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Mechanosensory Projections to Cerebral Cortex of Sheep

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ABSTRACT This study mapped the mechanosensory projections to cerebral cortex of sheep, to complete earlier partial maps and to relate cortical projections to the organization previously determined in ventrobasal thalamus. Tungsten microelectrodes were used to explore thoroughly the walls and depths of cortical sulci as well as the previously studied gyral crowns, for regions responsive to mechanical stimulation of peripheral receptors, in sheep anesthetized with Dial-urethane or nitrous oxide with either halothane or methoxyflurane. Earlier findings of a large projection from the ipsilateral mouth, lips and nose were confirmed. In addition, a small representation of the contralateral body and limbs was found which corresponds in most respects to the "second" sensory area (SII) of other mammals. In the primary (SI) sensory cortex, representations of the body and limbs were not found despite thorough fine-grain mapping. Responses possibly representing a vestige of primary sensory cortex, and mechanosensory responses in claustro-cortex, were also observed.

This study completes our electrophysiological mapping of mechanosensory projections in the bulbo-thalamic pathway in sheep. Previous studies analyzed projections to the dorsal column nuclei (the cuneate-gracile complex) and the spinal trigeminal nucleus (Woudenberg, '69), and to the ventrobasal thalamus (Cabral and Johnson, '71).

The projections in this mammalian mechanosensory path vary drastically from species to species. The variations directly reflect behavioral specializations; the animal's ability to gather information from, and respond to, the environment (e.g., Adrian, '43; Rose and Mountcastle, '59; Welker et al., '64; Johnson et al., '69; Pubols and Pubols, '71; Cabral and Johnson, '71; Welker, '73, '74). Sheep are artiodactyls, an order of mammals exemplifying an extreme of specialization. Their behavioral and structural devotion to excellence as plant-consuming systems gives rise to many questions concerning related specialization in their brains. Our studies take up one of these questions, that of the organization of the major tactile information system in such an animal.

Among the earliest physiological studies of sensory projections to cerebral cortex were those of Adrian ('43) and of Woolsey and Fairman ('46) on various hoofed mammals, including sheep. Methods available at that time restricted study largely to the exposed gyral crowns; sulcal banks were not easily reached with their recording electrodes. The partial maps they obtained nevertheless revealed two notable features of the organization of sensory cortex in sheep: (1) a predominance of ipsilateral, rather than the contralateral, projections which are usually seen in mammals; and (2) a surfeit of projections from the mouth with a dearth of projections from the body and limbs. Our map of projections to ventrobasal thalamus showed a similar predominance of ipsilateral projections from the mouth and nose; but there was in addition a small, but otherwise typical, mammalian projection from the contralateral body and limbs.

In the present study, the use of microelectrodes made possible the thorough exploration of cortex in sulci as well as on gyral crowns; thus we were able to assemble a complete map of the projections to sheep cortex. Our map includes projections from the contralateral body and limbs; but these are different from what we expected based on earlier findings in other mam-

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mals, and in the thalamus of sheep. The expected arrangement would be a representation of the body in the primary (SI) sensory cortex, medial to the representation of the face, with the trunk located posteriorly and the limbs projecting forward therefrom. This is not what we found.

