Localization in somatic sensory and motor areas of human cerebral cortex as determined by direct recording of evoked potentials and electrical stimulation

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This paper reports and illustrates in figurine style results obtained by electrical stimulation of the cortex in 20 patients and by recording of cortical evoked potentials (EP's) in 13 of these patients, whose surgery required wide exposure of the Rolandic or paracentral regions of the cortex. This study is unique in that cutaneous receptive fields related to specific cortical sites were defined by mechanical stimulation, as is done in animals, in contrast to electrical stimulation of peripheral nerves at fixed sites, as in scalp EP recordings. Observations were made on pre- and postcentral gyri, on the second somatic sensory-motor area, on the supplementary motor area, and on the supplementary sensory area. In two patients with phantom limb pain, the pain was elicited in one on stimulation of the postcentral arm area, and in the other on stimulation of the supplementary sensory leg area. Surgical removal of these areas had the immediate effect of abolishing the phantoms and the pain. Long-term follow-up review was not possible. In one patient with severe Parkinson's disease, stimulating currents subthreshold for the elicitation of movement resulted in disappearance of tremor and rigidity for short periods after stimulation of the precentral gyrus. The possible patterns of organization of the human pre- and postcentral areas are considered and compared with those of the chimpanzee and other primates. In patients in whom data from pre- and postcentral gyri were adequate, it appeared that the precentral face-arm boundary is situated 1 to 2 cm higher than the corresponding postcentral boundary.

Key Words • evoked potential • cutaneous receptive field • paresthesia • motor cortex • supplementary motor area • supplementary sensory area • second somatic sensory-motor area • phantom limb pain

The observations described in this paper were made more than 25 years ago, but the material has not been fully analyzed and prepared for publication until now, although it has been the subject of partial reports to a number of scientific audiences. The work began with Dr. A. Earl Walker at the Johns Hopkins Hospital (Fig. 1) in July, 1948, just before the senior author left for the University of Wisconsin. It was resumed at Wisconsin early in 1949. In spite of the passage of time and the recording of evoked potentials (EP's) from the exposed cortex in a number of studies, including three in which former associates, Celesia, Hirsch, and Lende, participated, we believe that this is the only study that has undertaken to define receptive fields for individual cortical points by systematic mechanical stimulation of the body surface, as is customary in animal studies. Rather, most studies of EP's in man have used the technique of "averaging" or "summating" potentials recorded with scalp leads and induced by limited percutaneous electrical stimulation of peripheral nerves, beginning with the work of Dawson in 1947. Nearly all studies in which direct cortical recordings were made also used this averaged potential method.

Recent review of our electroencephalographic (EEG) records has led us to adopt the method used in the present illustrations to show the relationships of the potentials evoked to the peripheral sites.
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stimulated. Our customary figurine technique, first used to construct somatotopic maps of the monkey, and later of other animals, where the potentials are almost exclusively initially surface-positive, could not easily be adapted to show surface-negative and surface-positive deflections. We have used this method in Fig. 7, and have also indicated the skin areas eliciting surface-positive potentials.

In addition to studying somatosensory localization by means of EP's, we have also used the classical procedure of electrical stimulation to arouse parasthesias and to induce movements on excitation of postcentral and precentral cortex. In one patient, some data were obtained from the second somatic sensorimotor area; from others, movements were elicited on stimulating the supplementary motor area, and in one the results appear to confirm Penfield and Rasmussen's localization of a supplementary sensory area on the medial aspect of the parietal lobe. In addition, stimulation of cortex was carried out in two patients with phantom limbs. Sensory and motor figurine maps have never before been constructed for the human cortex, so far as we are aware. An interest of the first author in these studies was to secure data from man for comparison with data obtained from a variety of laboratory animals.

Clinical Material

This report is based on studies made on 20 neurosurgical patients, whose disorders required wide exposure of the Rolandic region of the cortex, including, in five cases, the paracentral lobules. The medial extent of the exposures is indicated in the text or in the figure legends. Studies were undertaken on another dozen cases without success in recording EP's and with minimal results from cortical stimulation, possibly because of the effects of the pathology on the sensory and motor pathways.

Most exposures were carried out under local anesthesia. The patients' consent to the studies to be made and their cooperation in their conduct had been secured, according to the practice of the period. During EP recording, the patients were under general anesthesia.

Evoked potentials were recorded in 13 cases from 103 postcentral sites, four precentral sites, and one second somatic sensorimotor area site. Movements were obtained from all 20 patients on stimulation of 186 precentral, 14 postcentral, one second somatic sensorimotor, and seven supplementary motor area sites. Parasthesias were induced on stimulation of 26 postcentral, two precentral, and five supplementary sensory area points. Far fewer postcentral than precentral stimulations were made, so these statistics do not indicate the relative excitability of the two gyri. Similarly, few attempts were made to record EP's precentrally. Nearly all results from the cases yielding positive effects are illustrated in the figures. Detailed records were not kept of sites yielding no results. No effort was made to record EP's beyond the central gyri.

Methods

Electrical Stimulation

In one or two cases, a 60-cycle half-wave rectified stimulus was used, but this proved less satisfactory than a full-wave 60-cycle stimulus, and in animal experiments it tended to release gas bubbles under the stimulating electrode. The 60-cycle AC stimulator was the same instrument we have used for stimulation of motor cortex in animals.

Our usual technique in the laboratory has been described elsewhere. In patients, the procedure was similar, except that the interval between stimulations was shorter than the 2 minutes thought necessary in animal studies to permit full return to "normal" and avoidance of an "extinction" period, which is more prolonged under pentobarbital-sodium than in patients under local or light general anesthesia. Stimulations in the patients were made under both of these conditions; local anesthesia was of course essential for the elicitation of subjective responses. Two-second stimulus trains were used in all patients. Stimulus strengths were maintained as near threshold as possible and determined for each site stimulated, in order to avoid epileptiform afterdischarges and to obtain minimal responses. Even so, some of the movements illustrated were probably elicited by stimuli after threshold levels, and occasionally afterdischarges were induced. The results of stimulations producing epileptiform movements are not illustrated. In all cases, the current strengths of stimuli, in root-mean-square values, are given either for each point or in the legend of the figure. Monopolar stimulation was used in all cases, usually with the "indifferent" electrode clipped to the cut edge of the scalp.

Evoked Potential Elicitation

In elicitation of evoked potentials, the need to indicate the time of stimulation on the EEG record led to the development of a small tapping device with a microswitch in its tip, which closed when the body surface was lightly tapped. The electrical signal thus generated deflected one of the pens of the inkwriter and allowed the time of stimulation to be related to deflections in the recordings of the other five channels, and so identification of EP's (see Fig. 5 B). This device

*60-cycle AC stimulator was manufactured in the Electronics Laboratory, University of Wisconsin Medical School, Madison, Wisconsin.
†Electroencephalograph and tapping device manufactured in the Electronics Laboratory, University of Wisconsin Medical School, Madison, Wisconsin.
provided a stronger mechanical stimulus than it has been our custom to employ in animal experiments, where the stimulus has generally been limited to moving the hairs on the body surface with an electrically activated lever bearing a camel-hair brush. The hair loss was generally clear when the tapping device was used. One could use a wisp of cotton and obtain a response, as shown in Fig. 5 B (Toe I, Touch). The use of this tapping device undoubtedly caused wider and deeper peripheral excitation than was desirable and this may account for some diffuseness in the topological relationships revealed, but it also facilitated exploration. In spite of this, in general, the method gave quite good results. All recordings are of single responses. A “summatiting” or “averaging” technique was not employed.

Recording of Electrical Activity

Recordings in nearly all patients were made with an early model, six-channel electroencephalograph with a band pass of 0.5 to 60 cycles. Three of the pen-drivers were mounted forward and three aft over the moving paper. The recorder compared favorably in its characteristics with other inkwriters of the period. All recordings were “monopolar.” As in our animal studies, our electrical recordings in man show maximal amplitude about 100 /µV. In all illustrations positivity is up; case numbers indicate year and sequence in which patients were studied. F = female; M = male.

FIG. 1. Case 48-1, M. Cathode ray oscillograms of evoked potentials recorded from the postcentral hand area in response to mechanical stimulation at six different loci. Maximal amplitude about 100 /µV. In all illustrations positivity is up; case numbers indicate year and sequence in which patients were studied. F = female; M = male.

Records of Stimulation and Recording Sites

For each cortical point stimulated electrically which gave a response, a small numbered tab was immediately placed on the cortex. When exploration was completed, a photograph was taken with all the tabs in place. Photographs also were taken for each placement of the recording electrodes (Fig. 3 A). In addition to these photographic records, the surgeon outlined the exposure and plotted on a standard Penfield brain chart all recording sites and each stimulation site that resulted in movement or paresthesia, using a centimeter tape to measure the distance of the point from midline and/or Sylvian fissure. In nearly all cases, the exposure extended from near the midline to near or below the Sylvian fissure. The photographs were subsequently used to produce the key insets of the figures, which show locations of stimulation and recording sites and the course of fissures in the region of interest.