METHOD

Subjects and subject preparation

The subjects were twelve ewes and two rams weighing between 34 and 110 kg. They were obtained from the flock of the MSU Endocrine Research Unit. Some had undergone ovariectomy or hormone treatments in the course of studies on reproduction. The animals were sheared, and were taken off feed to empty the rumen, one day before experimentation. The next day they were injected intraperitoneally (IP) with 2.2 mg atropine sulfate per kilogram of body weight to control secretions in the respiratory tract. They were then anesthetized either by IP injection of barbiturate or by inhalation of gaseous anesthetic. In all cases the trachea was cannulated. The barbiturate used for long-term anesthesia was Dial-urethane buffered with NaOH; dosage was 144 mg/kg diallylbarbituric acid and 463 mg/kg urethane. When needed to eliminate nociceptive reflexes, usually after eight to ten hours, additional IP doses of anesthetic, one-quarter the original dose, were administered. For gaseous anesthesia, animals were tranquilized by intramuscular injection of 1.16 mg/kg promazine hydrochloride, and briefly anesthetized with intravenous sodium thiopental with sodium pentobarbital during insertion of the tracheal cannula. Anesthesia was thereafter maintained with halothane (1.5% in a mixture of 1000 cm^3/min NO_2 and 350 cm^3/min O_2) or with methoxyflurane (administered through an evaporator into a mixture of 900 cm^3/min NO_2 and 400 cm^3/min O_2). With methoxyflurane, body movements were minimized by intramuscular administration of phencyclidine hydrochloride, 4.12 mg/kg with additional doses when necessary. To maintain body fluids and nutrients, saline or 5% dextrose in saline was administered IP at four-hour intervals. A mechanical respirator was used when necessary. Experiments typically lasted 36 to 48 hours.

The head of the animal was securely fixed by means of screws placed in the skull which were fastened with dental acrylic to bars of a specially designed headholder. This headholder allowed the head to be placed in different positions in different experiments. The body was suspended on a frame which passed under the axillae and inguinae of the limbs on either side of the abdomen and thorax, leaving the limbs, sternum and abdomen available for stimulation.

The brain was widely exposed by removal of the bone and dura mater overlying the left cerebral hemisphere. The exposed cortical surface was protected at all times under a pool of warmed paraffin oil. This surface was photographed through the oil, and an enlarged print was made for recording the sites of electrode placements during the experiment.

Recording apparatus

Tungsten microelectrodes were manufactured using the method of Hubel ('57), except that in later experiments they were insulated with glass as described by Baldwin et al. ('65) with D. L. Clark's modification of etching the glass near the tip with HF to provide fine control over the area of uninsulated surface. Best results were obtained when this uninsulated surface extended 30 to 60 μm back from the tip; the maximum shaft diameter, including the glass coating, was 60 μm.

For recording, the microelectrode was clamped in a shielded holder; and from it signals were passed through 80 Hz low and 10 kHz high filters, amplified and displayed through an audio monitor and an oscilloscope. These signs of neural activity were frequently recorded on magnetic tape, and for permanent visible reproduction they were played from the tape through a storage oscilloscope from which they were photographed.

Mapping procedure

A microelectrode was introduced into the cortex in a series of regularly spaced penetrations, usually in rows 1 mm apart, with penetrations within a row 0.5 or 1 mm apart. Surface blood vessels often prevented such regular spacing, however. Since the head could be placed in different positions in different experiments, the planes of the rows of penetrations were varied from experiment to experiment. This permitted a wider sampling of intracortical spatial relationships.

During the slow passage of an electrode through the cortex, the body surface was stimulated until "drivable" unit activity was encountered. Samples of such activity are illustrated in figure 1. Stimulation was performed manually, using fine instruments such as wooden rods, plastic tubing and a cat's vibrissa. For a very fine stimulus, the finger of the experimenter was placed in contact with the hair or skin of the sheep with a pressure just sufficient to cross the experimenter's tactile threshold. All stimuli were at room temperature (20° to 24° C) in order to avoid temperature-dependent effects. A response was considered "drivable" if each and every application of the stimulus to the receptive field evoked unit activity.

When such activity was encountered, electrode movement was stopped and the peripheral receptive field was carefully delineated, using minimal adequate stimulation. Samples of the response activity were recorded on magnetic tape, along with a verbal description of the electrode coordinates and the receptive field. These descriptions were also summarized in a written protocol, and the receptive field was drawn on a photograph of the relevant part of the sheep's body.

For marking the location of responding units of special interest, microlesions were made by passing 40 μamp D.C. through the recording electrode as anode.

Histological procedures

At the conclusion of each experiment, the plane of electrode penetrations was preserved by inserting pieces of hypodermic tubing at the boundaries of the investigated area, using the electrode holder and micromanipulator for their placement. Then the sheep was perfused through the heart with normal saline (0.9% NaCl) followed by a mixture of one part formalin and nine parts normal saline. After 24 hours, the brain was removed and photographed, and a block of tissue containing the tracks of electrode penetrations was trimmed by cutting along the planes of the inserted tubing. The block was dehydrated in ethanols, embedded in celloidin, and sectioned at 25 μm intervals in the plane of rows of electrode tracks. Alternate sections were stained with thionin for cell bodies, and with hematoxylin for myelinated fibers. Sections were examined microscopically to identify electrode tracks and localize the marking lesions.

RESULTS

Responses to mechanosensory stimulation were obtained at 207 loci in 429 electrode penetrations from 14 sheep. The large number of penetrations yielding no responses served to demarcate the boundaries of the somatic sensory region of neocortex.

Location of somatic sensory cortex

This region was located similarly in all of the sheep, and under all of the anesthetic conditions that we used. As illustrated in figure 1, this region lies where three "constant" sulci occur in sheep neocortex (Landacre, '30). These are the coronal, diagonal and anterior suprasylvian sulci. Several smaller sulci may occur in this region in a given specimen; Landacre termed these variable sulci as "inconstant," and he classified them as branches (rami) of the anterior suprasylvian sulcus.

All responses meeting our criteria were encountered lateral to the coronal sulcus. Except in its variable anteriormost branchings, the diagonal sulcus marked a ventrolateral limit to the responsive region. Responses were found on both sides of the anterior suprasylvian sulcus, but never more than a few millimeters caudal to the posterior lip of the sulcus. These three constant sulci are quite deep, as shown in figure 1B.

Responses were often encountered in the depths of the anterior suprasylvian sulcus, but not in the depths of the coronal or diagonal sulcus.

Relation of responsive loci to cortical lamination

The zone from which evoked unit activity could be recorded was confined to the outer stripe of Baillarger which is characteristic of mammalian sensory cortex (fig. 6) and which is the region of most thalamocortical terminals (e.g., Jones and