Figurine Maps

Three types of figurines are to be found in the illustrations.

Motor Figurines. Motor figurines illustrate the motor effects of cortical stimulation by indicating, with solid black or hatched “Zipatone,” for stronger and weaker movements, the parts of the body in which the movements took place. Direction of movement is either indicated by letter labels (F = flexion; E = extension) or sometimes by arrows to indicate fanning of the fingers or apposition of thumb and fingers; occasionally, as in Figs. 10 and 14, upward pointing arrows indicate extension and downward pointing arrows indicate flexion. Other arrows at the wrist, ankle, shoulder, and hip are used to indicate the direction of movement. Extension and flexion of the elbow, knee and ankle, ulnar, and radial deviation of the wrist and fingers, abduction by a circle with a dot in the center, and elevation or depression of the shoulder girdle by a triangle pointing in the direction of movement. For the face, “Zipatone” has been placed on the figurine to show the locus of the response, and arrows show elevation of the lids, direction of eye movements, closure, opening, or deviation of the jaw, and protrusion or retraction of the tongue.

It should be pointed out that all figurines representing the precentral and supplementary motor areas show ipsilateral rather than contralateral views of the body with respect to the side of the brain stimulated, as is the case with figurines relating to precentral evoked responses. This is to preserve the appropriate orientation of individual figurines within the cortical localization patterns of these areas, as we have explained elsewhere. Figurines of the postcentral, sec-
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Sensory Paresthesia Figurines. Sensory paresthesia figurines illustrate with dotted “Zipatone” the areas of the body to which the patient referred the sensations elicited.

Evoked Potential Figurines. Typical EP’s elicited by stimulation of the body surface and excised from the EEG record have been mounted near an outline drawing of the relevant part of the body, with arrows indicating the sites stimulated. When the stimulus was applied to a surface not visible in the drawing, the site of stimulation and the response are indicated by a star, and arrows are used to connect the two. In Fig. 7, cross-hatched “Zipatone” has been applied to each sensory figurine to indicate the skin area yielding initially surface-positive potentials. Since only limited time was available in which to make observations, it was not possible to stimulate in any given patient all parts of the body surface. Individual parts of the body were explored more completely in some cases than in others. The results, therefore, are less adequate than those obtained in animals, where one is not limited by time. Even so, the five recording channels of the EEG made it possible to collect data more rapidly than a single-channel cathode ray oscillograph would have permitted.

Recordings were made with the aid of a Marshall-Walker 16-electrode array‡ (Fig. 3 A). One electrode served as the reference lead and was placed remotely from the Rolandic region, either on the cortex or more frequently on the moist inner surface of the scalp or on the reflected dura, as indicated in the figures by an asterisk. The locus was not standardized. With the other 15 electrodes, connections could be made quickly by a switch to five of these at a time. Adequate grounding of the patient was essential to avoid 60-cycle pickup.

Anesthesia

Although the cortex was stimulated under either local or general anesthesia, all recordings were made under general anesthesia induced by pentothal, nitrous oxide and oxygen, or ether. As in animals, the best results were obtained at deeper levels of anesthesia.

Results

The EP’s recorded with a cathode ray oscillograph from one of Dr. Earl Walker’s patients at the Johns Hopkins Hospital are shown in Fig. 1. (See Marshall and Walker77 for an EEG recording from one of those cases.) The surface-positive deflections, generally followed by a smaller negative wave, are superimposed on low-level spontaneous brain activity. The cortical recording site is in the hand rather than in the finger area of the postcentral gyrus. Stimulation occurred at the very beginning of the sweep, which was tripped by the stimulator (one we used in the laboratory for animal studies). The initial positive deflections are approximately 100 μV in amplitude. Latency to onset was around 15 to 18 msec; time to the peak of the positive deflection was between 22 and 30 msec. The duration of the positive phase was about 15 msec in the four upper responses and nearly twice as long in responses to stimulation of the base of the thumb and the palm, where the negative component was absent.

Figure 2 illustrates with sample EEG recordings, made with the Gilson EEG, the effect of rate of stimulation on the amplitude of the response, which progressively diminishes as the rate of stimulation increases, an effect well known from animal studies.89 Full amplitude is achieved, when the rate of stimulation is around 1/sec. In these records with the slower stimulation rates, the rapid initial positive deflection is followed by one or two slower positive deflections. The first of these later deflections may also be seen in Fig. 1. In this patient, background activity was minimal during this recording time, and the potentials are surface-positive without a following negative phase.

The form of the EP varied considerably from patient to patient, as will be seen in succeeding illustrations, and even in the same patient, depending on the state of the brain’s activity. This variation is

‡Marshall-Walker electrodes manufactured at the Johns Hopkins Hospital, Baltimore, Maryland.
FIG. 3. Case 50-6, F. A: Photograph of the right hemisphere showing: 1) sites of electrical stimulation (upside-down numbers) along the precentral lip of the central sulcus, 2) Marshall-Walker electrodes in place postcentrally, and 3) five recording sites from a second placement of the electrodes on the upper postcentral gyrus. B: Drawing traced from the photograph showing the precentral motor points and the postcentral recording sites. The stippled circles are centered over the sites from which the correspondingly numbered tracings in Figs. 4 and 5 were recorded. This drawing is also similar to the key of Fig. 7 (inset). Scales are in centimeters. Med indicates the medial edge of the exposure at the midline. The asterisks mark the “indifferent” electrode sites; the one at the Sylvian fissure for the electrodes shown in A, and the one at the midline for sites 17 to 21.

Also seen in animals, where under deep anesthesia the responses are surface-positive and become diphasic (positive-negative) only as the level of anesthesia lightens.

Figure 3 A illustrates one arrangement of the Marshall-Walker electrodes on the postcentral gyrus. The numbered tabs on the precentral gyrus mark motor stimulation points, while Numbers 17 to 21 on the upper postcentral gyrus identify some of the recording sites of a second setting of the electrodes. The precentral tabs are upside down, because the surgeon faced the brain from the vertex. Figure 3 B is a drawing traced from the photograph and shows the motor points precentrally and the recording sites, centered within the numbered circles, postcentrally.

Recordings made from Points 7 to 11 in the postcentral arm area on tapping the tip of Finger III are shown in Fig. 4 A. The top channel signals the time of stimulation. Alignment of the pens is shown at the left, and 50-µV calibration signals are at the right. The EP's are initially surface-positive at points 10 and 8 and initially negative at the other three sites, while the form is different at each of these three sites. The onset of the initially positive deflections appears to precede in timing the onset of the initially negative deflections.

Figure 4 B gives recordings from Points 17 to 21 to tapping the tip of the hallux. The deflection is initially positive at sites 19 and 18, while the responses are initially negative at Points 21, 20, and 17. Again the initially positive deflections lead in time the initially negative ones. In Channel 17 the initial negativity is quite small but clearly present. We may assume that the recording site is close to a surface-positive
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Fig. 4. Case 50-6, F. A: Nine seconds of electroencephalographic recordings from electrode sites illustrated in Fig. 3 B, indicated by the numbers at the left, showing potentials evoked by tapping the tip of left Finger III. Positive deflection is upward. Top line signals time of stimulation. Scratch lines and amplitude calibrations for recordings are mounted at the left and right sides of A and B. Interval between vertical lines is 200 msec. B: Recordings made from sites indicated by numbers at the left, while tapping the tip of Toe I. All recordings were made with the patient under deep ether anesthesia.

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FIG. 5. Case 50-6, F. A: Recordings made while tapping the tip of the patient's heel. B: Comparison of recordings made at electrode sites indicated at the left (see Fig. 3 B) to touching Toe I with a wisp of cotton and tapping Toe I, Toe V, and heel. Calibration at right.
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Fig. 6. Distribution of initially positive and initially negative evoked potentials (EP's) over the postcentral gyrus displayed at the electrode sites at which they occurred (see Fig. 3 B). The heavy lines (CS) are the central sulcus. The lighter lines at left and right indicate the sulci behind and ahead of CS. A: Case 50-6, F. Responses to tapping the tips of the fingers. B and C: Responses to stimulations at sites indicated by arrows on the figurines below the plots. At the right in C are shown the effects of tap and cotton stimulation of the hallux. D. Case 50-8, F. Responses to tapping the tips of Fingers I to V. Compare with the figurine map of Fig. 14.