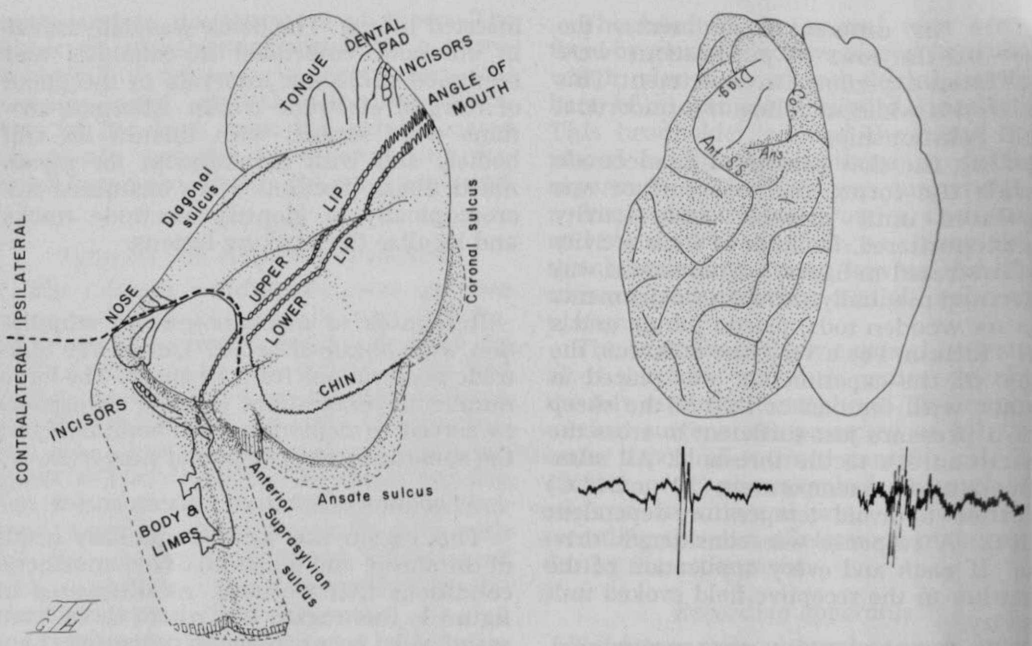

Fig. 1A Approximate locations of projections from peripheral receptors to sensory cerebral cortex in sheep. The diagram at right shows the location of the sensory cortex (the unstippled region) on the left cerebral hemisphere between or along the ansate (Ans.), anterior suprasylvian (Ant. s.s.), coronal (Cor.) and diagonal (Diag.) sulci. The diagram at left shows the sensory region as dissected free from the rest of the hemisphere, as in photograph at right, and with the anterior suprasylvian sulcus spread open. The location of projections forming sensory representations of major body parts are indicated. Particularly prominent are projections from the glabrous, papillated lips and the neighboring hairy skin. At lower right are examples of activity of neural units in response to mechanical stimulation. That on the left is a relatively isolated unit (11a in animal 29; fig. 6) responsive to stimulating the upper lip; that on the right is a unit cluster (4a in animal 31; fig. 3) responsive to stimulating hairs above the upper lip.

Powell, '70). This was in contrast to our experience in cats and other carnivores, where a column of responsive tissue extended through several cortical layers (Rubel, '71; Welker et al., '64). Instances in which two or more responsive locations were encountered in a single penetration were invariably cases where the electrode encountered the stripe at two or more locations in cortical folds (e.g., figs. 3A, 4C). In a few cases, in the wall of the anterior suprasylvian sulcus, the path of the electrode followed along the stripe for some distance, and here we found a succession of projections from closely related peripheral receptive fields (fig. 6).

Somatotopic organization

Figure 1 illustrates the general pattern of projections from peripheral receptive fields. In the greater portion of this sensory region, ipsilateral tissues on and around the lips and nose were represented predominantly. Projections from teeth, dental pad and tongue were found more anteriorly, where the variable terminal branches of the diagonal sulcus approach, and in some cases meet, the coronal sulcus; these projections were always ipsilateral. Projections from the contralateral head and body were found on or near the banks of the anterior suprasylvian sulcus; projections from the postcranial body were located on the posterior bank of the sulcus and were, with one exception, always contralateral.

There are two representations of the lower lip and chin. A large ipsilateral representation lies along the lateral bank of the coronal sulcus. A smaller representation lies near the anterolateral end of the anterior suprasylvian sulcus, and has a contralateral component posterior to and possibly continuous with an ipsilateral component (figs. 1, 4C).

The projections were almost always in somatotopic order, that is, projections pre-

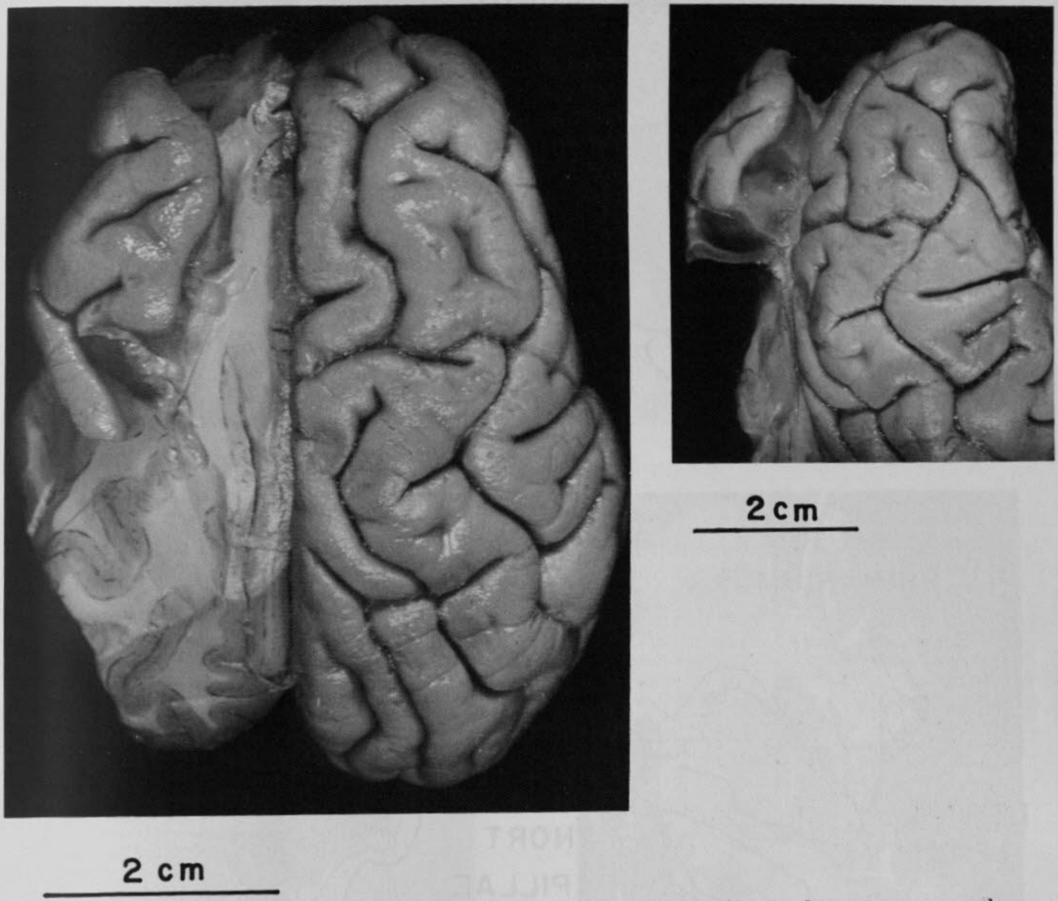

Fig. 1B Photograph of a sheep brain with the left hemisphere dissected away to expose the sensory region on all sides, as viewed from dorsal and medial sides. Note depth of sulci.

served the topological relationships of their peripheral receptive fields. Two of the seven cases that were not in somatotopic order are shown in figure 4B (P5) and figure 8 (P35), respectively.

Projections from surfaces inside the mouth

The tongue is somatotopically represented, with projections from the tip of the tongue anterior to those from more posterior regions of the tongue (fig. 3A). All tongue representations found were ipsilateral. These are the most anterolateral projections, and they lie anterior to the medial end of the diagonal sulcus and somewhat lateral to the coronal sulcus.

Medial to the tongue projections are those from the ipsilateral incisors and dental pad (figs. 2, 3B). Projections from the lower incisors and adjoining gums are located most medially, along the lateral bank of the coronal sulcus. We did not find projections to the cortex from the molar teeth, although these probably exist, since there is a small representation of the molars in the ventrobasal thalamus of sheep (Cabral and Johnson, '71). Responses to stimulation of tongue and teeth were very difficult to obtain. This projection lies in a protuberance of cortex that was easily compressed, damaged and rendered unresponsive during the removal of the overlying skull which is very thick at this location.

Just lateral to the representation of the lower incisors are projections from the dental pad at the front of the palate, into which the incisors insert when the mouth