A clear, initially surface-positive deflection was recorded at Site 19 in response to stimulation of the heel (Fig. 5 A). There is also a smaller initial positivity at Site 18. At Point 20 the response is virtually negative, while there are no clearly correlated deflections at Sites 21 and 17. In this case simultaneous recording on a single channel of the activity induced at these five sites would yield a positive-negative sequence, in which again the negativity would dominate.

Recordings from Points 17 to 21 on stimulation of Toe I to touch and tap and to tapping Toe V and the heel are compared in Fig. 5 B. Light touch with cotton wool gave the least complex EP's, with a very slight initial negativity preceding a strong positive-negative sequence at Site 17. The recording site here is
presumed to be close to a site yielding an initially positive response. Responses at Sites 18, 19, and 20 are negative, and appear to begin simultaneously with the slight initial negativity at Site 17. Again addition of the responses at Sites 17 to 20 would give a negative response and would swamp the positivity of Site 17, which occurs during the period of the negativity. As measured from the records, the negativities add up to 190 µV, while the positivity equals 50 µV. Since the negativity begins before the positivity, only a negative deflection would result. The responses to tapping Toe I are more complex than those to touch. An initially negative series of potentials appears at Point 21, and all other sites now yield some initial positivity. When stimulation is shifted to Toe V, an initially positive response occurs at Point 18, while initially negative deflections occur at Sites 17, 19, and 20, and there is no clearly correlated event at Site 21. Shifting stimulation to the heel results in initially positive potentials at Points 18 and 19, and perhaps at 17, while at Point 20 the response is strongly negative.

It is clear from Fig. 5 B that the best surface-positive deflections to stimulation of the three separate parts of the foot occur at different cortical recording sites. It is the surface-positive deflection which defines somatotopy in the postcentral gyrus. This is demonstrated in Fig. 6 and again in the evoked response figurine map of Fig. 7 for this patient.

Figure 6 shows the distributions of surface-positive and surface-negative potentials over the postcentral gyrus, when different sites on the body surface were tapped. The loci of the surface-positive potentials are fairly restricted, while the initially negative potentials surround the positive ones more widely. The positive focus shifts up the gyrus as the stimulus moves from thumb to little finger (Fig. 6 A). A similar shift is seen in Fig. 6 D for another patient. In addition, one sees in the latter case the appearance of a second surface-positive focus higher up on the gyrus, in what is presumably the area for the whole hand, as distinct from the finger area. The stimulus sites move from the shoulder to the costal margin, to the knee, to the anterior leg, and finally to the hallux (Fig. 6 B). The surface-positive potentials shift accordingly and the surface-negative deflections continue to be widespread. Similar relationships are seen for stimulation of different aspects of the foot (Fig. 6 C).

Figure 7 illustrates in figurine style the EP's obtained by stimulating each cutaneous site, to which the responses are related by the indicating arrows, for 21 points on the postcentral gyrus. The motor sequence of the precentral gyrus is illustrated by 18 motor figurines. Again, in nearly all of the EP figurines, both initially positive and initially negative responses are seen. The systematic shift in initial positivity (indicated by cross-hatching) corresponds to the somatotopic sequence in the postcentral sensory area. For the figurine nearest the calibration signal, all responses are negative except those evoked by stimulation of the elbow. Had the shoulder been stimulated, surface-positive potentials might have been evoked from the shoulder.

A number of features of the motor and sensory sequences may be noted. Precentrally the leg is clearly represented in this patient on the dorsolateral surface of the hemisphere for 1.5 cm from the midline, while the point causing movement of thoracic and upper back muscles lies 2.3 cm from the midline. Note that the back muscles are represented at Points 6 and 9 (Fig. 3 B). The sequence of representation from the elbow through the fingers is that usually reported. Immediately lateral to the thumb representation, conjugate deviations of the eyes were elicited; in one case, upward movement of the eyes was associated with action of the frontalis muscle. Movement of facial muscles and closure of the eyelids were obtained from more lateral points. From one of these, contraction of the dorsal neck muscles was produced.

The postcentral sensory map again shows the leg represented well onto the dorsolateral surface as far as 2.3 cm from the midline and possibly farther in unmapped cortex. Caudally near the postcentral sulcus, the thorax and proximal arm are represented 4.5 cm from the midline. The receptive fields for these points were not completely defined. Even in the classical hand and finger region of the gyrus, responses were obtained from stimulation of the cubital and antecubital aspects of the elbow.

Another feature evident in this map is the fact that postcentrally EP's to stimulation of the fingers were recorded lateral to the precentral boundary between the hand and face areas and it is probable that the lateral limit of finger representation was not reached. This feature of the postcentral sequence will be pointed out in three other patients, where data for pre- and postcentral sequences were obtained (Figs. 13, 18, and 21).

Figure 8 illustrates the motor sequence of another

![Fig. 7. Case 50-6, F. Evoked potential (EP) and motor figurine maps. Arrows from EP's indicate skin sites at which mechanical stimuli were applied. Each EP is a single response cut from the EEG paper. Stars indicate sites on body surface not visible in the drawings and their EP's. The parallel vertical thin lines on some of the EP's define 200 msec intervals. Numbers under the motor figurines (mA) are near-threshold values of the 60-cycle AC stimulating currents (root-mean-square values). For symbols see Figurine Maps, in text. Inset: Dots in key and in all subsequent keys indicate EP recording sites; circles are electrical stimulation sites. Letters a-d are motor points corresponding to figurines a-d (upper right). Indifferent electrode sites marked by asterisks. See legend of Fig. 3.](image-url)
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patient for 11 precentral points from foot to pharynx. Short runs of initially positive EP's obtained on tapping the hallux and four sites on the arm are shown for two postcentral sites. The postcentral foot point is 1.5 cm from the midline. The responses illustrated in Fig. 2 were recorded from the arm point in this patient. The receptive field was not completely defined for either of these sites.

The motor effects of stimulating nine precentral points and the evoked potentials recorded at six postcentral sites are shown in Fig. 9. Nearly all of these are surface-positive. The inset strip of EEG record shows the reproducibility of the deflections at one site to stimulation of the index finger. Although exploration of the body surface with the stimulator was limited, there is a reasonable correspondence between the pre- and postcentral data for the hand.

Figure 10 shows results obtained on stimulating seven precentral sites and EP's recorded from eight postcentral points. The exposure in this case extended to the midline, and it appears that the leg is not represented on the dorsolateral surface of this hemisphere. The EP's from the hand are all strongly diphasic and mainly initially surface-positive. Those from the upper arm are surface-positive and do not show the diphasicity of the hand points.

**Fig. 8.** Case 50-2, F. Evoked potentials recorded at two postcentral points for the hallux and arm, and motor figurines for 11 precentral sites. All motor points were stimulated at 1.0 mA. For symbols see Figurine Maps, in text.

**Fig. 9.** Case 50-7, F. Motor and evoked potential (EP) responses. Stars indicate hidden stimulation sites on the palmar aspect of the hand. All precentral motor points were stimulated at 1.0 mA. The broken line surrounding the inset outlines the exposure. The medial edge is 3.0 cm from the midsagittal line. The sample EEG shows the reproducibility of the response to stimulating the tip of the index finger. For symbols see Figurine Maps, in text.
Fig. 10. Case 50-4, F. All precentral motor points were stimulated at 1.0 mA. Arrows indicate direction of movement: a downward pointing arrow means flexion, an upward pointing one extension. In the inset, the Sylvian fissure is at the bottom. All evoked potentials are initially surface-positive. For symbols see Figurine Maps, in text.
FIG. 11. Case 59-9, F. In this patient all evoked potentials (EP's) were initially surface-positive at the three postcentral sites studied. Question marks on the shoulder suggest that EP's might have resulted had the shoulder been stimulated. For symbols see Figurine Maps, in text.

In Fig. 11, three postcentral points in the arm area were studied and all the EP's recorded were surface-positive with little afternegativity. It is quite likely that stimulation of the shoulder would have yielded EP's at all three sites, since response amplitude was increasing as stimulation advanced up the arm. Two precentral points yielding adduction of the shoulder are located directly opposite these sites. The motor sequence in this case very clearly illustrates the classical view of the precentral motor map of the finger area. Since the surgical exposure again was to the midline and the highest sensory arm point is situated 4.0 cm from the midline, it is probable that the leg area of this patient extended well onto the dorsolateral surface.