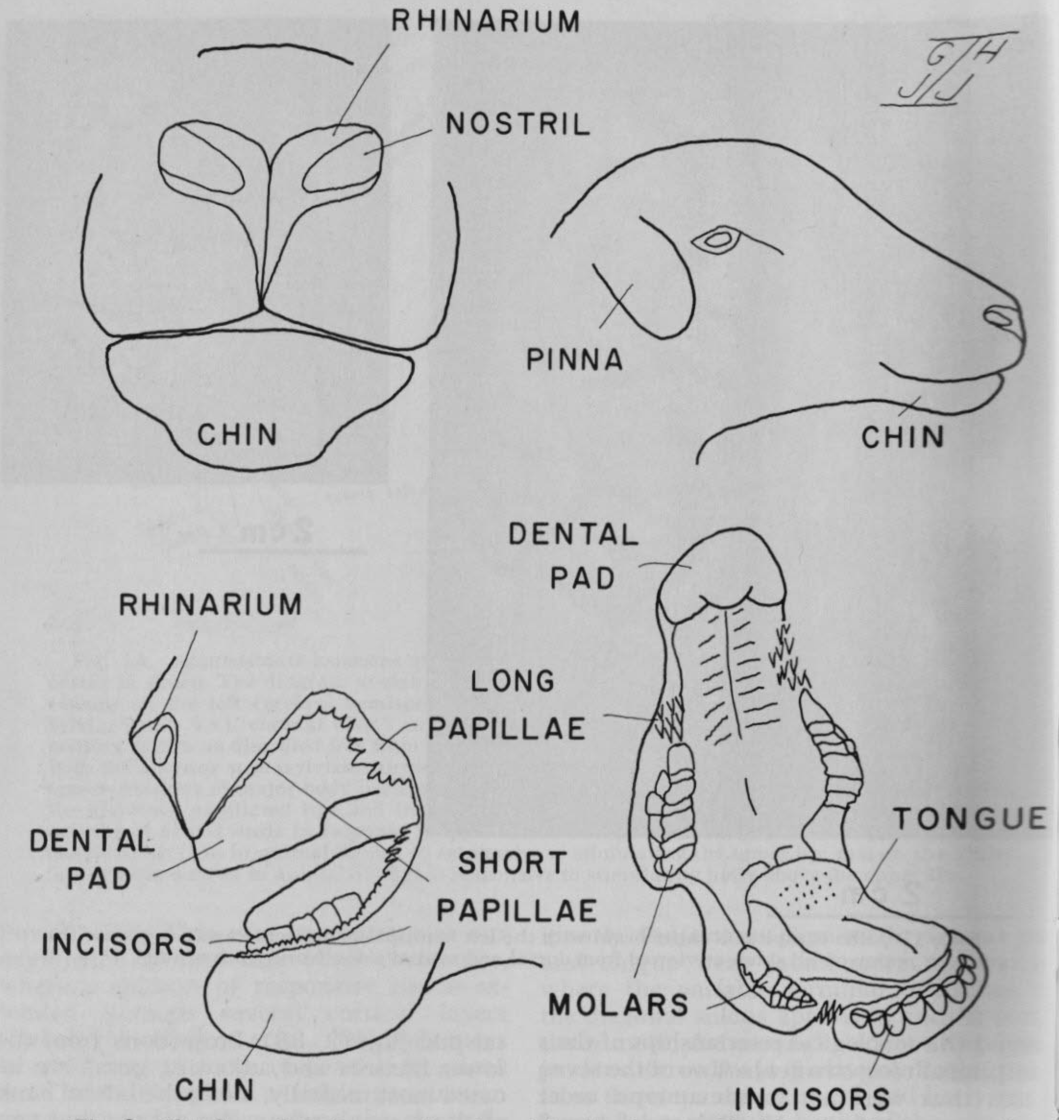

Fig. 2 This figure is both an explanation of the figurines used in following diagrams, and an illustration of the sensitive peripheral regions giving rise to the major mechanosensory projection to the sheep brain. In the photograph at lower left, the mouth is propped open and the upper lip retracted to reveal the short and long papillae, dental pad and incisors. At lower right the mouth has been dissected free and opened to reveal internal surfaces.

is closed (sheep and other bovid artiodactyls have no upper incisors).

In summary, the sequence of cortical projections of mouth parts, going from antero-lateral to postero-medial on the cortical surface, is as follows: tongue, dental pad, lower incisors and gums (fig. 3). This is a faithful reflection of the order of projections found in ventrobasal thalamus, going from ventral to dorsal in the medial portion of the sensory thalamic nucleus (fig. 9). The medial tip of the diagonal sulcus, in at least some cases, invades the region containing projections from the incisors and dental pad.

Projections from the lips and peri-oral hairy skin

Projections from the peri-oral regions occupy the largest portion of the somatic

Figure 2

sensory region of sheep neocortex, almost the entire "cap" of the "mushroom" enclosing the thalamocortical projection fibers between the coronal and diagonal sulci (figs. 1, 4, 5). The most anterior of these projections are from the ipsilateral "corner of the mouth," where the upper and lower lips join on the side of the face (fig. 4A). Posterior to this, medially, along the lateral bank of the coronal sulcus, are the representations of the ipsilateral lower lip and the adjoining hairy skin between the lip and the chin. Lateral to these mandibular projections is a large field of projections from the ipsilateral upper lip and hairy skin over the maxilla (fig. 5). More posteriorly, the projections encountered are from receptive fields successively closer to the midline of the face. In the region where projections from the upper lip and the lower lip adjoin, there is usually a minor sulcus or sulcal group, which Landacre ('30) called an anterior ramus or rami of anterior suprasylvian sulcus. This sulcus does not consistently mark a boundary between the upper and lower lip projec-

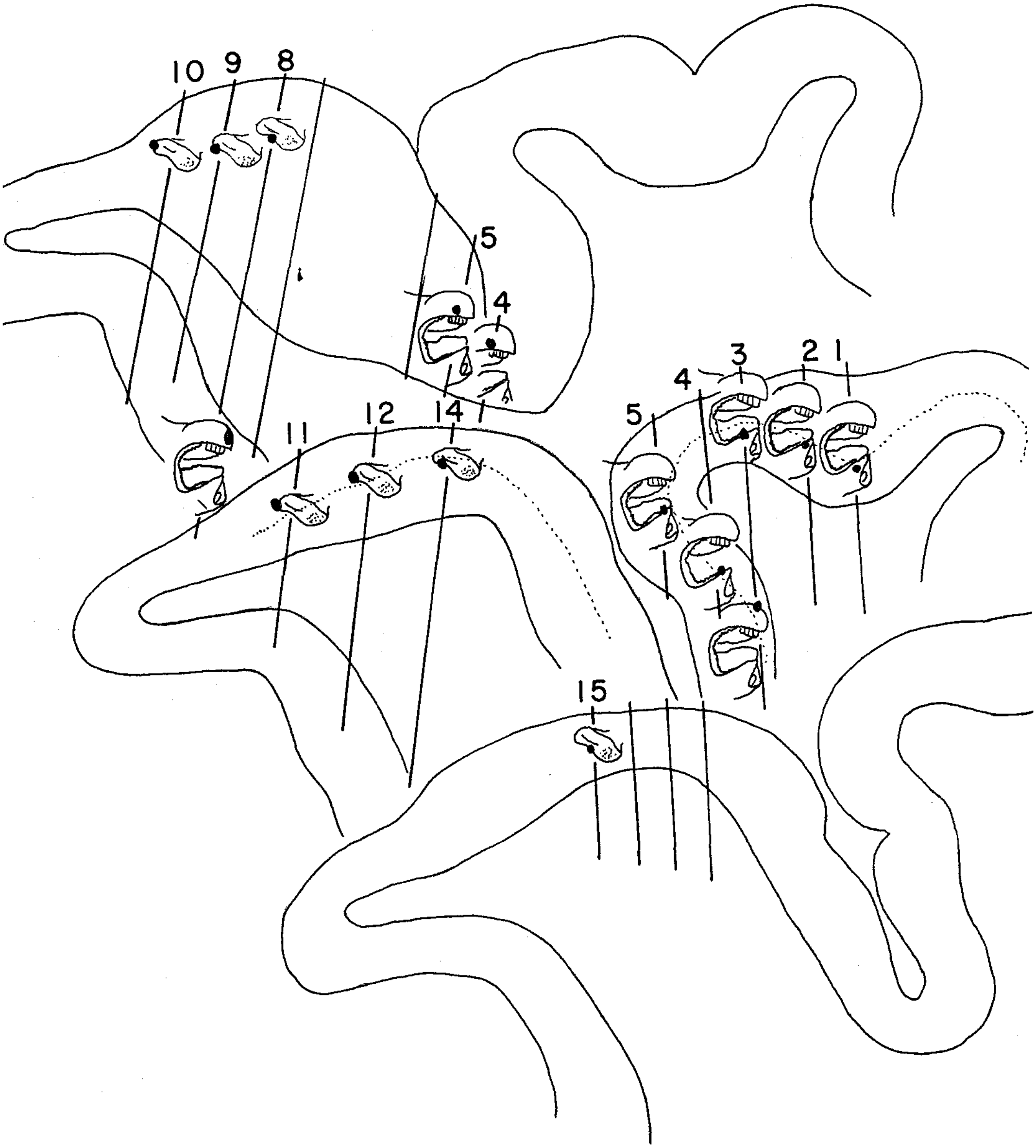

Figure 3A

Fig. 3 Location of mechanoreceptive projections from tissues inside the mouth. In this and following figures the black spot on each figurine represents the receptive field from which unit discharges could be activated. See figure 2 for explanation of figurines.