Six postcentral EP figurines and two precentral motor figurines are shown in Fig. 12. In addition, the legend lists the movements of the face induced by stimulation of the seven precentral points, C to J. There is an apparent lack of correspondence between the motor figurines for fingers and wrist and the EP figurines for the arm, in which the responses are

FIG. 12. Case 50-11, F. All evoked potentials are initially surface-positive except in response to stimulation at one hand point. Contralateral movements elicited from the lettered sites, from above downward, were: J, retraction of angle of mouth; H, retraction of angle of mouth and movement of lower lip; G, lower lip rolled against teeth, contraction of platysma and closure of jaw; C, contraction of orbicularis oris of both lips and deviation of jaw to contralateral side; D, contraction of buccinator and orbicularis oris, and movement of tongue; E, closure of jaw; F, chewing movement followed by swallowing. For symbols see Figurine Maps, in text.
Figure 13 illustrates the evoked potentials recorded from 13 postcentral sites and the movements elicited by stimulation of 16 precentral points. The lower 10 EP figurines have been enlarged in the inset to provide better visibility of individual responses. Again we see both positive and negative initial deflections. Data for the top three EP figurines are probably incomplete, since only the fingers were stimulated. The pattern of localization of the lower postcentral figurines is not quite according to expectation, since surface-positive potentials from the ulnar side of the hand occur at the central sulcus lateral to the point just above, which gave best response from the thumb, neck, and chin, while the point immediately caudad and those more laterad gave positive potentials from the whole hand and the chin and other parts of the face. Note also that surface-positive responses to stimulation of the forearm and of the shoulder and neck were obtained in a region classically considered the finger area. The dorsal edge of the exposure was "close to the midline," and it can be seen that only digital and wrist movements were obtained from the upper precentral...
FIG. 14. Case 50-8, F. Sensory and motor figurine maps. Arrows pointing downward signify flexion, upward-directed arrows mean extension; others indicate directions of movement. The scale at the left of the inset key is in centimeters. For other symbols, see Figurine Maps, in text.

The leg area, therefore, was probably entirely on the medial aspect of the hemisphere. Again we see that conjugate deviation of the eyes was elicited on stimulation of the upper part of the face area close to the central sulcus, and again the boundary between hand and face areas postcentrally falls approximately 2 cm lateral to the highest face point precentrally.

In Fig. 14, EP figurines are given for 12 postcentral sites and motor figurines for two postcentral and six precentral points. Again the potentials are initially either positive or negative. The EP data are probably incomplete, since stimulation was limited to the fingers. The pattern for the fingers, however, is quite clear. The exposure in this patient reached to within 1 cm of the midline. The motor point yielding movement at the shoulder is, therefore, about 4 cm from the midline, which would permit partial representation of the leg on the dorsolateral surface.

Figure 15 illustrates the EP's recorded at five postcentral sites and movements elicited from one postcentral and nine precentral sites. A striking feature of the EP data is the extent to which the whole arm yielded responses, in what, from the precentral map, appears to be the finger area. As can be seen, these were recorded close to the central sulcus.

FIG. 15. Case 50-5, F. Sensory and motor figurine maps. The medial edge of the exposure is at the midline. All unlabeled motor points were stimulated at 1.0 mA. For symbols see Figurine Maps, in text.
FIG. 16. Case 50-10, F. Five precentral motor figurines; three precentral and 10 postcentral evoked potential figurines. At top left is shown a series of responses evoked by tapping the ulnar side of the hand. The medial edge of exposure is at the midline. For symbols see Figurine Maps, in text.

Exposure in this patient extended to the midline. The leg areas are, therefore, entirely on the medial surface of the hemisphere.

In Fig. 16 are illustrated EP's recorded at 10 postcentral and three precentral sites. This was one of the few cases where attempts were made to record EP's from the precentral gyrus. Movements were obtained from five precentral sites. The segment of EEG record at the upper left shows that responses to stimulation of the ulnar side of the hand occurred with fairly constant amplitude of about 200 μV, except during the periods of fast spontaneous activity. The large response to stimulation of the ulnar side of the forearm, shown in the second figurine from the top, indicates that potentials probably could have been evoked by stimulation farther up the arm. Note that the EP's are mainly surface-positive both pre- and postcentrally.
FIG. 17. Case 50-1, M. Results from the right and the left (L) hemispheres of this patient have been combined. All motor points not labeled were stimulated at 0.8 mA. The two lowest points on the postcentral gyrus, one motor and one sensory, are in the second somatic area. The medial edge of the exposure was close to the midline, the lateral edge at the Sylvian fissure. For symbols see Figurine Maps, in text.

Figure 17 combines in one map the results obtained at two different operations on the two hemispheres of this patient. Figurines labeled L illustrate data from the left cortex. Evoked potentials were recorded at six postcentral sites, from one precentral site, and from one site at the lower end of the postcentral gyrus, which must be classified as a second somatic area point. The latter is close to a point from the left hemisphere, which on electrical stimulation gave plantar flexion of the foot. Three postcentral points of the left hemisphere yielded sensory paresthesias (stippled markings) and 19 precentral points (four from the left hemisphere) produced movements. The platysma was activated from seven precentral points. The exposures over both hemispheres reached within 0.5 cm of the midline. The leg areas, therefore, were on the medial surfaces.

In addition to the data illustrated in the figure, this patient, who had severe Parkinson's disease, exhibited marked inhibition of the tremor and disappearance of rigidity, when the precentral motor cortex was stimulated. The inhibition occurred at current values below threshold for production of movements. Tremor disappeared for short periods in the arm,
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Fig. 18. Case 49-1, M. Skin areas to which paresthesias were referred (stippled areas), when points on the postcentral gyrus were stimulated. Motor figurines at right illustrate movements, also elicited by paresthesia-inducing stimuli at five of the postcentral sites. Note the agreement between motor and sensory effects. The two precentral motor points at the left, when stimulated, also inhibited speech. All stimulations were at 0.5 mA. The stippled area in the key, next to the Sylvian fissure, marks the site of a brain scar. Note that evoked potentials were elicited by taps from wider areas of skin than those to which paresthesias were referred on stimulation of neighboring cortical sites. Heavy lines both represent the central sulcus. For other symbols see Figurine Maps, in text.

When points in the arm area were stimulated with the weaker stimuli, but might cease also in the leg with stronger stimuli. The effect was very striking. Not only did the tremor disappear, but so did the rigidity. Since the cortical exploration was made under local anesthesia, it was possible to ask the patient to squeeze one's hand. When tremor and rigidity were present, hand squeezing was not very well executed and the grip was weak. When the request was made after tremor and rigidity were abolished by cortical stimulation, the movement was strong and easily executed. In one other patient with Parkinsonism, cortical stimulation on the inhibition of tremor were studied but not reported here, similar effects of cor-
tioned. Postcentral stimulation occasionally inhibited the tremor, but usually it did not.

Figure 18 illustrates by stippled markings the cutaneous areas to which paresthesias were referred, when 12 cortical sites were stimulated, and the potentials evoked at 11 sites by tapping the body surface. In addition, movements, as well as paresthesias, were elicited from five postcentral points. These results are illustrated by the motor figurines at the right, where the central sulcus is duplicated. From two precentral
points, facial movements were obtained. It will be noted that, in general, there is good correspondence between the movements obtained on postcentral stimulation and the parts of the hand, to which paresthesias produced by the same stimulations were referred. There is less good agreement between the distributions of the paresthesias and the EP's, perhaps because the tapping device stimulated the hand more widely than at the site of the tap. Attention should be directed to the fact that the postcentral face-arm boundary is at least 2 cm below a comparable precentral boundary. The leg area in this patient appears confined to the medial wall.

Motor results of stimulations carried out on two patients are shown in Fig. 19. All sites are precentral except for one postcentral site in A. The stimulus sites in the lower part of A are along the upper lip of the Sylvian fissure. Note in B that conjugate movement of the eyes was again obtained close to the central sulcus above the area for facial muscles.

In Fig. 20, the results of stimulating 13 dorsolateral precentral sites and three postcentral sites on the medial wall are given. The precentral map is of especial interest, because of the distribution of points from which elbow, shoulder, and neck movements were obtained. These surround rostrally the finger points near the central sulcus. The paracentral postcentral points all elicited movements of the legs, while...
Localization in human cerebral cortex

FIG. 21. Case 51-4, F. Fourteen dorsolateral precentral and three paracentral motor points are illustrated, also one supplementary motor point and two postcentral paresthesia points. The area marked by stippling indicates the site of a meningioma of the falx. All unlabeled points were stimulated at 0.5 mA. Scale below the key is in centimeters. For symbols see Figurine Maps, in text.

the more caudal one also caused movement of the lower back musculature.

In Fig. 21 are illustrated the motor effects of stimulating 14 precentral points on the dorsolateral surface and four on the medial surface of the hemisphere. Three of the latter are situated just beneath the medial end of the central sulcus close to the boundary between precentral and postcentral cortex in a position, which on Brodmann's map of 1908 would be in Area 4. The most rostral point is in the supplementary motor area. In this patient the area related to the leg extends onto the dorsal surface of the hemisphere. The point eliciting contraction of the abdominal muscles is located 2 cm from the midline. However, the pattern in the arm area contrasts with that in Fig. 20. Here the finger area occupies the full width of the precentral gyrus and there is no evidence of upper arm representation rostral to the digital area, as there was in Fig. 20. Paresthesias were aroused on stimulation of two postcentral finger points. Again it should be noted that these two points are situated more laterad than are the precentral points, which caused movement of these same digits. One rostral point on the medial wall is in the supplementary motor face area. The figurine illustrates only the fact that bilateral movements occurred in both lips. Besides repetitive protrusion and compression of the lips, the tip of the tongue was brought in contact with the upper incisors and a rapid "T-T-T-T" sound was emitted. The right angle of the mouth was also brought.
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forward as a part of the lip movement and there was some opening and closing of the jaw in synchrony with the "T" sound.

Figure 22 illustrates movements obtained on stimulation of the medial wall of the right hemisphere. Three of the sites for the lower limb are in the precentral motor area, while six sites are in the supplementary motor area. Of these, two gave movements in the leg, with which movement of the lower back was associated at one point, while four elicited movements of the face, tongue, eyes, and jaw, and vocalization or inhibition of vocalization. Tongue movements were bilateral at two points and lip and eye closure movements were bilateral at another point. Arm movements were not elicited, perhaps because arm foci were in the fissure ahead of the leg points.

Case Reports

Two patients with phantom limb pain were studied prior to removal of the cortex related to the missing part.

Case 51-3

The first of these patients had had the left leg amputated above the knee 13 years before and now complained of intractable pain in the phantom. Four precentral points were stimulated in the arm area with results illustrated in Fig. 23. The most medial of these was 2.5 cm from the midline. Two postcentral points in the arm area also were stimulated. One caused flexion at the metacarpal-phalangeal joints of the lateral three digits, strongest in the little finger. The other yielded tingling over the ulnar aspect of the forearm.

Three motor points were stimulated on the medial wall of the hemisphere; two of these, one precentral and one postcentral, resulted in movements at the hip without any accompanying sensation; the third, the most rostral point, gave flexion of the stump at the hip and the patient also reported flexion of the knee and plantar flexion of the foot and "some pain, but only mildly like the usual pain," in the phantom foot.

Five points were then stimulated on the medial wall of the hemisphere well behind any expected extent of Brodmann's Areas 3, 1, and 2, in what is probably Penfield's supplementary sensory area. Two of these, adjacent to the cingulate sulcus, yielded nonpainful paresthesias at the base of thumb and index finger and on the ulnar aspect of the arm near the elbow. Both of these sites also gave rise to effects which she referred to the heart, a change in heart rate and a "gone feeling in the heart." Stimulation at three points, one at the margin of the hemisphere on the dorsal surface and two in the paracentral lobule, resulted in sensations referred to the phantom, similar in character to the phantom pain she was accustomed to experience. The more caudal point on the medial wall, when stimulated, caused the patient to exclaim: "Whew! That was a dandy! It was of the same type, but not so intense as I usually have. It was on the under side of the foot on the big toe side." The point just ahead of this one gave rise to tingling and pain, "but not bad," on the little toe side of the sole and the lateral aspect of the foot. The point on the dorsal surface of the hemisphere resulted in pain referred to the center of the sole. "It was just like somebody took a knife and slit the center of the sole."
Localization in human cerebral cortex

Fig. 24. Case 49-2, M. Patient with intractable phantom-limb pain in right arm amputated at the upper third of the humerus. Painful paresthesias induced by stimulation at all sites except the three for the face. Postcentral stimulation at 0.5 mA; precentral at 0.6 mA. Medial edge of exposure 1 cm from midline. For symbols see Figurine Maps, in text.

It is of interest, in relation to Campbell's report on Betz cell atrophy in motor cortex in longstanding amputees, that the precentral motor cortex in the leg area of this patient was grossly atrophied, sufficiently to admit the surgeon's finger tip (hatched area of the key).

Following cortical exploration, the area indicated in the key figure by stippling was excised under local anesthesia. Immediately on removal of this region of cortex the patient lost awareness of the phantom limb. In response to repeated questions about the phantom, she replied: "I just don't know, doctor, where the foot is. I can't tell. I always knew before, didn’t I?" After surgery the patient was able to recognize contacts with all parts of the body except over the stump of the left leg.

When seen some 6 months after surgery, the patient reported that the phantom was still present but was no longer full-sized, extending only about 6 inches beyond the stump. She was not aware of the knee or of the big toe, but she could still "feel" toes IV and V and the lateral aspect of the foot and the heel. The phantom pain had not entirely disappeared but was less intense.

Case 49-2

Some 21 months previous to admission, the second patient had caught his right hand in a hay-baler and had his whole arm pulled into the machine. Injury was so extensive that the arm had to be amputated at the junction of the upper and middle thirds of the humerus. A phantom hand had existed ever since the accident, and pain in it was constantly present and could be accentuated by pressure on the stump and its neuromata. Although the whole hand was involved, the pain was most constant in the middle and ring fingers, and less constant in the thumb. Partial relief came from twice removing the neuromata but the pain never disappeared. At times the pain was "severe enough to cause nausea."

Figure 24 shows eight postcentral points, which yielded paresthesias on stimulation, and two precentral points. One of the latter gave a "hot sensation, like touching a live wire," throughout the whole hand and arm and movement of the stump at the shoulder occurred. Stimulation of the other point caused inhibition of speech. All the postcentral points stimulated, except those for the face which produced a sense of warmth, gave rise to an intense burning sensation referred to the skin areas indicated in the figurines. He described the paresthesia as "like my usual pain" and compared it to an electric shock or "like sticking the hand in hot water." Stimulation of the most dorsal point involved the whole hand in the phantom pain and also resulted in a sensation of movement at the wrist.

At surgery, the whole postcentral arm area was removed. At no time in the immediate postoperative period did the patient admit any awareness of the phantom limb. Pain persisted on palpation of the neuromata in the stump but did not radiate into a phantom, as it had previously done. Long-term follow-up review was not possible, since the patient died in another accident within a year.

Discussion

Evoked Potential Studies

The observations described in this paper differ in one important respect from all other EP studies reported on man up to this time. Mechanical stimuli applied to the body surface were used to define receptive fields of potentials evoked at specific cortical sites, as in animals, instead of using fixed
sites for percutaneous stimulation of median and ulnar nerves or of nerves in the leg, as has been the common practice in scalp recordings on man, since the initial work of Dawson. More localized electrical stimulation, limited to individual digits, has been employed by Desmedt, and others. In several studies, light touch and pinprick applied to face and tongue caused good EP's. Similarly, Jasper, in discussing the paper by Goldring, mentioned light touch as an effective stimulus. However, no receptive field mappings by these individuals with these stimuli have been reported to our knowledge. The advantage of using mechanical stimuli to explore the body surface is that one can thereby define the receptive fields for given cortical recording sites and thus study in man the somatotopic organization of the postcentral gyrus, as has been done in animals. One can, of course, at the same time, with multiple electrodes, map the distribution of EP's on the cortex to mechanical stimulation of specific sites on the body surface, as shown in Fig. 6.

While in general it is difficult in any species to use EP's for mapping studies in the presence of normal brain-wave activity, we were able to observe individual EP's under favorable conditions of general anesthesia, as have others.

**Characteristics of Evoked Potentials Recorded Directly from Cortex**

The amplitudes of EP's in man are very much less than in animals. In this study the initial positive deflections of individual responses ranged from 50 to 200 $\mu$V, but were usually less than 100 $\mu$V. This lower amplitude in man may be due to the greater thickness of cortex above Layer IV, in which cortical afferents terminate to provide the source of the surface-positive potentials. Maximal EP's in cat and monkey usually exceed 200 $\mu$V and range up to 500 $\mu$V. In the thinner auditory cortex of the rat, the amplitude may be as great as 1500 $\mu$V (unpublished material) and as high as 1900 $\mu$V in the visual cortex of the rabbit.

Potentials recorded directly from the cortex, as shown in the illustrations of this paper, varied in form from patient to patient and at different times during an observation period in the same patient, as well as from site to site. Among the reasons for the variability may have been changing levels of anesthesia and the type of anesthetic. We saw no relation to the clinical status of the patient, although we are aware that such a relationship may exist in epileptic patients. The potentials might be initially surface-positive without any afternegative phase, as in Fig. 2. In other cases, all recordings were initially surface-positive with a succeeding negative deflection, as in Figs. 1, 10, 11, 17, and 18 and in most of Figs. 9, 12, and 16. In still other patients (Figs. 4, 5, 7, 13, 14, and 15), there were responses which were initially positive and others which were initially negative. Any particular cortical site could yield both types, but whether they were initially positive or initially negative at any given cortical point depended upon the peripheral site of stimulation. This is well illustrated in Figs. 6 and 7. In general, the surface-positive potentials were obtained on stimulation of a more restricted portion of the body surface than were the initially negative potentials. Thus somatotopy was defined by the initially positive potentials.

If the cortical distributions of potentials evoked by fixed peripheral sites of stimulation are studied, as in Fig. 6, it is seen that again the surface-positive potentials shift systematically with the peripheral locus, and the localizing, initially surface-positive potentials are surrounded over a wider area of cortex by initially negative responses.

As seen in Figs. 4 and 5, the latencies of the surface-positive responses generally are shorter than those of the surface-negative responses, although this may not always be so. The explanation of the surface-negative responses is not clear. Initial negative potentials are seldom seen in animals under pentobarbital anesthesia. This may be because of the deeper anesthetic state under which animals are studied. Certainly most of our patients were under lighter general anesthesia than were our animals. It is possible, then, that the two classes of responses seen may be related to depth of anesthesia, although we have no estimate of the relative depth in different patients. Since the surface-positive response in animals signals the arrival of an evoked volley, it is possible that, after the arrival of such a volley in man, a transcortical transmission in Layer I of the cortex occurs slightly later, giving rise to the surface-negative potentials. These resemble the surface-negative potentials recordable in animals and man from cortex near an electrically stimulated site (direct cortical response). Analysis of the initially negative responses would require recording in depth. If they are due to activity in the superficial layer of the cortex, as with the direct cortical response, it should be possible to determine this.

It does not seem likely that the initially negative potentials of our single response recordings are volume-conducted from subcortical sites. The latencies of the negative, relative to the surface-positive potentials, do not support this view. Furthermore, in animals, where the EP's are of much greater amplitude than in man, initially negative potentials are seldom seen, even though subcortical levels of the afferent pathway are nearer to the recording sites.

Since we made no recordings from the scalp, we have no personal experience upon which to compare records taken from scalp with those taken directly from the brain. From a survey of the literature, it is
not entirely clear how the two relate. Those who have reported directly from cortex have reported both initially positive and initially negative potentials, but in general systematic, closely spaced detailed mappings of cortical responses to show the distribution of initially negative and positive potentials have seldom been made. Broughton et al. and Goff et al. have both reported with scalp and brain leads an inversion of initially surface-positive potentials at the central sulcus and have interpreted the inversion as due to a dipole on the posterior wall of the central sulcus. Our direct recordings at 0.5-cm steps show that in some patients localized surface-positive potentials of the postcentral gyrus tend to be surrounded for some distance by initially surface-negative potentials as illustrated in Fig. 6. We believe these widespread "inversions" cannot be interpreted as reflections of dipoles in the central sulcus. Furthermore, such reversals are not seen, as they should be on the dipole hypothesis, in monkeys and chimpanzees under barbiturate anesthesia, where large surface-positive EP's occur both on the surface of the postcentral gyrus and on the caudal bank of the central sulcus. Even when dorsal roots are stimulated, there are only rather small negative potentials at the margin of the cortical response area. In the two patients (Figs. 16 and 17) in whom EP's were recorded precentrally, the responses were initially surface-positive. There were no initially negative responses. An example of initially negative EP's observed in animals is that recorded in the peristriate cortex of the marmoset, where the cortex is quite unfissured.

Patterns of Sensory and Motor Localization in Post- and Precentral Gyri

Because of the limited time during which potentials could be evoked and cortex stimulated, it was not possible to map more than a limited number of cortical sites in a given patient. The patient most extensively studied was that illustrated in Fig. 7. Even here, it is clear from study of the map that exploration of the body surface was incomplete. For example, it is not likely that a given cortical site will have more than one receptive field, such as those indicated for arm and thorax (Points 2, 3, and 4, Fig. 3 B). Here the body surface was not sufficiently explored to define fully the receptive fields for these points. The same may be said of Sites 12 to 16 (Fig. 3 B), where the ocelar nal aspect of the arm was not stimulated, and for Sites 7 to 11, where the antecubital aspect was not explored. This limitation probably applies generally to our material. The results illustrate what is potentially possible, but it remains for future studies to provide more detailed maps, which will permit a full comparison of the topographical patterns of man and his nearest primate relatives.

It should be recalled that the stimulator used to explore the body surface of our patients delivered a stronger stimulus than the tactile stimulator generally employed to move hairs on an animal's body. This no doubt caused spread of the stimulus beyond the site of the tap and resulted in larger receptive fields. However, it is not likely that the stimulus spread was great. The effect generally was comparable to that felt when one taps one's finger with a light reflex hammer. In this situation, in addition to contact with the finger tip, movement of the finger and adjacent parts of the hand may occur but the subject recognizes where the tap was applied. Furthermore, if, while holding the patient's hand (which on stimulation resulted in evoked potentials), the observer's hand is tapped strongly enough to shake the patient's, evoked responses need not occur. The wider activation of cortex by the tap than by cotton wool stimulation is seen in Fig. 5 B (Toe I, Touch; Toe I, Tap) and in Fig. 6 C (tap, second from right; touch, far right). In Fig. 18, the EP method defined larger receptive fields than the areas of paresthesia produced by electrical stimulation of nearby cortical points. Of course, it is possible that the patient reports only the area for which the most intense sensation is aroused and not the whole area.

The common textbook illustrations of the patterns of localization in the pre- and postcentral gyri are either ladder-like arrangements of the names of the parts represented, such as that of Foerster, or the "homunculi" of Penfield, et al. These are based on data accumulated from a relatively small number of points in each of a large number of patients. Superposition of data from many patients, as in the paper by Penfield and Boldrey, indicates extensive areas of cortex devoted to particular body parts, although in individual patients there may be relatively smaller areas. One reason for this difference appears to be the variability in the position on the central gyri at which particular parts of the body are represented, as we have found for the leg in the present study. This variability is seen in animals, although to a lesser extent. Somatotopic maps for animals are commonly based on data collected for considerable portions of the area under study in individual animals. This is not possible, of course, in man.

Another difference between studies on man and animals is the fact that most sensory and motor data on man have been collected from the exposed surfaces of the central gyri, whereas in animals the banks of the central and other fissures also have been explored after removing adjacent cortex. This means that large portions of the sensory and motor areas on the walls of the central sulcus of man have been less thoroughly studied than have the exposed surfaces. In fixed brains, which we have examined, the central sulcus was nearly twice as deep as the width of each gyrus. This means that little more than a third of the sensory and motor areas on the dorsolateral aspect of the hemisphere is generally available for study. For man there are few reports on data collected from the walls of the central sulcus. Penfield and Rasmussen illustrate in their Fig. 8 data for the rostral bank of the
were especially favorable for the case illustrated in 500 J.

gyrus in Fig. 7, one rostrally in the paramedian well as of the epaxial musculature, the representation monkeys. Perhaps the conditions of local anesthesia which produced movements of the digits extending onto the rostral bank of the central sulcus. This basic plan is already evident in the rat. It has also been found in the brain of Ateles ater. Earlier accounts of the motor area in monkeys failed to define the epaxial representation, with the result that the localization pattern tended to resemble that attributed to man. The apparent reason for failure to identify earlier the epaxial representation is the higher current required to stimulate this region of the cortex. Stimulation of epaxial representation may account for the adverse movements elicited in monkey by the Vogts, and in man by Foerster, who was known to use stronger stimulation.

In most of the patients reported here, only a line of points along the lip of the central sulcus was stimulated. However, in some patients more rostral points were also included. The area studied in Fig. 20 appears to extend the length of the arm area. The localization pattern is of special interest, because points yielding movements of the elbow and shoulder surround rostrally points nearer the central sulcus, which produced movements of the digits. The pattern is more like the pattern of representation in the monkey than that classically described for man. These observations raise the possibility that the pattern in man has not been defined for the same reason that the epaxial representation was not found earlier in monkeys. Perhaps the conditions of local anesthesia were especially favorable for the case illustrated in Fig. 20, since all thresholds were relatively low. In one other patient (Fig. 8), movements of elbow and shoulder in association with movements of fingers and wrist were seen throughout most of the arm area stimulated. If stronger currents generally are required to excite more rostral levels of the precentral gyrus of man, the general practice of keeping currents close to the threshold of points near the lip of the central sulcus could account for failure to elicit movements of proximal limb from the rostral part of the gyrus, as well as of the epaxial musculature, the representation of which is seldom illustrated for man. In our material there are seven instances in which the epaxial musculature was activated: three on the precentral gyrus in Fig. 7, one rostrally in the paramedian precentral area of Fig. 22, one in the supplementary motor area of this same patient, one posteriorly in the paracentral postcentral sensory cortex shown in Fig. 20, and another (dorsal neck muscles) on the precentral gyrus of this same figure. In another patient (Fig. 21), responses were also obtained from the full width of the precentral gyrus at low thresholds. Here it appears that the hand area may extend into a well developed precentral sulcus.

Another feature of interest in the precentral motor sequence is the occurrence of movements of the eyeballs from points close to the central sulcus (Figs. 7, 8, 13, 19 B and 20). In four of these cases, the movements were bilateral and conjugate, in two they were contralateral only. In all cases, the sites were the highest points in the face area, adjacent to the thumb above and medial to those yielding closure or elevation of the lids below. Similar localization for eye movements has been reported by Foerster and by Penfield and Rasmussen. Movements of the eyeballs in monkeys are produced by stimulation of cortex in the inferior precentral sulcus and on the surface of the gyrus ahead of this sulcus. This region of cortex is directly adjacent to the area yielding movements of the eyeballs from the rostral and more medial parts of the face area of the monkey. The findings in man, then, show relationships similar to those in the monkey except for the fact that the sites yielding eye movements come closer to the central sulcus than those in the monkey. Apparently, the frontal eye field in man extends onto the precentral gyrus from more rostral frontal cortex.

An interesting effect in a case of Parkinson’s disease was seen in the patient whose sensory and motor data are illustrated in Fig. 17. This was the striking way in which stimuli, subthreshold for movement, applied to the precentral gyrus, caused cessation of the marked tremor and strong rigidity which this patient exhibited. The results suggest the possibility that subthreshold electrical stimulation through implanted electrodes might be used to control these symptoms in Parkinsonian patients.

Our data also raise questions about the patterns of localization in the postcentral gyrus. In Fig. 7 the postcentral pattern opposite the precentral finger area shows that more of the arm than the fingers is represented. This is true also for Figs. 12, 13, and 15. These cases suggest that the organization of the postcentral sensory area may mirror that of the precentral motor area, as illustrated by Fig. 20, and that the walls of the central sulcus may be concerned principally with representation of the fingers, as they are both precentrally and postcentrally in the monkey and chimpanzee.

In this connection, it is of interest that Penfield and Boldrey, in their composite figures of sites yielding sensations and movements of digits and other parts of the arm, show (in Figs. 12 to 15) that the digits are represented in narrow strips of the pre- and postcentral gyri along the lips of the central sulcus, while other parts of the arm have wider representation both pre- and postcentrally.
Localization in human cerebral cortex

In describing the individual figures, attention was called to the relation of the pattern to the medial edge of the hemisphere, whenever this was possible. In only four of the patients was there clear evidence that the leg representation extended onto the dorsolateral aspect of the hemisphere (Figs. 7, 8, 21, and 23). In six others (Figs. 11, 14, 19 A and B, 20, and 22), this was considered possible. In five (Figs. 10, 13, 15, 17, and 18), the leg area clearly did not extend onto the dorsal surface, while in the remaining five (Figs. 1, 9, 12, 16, and 24), the sites studied were too far from the midline to permit a judgment.

Most illustrations of the Rolandic sensory and motor areas of man show the leg area extending well onto the dorsolateral surface, as it does in the monkey and chimpanzee. However, reported finding the motor leg area situated entirely on the mesial aspect of the hemisphere in 14 consecutive cases that he studied. The results reported here indicate that there is considerable variability from patient to patient in the position of the leg-arm boundary in the Rolandic areas. This view also has been stated by Penfield and Rasmussen.

Another feature of the sensory and motor sequences, as generally described, is that particular parts of the body are represented at the same mediolateral level precentrally and postcentrally. In four patients in this series, we had the opportunity to compare the pre- and postcentral sequences and found that the face-arm boundary was situated more laterally on the postcentral gyrus than on the precentral. In Fig. 7, even though the lateral limit of the postcentral finger area probably was not quite reached, it is clear that the precentral face-arm boundary is more than 1 cm above the lowest postcentral finger point. In Fig. 13, again the postcentral finger points are seen to extend well below the uppermost precentral face point for a distance of 2 cm. In Fig. 18, although the precentral boundary between face and arm was not defined, the higher of the two precentral face points is again at least 2 cm above the postcentral face-arm boundary. In Fig. 21, there is a discrepancy in the levels of the sensory and motor representations along the central sulcus with precentral lying higher than corresponding postcentral foci. Figures 10 and 12 also suggest that a similar lateral shift of the postcentral sequence exists in these cases.

A less striking difference in the level of the face-arm boundaries of the pre- and postcentral representations is evident in macaque, spider, and cebus monkeys, and in the gibbon and chimpanzee. The greater need for cortical representation of motor than of sensory functions of the head, especially in man, may explain the upward shift of the face-arm boundary precentrally. However, this boundary in primates tends to run in a mediolateral direction from the rostral border of the motor cortex to the caudal border of the sensory cortex. If this direction is maintained in man, the great depth of the central sulcus would result in a greater lateral shift of the face-arm boundary, when it emerges from the central sulcus onto the postcentral gyrus. Celesia has revised the Penfield homunculi to take this difference into account.

While we have just suggested that the organization of the pre- and postcentral arm areas may be more like their organization in the macaque than has been thought, the leg areas are clearly arranged as are the leg areas in the chimpanzee and gibbon. In all three, the leg is extended toward the cingulate sulcus with the toes near that sulcus and the hip either near the rim of the hemisphere or on the dorsolateral surface. This arrangement differs from that in tailed primates, where the tail is represented most medially. Next to it, postcentrally, is the postaxial aspect of the leg followed by the foot, then the preaxial leg and the trunk. We have suggested that these differences in the arrangement of the leg area may be related to the absence of the tail in higher primates, with the result that enlargement of the cortical leg area has been free to take place by growth toward the cingulate sulcus unhindered by the presence of an already established tail area. The general plan of organization in the pre- and postcentral areas in the chimpanzee has been diagrammed elsewhere by Woolsey (see his Fig. 3.4).

In our patients, we did not have occasion to make observations on the representation of the genitalia. Earlier illustrations of Penfield, et al. (for instance Fig. III-36 in Penfield and Jasper and Fig. 17 in Penfield and Rasmussen) show the genitalia represented beyond the toes on the medial wall of the hemisphere, although Penfield and Rasmussen state that the relationship is not clear. In the gibbon and chimpanzee, the genitalia are represented in a more natural relation to the anus, buttocks, and lower abdomen. In the chimpanzee this representation may be entirely on the posterior wall of the central sulcus (see Fig. 3.3 of Woolsey). Penfield and Rasmussen described a patient in which sensations referred to the genitalia were elicited on stimulation of the postcentral gyrus on the dorsal surface of the hemisphere near the hip representation. If the genitalia in man are represented on the caudal bank of the central sulcus, as in the chimpanzee, lack of data concerning them is understandable. It seems probable that localization of genitalia beyond the toes on the medial wall is the result of stimulation of a genital focus in the supplementary sensory area. Either the supplementary focus or one near the postcentral hip area or both could have accounted for the symptoms of nymphomania reported by one of us.

Second Somatic Sensory-Motor Area

In only one of the patients of this study was there evidence for a second somatic sensory-motor area (Sm II). The results are illustrated in Fig. 17, where data from both sides are illustrated together on the right hemisphere. The two lowest points just above the Syl-
vian fissure postcentrally are considered to be in this area. The more lateral one yielded excellent EP's on stimulation of the tip and base of the contralateral thumb. These were the only sites stimulated, so the extent of the receptive field was not determined nor was the ipsilateral hand stimulated. Just above the hand point is one from the left hemisphere, which on cortical stimulation yielded plantar flexion of the contralateral foot. These observations are consistent with the view derived from animal experiments that the leg is caudal to the arm in Sm II and that the apices of the limbs reach toward the Rolandic region. The sites in Fig. 17 lie within the region from which Penfield and Rasmussen were able to elicit by cortical stimulation sensory, motor, and inhibitory effects for the contralateral arm and leg, and occasionally for the ipsilateral limbs in their second somatic area. Stimulation by them of cortex of the upper bank of the Sylvian fissure with a penetrating, insulated electrode produced effects in the leg.

In another patient, not included in this report, points "along the upper posterior margin of the Sylvian fissure" gave responses to "stimulation of either side of the body."76

Hirsch, et al.,30 studied a patient from whom one temporal lobe had been removed 10 years before. Using a "summatung" technique and electrical stimulation of nerve, they recorded from the upper bank of the Sylvian fissure relatively large negative responses preceded by a small positive deflection on stimulation of contralateral and ipsilateral sides of the body. The latencies of these responses were longer (30 to 50 msec) than for postcentral responses (25 msec). In this respect the second sensory responses in man resemble those of the monkey and the chimpanzee, or that there is a motor area that extends than in the squirrel monkey, macaque, and chimpanzee (unpublished material).

Penfield and Rasmussen44 also reported effects upon the arm and leg from stimulation of cortex above the Sylvian fissure and rostral to the level of the central sulcus. This suggests either that the second sensory area is more extensive anteroposteriorly in man than in the squirrel monkey, macaque, and chimpanzee, or that there is a motor area that extends rostral to Sm II, as was reported for the monkey by Sugar, et al.48 Although we have looked for a motor area in this region separate from Sm II, our data indicate complete overlap of sensory and motor representations in Sm II. The question obviously deserves further study.

The Supplementary Motor Area

The term "supplementary motor area" (Ms II) was first used by Penfield and Welch,46 who are responsible for redirecting attention to the representation of body musculature in this region of the cortex, a region also studied by Bates in 1953. However, Horsley and Schäfer in 1884 and 1888 first clearly established the representation of head, arm, and trunk in this region, although Ferrier in 1890 wrote that he "had to some extent noted" these effects in his first experiments on the monkey in 1873. The map of the monkey by Horsley and Schäfer was transferred to the human brain by Mills in 1889. His map corresponds rather well with the current locale of the supplementary motor area in man. Similar results obtained by the Vogts in monkeys and by Foerster in man also were the result of stimulating this region of cortex.

In two of our patients, movements were obtained on stimulation of the medial wall of the hemisphere rostral to the precentral leg area. In one of these (Fig. 21) a single site was stimulated, which yielded bilateral movements of the lips and tongue and a repetitively vocalized "T-T-T" sound. The site was situated near the upper rim of the hemisphere, 2.5 cm ahead of the central sulcus. Similar repetitive vocalizations from this region of the cortex have been reported by Brickner and by Penfield and Rasmussen. It is of interest that, within a week after this characteristic vocalization had been produced, Dr. R. A. Kuhn, who had been present in the operating room, was called to see a patient in the Student Health Clinic. During the examination, the patient developed an epileptic attack, which began with repetitive vocalization very like that induced by the cortical stimulation. Dr. Kuhn thereupon remarked, "This patient must have supplementary motor area epilepsy." When diagnostic studies were completed and surgery was undertaken, a small meningioma of the falx pressing bilaterally upon the supplementary motor area was found. For 3 days after the operation, this patient had a slight motor aphasia and a weak contralateral forced grasp reflex.

In the second patient (Fig. 22), seven sites were diagnosed as lying within the supplementary motor area anterior to the precentral leg area. Two of these sites produced movements of the hip, knee, and lower back. Four yielded movements of facial muscles and tongue, and inhibition of speech.

In one other patient, not included among the cases illustrated in this report, the supplementary motor area was stimulated about 2 cm rostral to precentral motor points, which had yielded movements of toes, foot, and knee. Biting movements, turning of the head, and retraction of the lower lip were observed.

In two patients with bilateral parasagittal meningiomas just rostral to the precentral gyrus, there was, after surgery, profound motor aphasia and strong forced grasp reflexes of both hands and the jaws, and in one of the patients there were grasp reflexes bilaterally in the toes.19 These patients also showed marked perseverations in movements involving the hands, including writing. These effects were temporary and began to clear after about 10 days. It is of interest, however, that both stimulation of the supplementary motor area and injury to it appear to affect the speech mechanism. Penfield and Roberts include the supplementary motor areas of both hemispheres in the cortical areas involved in speech mechanisms. Chusid, et al.,13 and Guidetti have
described speech disturbances associated with lesions in this region. Lesions of the supplementary motor areas in monkeys have led us to the conclusion that the forced grasping in this animal, originally described by Richter and Hines, is related primarily to removal of the supplementary motor area. The effect is more enduring with bilateral lesions. Similar conclusions were also drawn by Penfield and Welch, and Penfield and Jasper reported the occurrence of a grasp reflex following ablation of the supplementary motor area in man.

**The Supplementary Sensory Area**

In one of our patients (Fig. 23), results of stimulation suggested that we were in the supplementary sensory area of Penfield and Jasper on the medial surface of the parietal lobe. Sensory effects were obtained from five sites in this region. Two, related to the opposite arm, were adjacent to the sulcus cinguli and three, related to the foot, were situated above these up to the margin of the hemisphere. This arrangement suggests that a supplementary face area should be either on the upper bank of the sulcus cinguli or, more likely, on the medial surface posterior to the arm and leg points. Such an arrangement would form a pattern mirror-imaged with the supplementary motor area on the medial wall precentrally. It also accords in general with the case illustrated by Penfield and Jasper in their Fig. III-43.

The supplementary sensory areas for the arm and leg were defined by Blomquist and Ambrogi Lorenzini in the squirrel monkey by recording the distribution of cortical potentials evoked on electrical stimulation of dorsal root fibers. A face area was not described. More recently, microelectrode recordings from the medial aspect of the parietal lobe of the monkey by Murray, et al., have yielded responses from the leg, arm, trunk, and head in cortex on the ventral bank of the cingulate sulcus and the medial surface caudal to this sulcus. It is probable that the supplementary motor and sensory areas account for the extrapyramidal motor areas on the medial and dorsal aspects of the frontal and parietal lobes in Foerster’s map of the human cortex.

**Postcentral Movements, Paresthesias, and Stimulus Thresholds**

Movements were obtained on postcentral stimulation from 14 points and paresthesias from 24 in this series of patients. Both movement and sensation might be produced by a particular stimulation, or movement or sensation alone. In Fig. 18, 12 postcentral sites were stimulated at 0.5 mA, of which five elicited both movements and paresthesias, while the rest gave only paresthesias. It appears that, in general, stronger stimuli are required for the elicitation of movements than of paresthesias. However, in some of our patients movements were obtained without paresthesias. Thresholds for postcentral stimulation resulting in movements and/or paresthesias generally were not significantly higher than for precentral stimulations. In the anesthetized monkey, production of movement by postcentral stimulation usually requires a considerably higher stimulating current than does precentral stimulation near the central sulcus (see Woolsey, Fig. 9). Penfield and Boldrey reported lower thresholds for postcentral than precentral stimulation, but they stated that Foerster had found the reverse. The character of the movements obtained by postcentral stimulation did not differ in any significant way from those obtained on precentral stimulation. In this our observations agree with those of Penfield, et al., but are not in accord with those of Libet, who found motor responses obtained by stimulation of the postcentral gyrus to differ from those elicited from the precentral gyrus both in threshold and in type of muscular activation. However, the character of the electrical stimulus was different. We used 60-cycle AC; Libet used rectangular pulses from an AFL model 104A stimulator delivered through an RF isolation unit.

**Phantom Limb Pain**

Two of our patients were seen because of phantom limb pain. In one patient (Fig. 23), cortical stimulation of the precentral leg area on the medial wall produced movement and pain in the phantom leg, which was only mildly like the usual pain. Stimulation of the postcentral leg area resulted only in movements. However, when more caudal cortex on the medial wall was stimulated, severe pain was produced in various parts of the foot, and nonpainful paresthesias were referred to the arm. In addition, the points related to the arm also gave rise to a feeling of fainting, a decrease in heart rate, and a “gone feeling in the heart.” The phantom limb and pain were abolished by removal of the area, which on stimulation gave rise to the pain, together with the leg portion of the postcentral sensory area on the medial wall. In the second patient (Fig. 24), pain in the phantom arm was aroused by stimulation of the postcentral arm area and relieved by its removal.

It was not possible to follow either of these patients long enough to know whether the surgery provided long-term relief from the phantom pain. Penfield and Jasper (p 99) reported a case of thalamic pain, in which cortical stimulation of the postcentral gyrus produced attacks of pain similar to those that occurred spontaneously. Removal of the postcentral gyrus relieved the patient for 18 months and then the pain returned. A further period of relief was obtained by removal of atrophied precentral cortex, but again the pain returned. Since the supplementary motor and sensory areas and the second somatic sensory-motor areas still remained, these areas may also have con-
tributed to the phantom pain, as the supplementary sensory area clearly did in one of our patients (Fig. 23).

The role of the cortex in the elaboration of pain has never been established, since stimulation of the cortex has produced few sensations of pain except in patients with pathological pain. Penfield and Boldrey reported eliciting a sense of pain 11 times in 163 patients. However, they also reported only 13 sensations of cold and two of heat, while most sites produced tingling (204), or electricity and numbness (131), and a smaller number (49) gave rise to a sense of movement. It is possible that in the patients with pathological pain the sensation of pain is aroused by corticothalamic connections activated by the cortical stimulation. Walker, however, has expressed the view that the cortex should be concerned with pain, since the thalamic centers receiving pain afferents undergo retrograde degeneration on cortical ablation. If central pain and temperature neurons have higher thresholds to electrical stimulation, as do their peripheral fibers, it is possible that threshold stimulation of cortex adequate to produce movement and tactile paresthesias may not be strong enough to activate normal pain and temperature mechanisms.

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