A. Responses in rows of penetrations oriented between parasagittal and horizontal planes in animal 28. Anteriormost were projections from the tongue, and the most anterior of these were from the tip of the tongue. The lower response in penetration 8 (P8) was to stimulation of chin hairs and was located on the lateral bank of the coronal sulcus, out of regular somatotopic order. Most midline responses were found considerably posterior to this level. More typical are the anterior coronal-bank responses in P4 and P5 from hairs along the lateral part of the lower lip. More posterolaterally, around the posterior bank of the diagonal sulcus, responses in penetrations 2–5 were from papillae of the upper lip. Deep in the sulcus, near the junction with the coronal sulcus, in P3, was a response from the chin hairs. The dotted line intersecting P 1–5 and 11–14 represents the outer stripe of Baillarger.

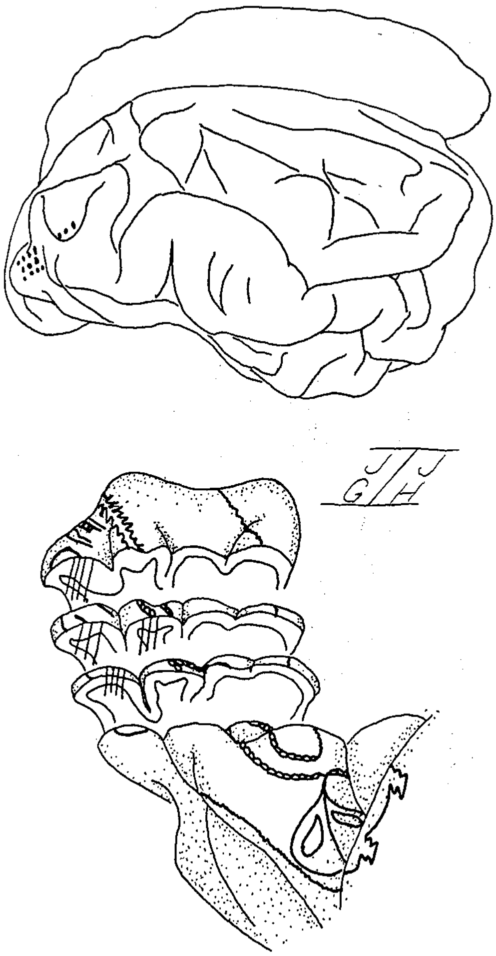

Figure 3A

tions, since upper lip responses were often found on the "lower lip side" and vice versa (e.g., P3 in fig. 5).

At the ventro-latero-posterior corner of the "mushroom cap" where the anterior suprasylvian sulcus merges with the diagonal sulcus, the projections encountered are from the ipsilateral glabrous skin around the nostrils and along the midline of the nose (fig. 4C). On the anterior bank of the anterior suprasylvian sulcus these projections are continuous somatotopically with those from the contralateral glabrous nose (figs. 4, 8).

Contralateral projections of the face and body in the anterior suprasylvian sulcus

The cortex of the fundus of the anterior suprasylvian sulcus receives projections from the contralateral side of the face (figs. 4, 7, 8). Going up the anterior bank of the sulcus, projections are from the contralateral face near the midline, and these are continuous with the ipsilateral and midline projections anterior to the sulcus (figs. 4, 7). Going up the posterior bank of the sulcus, projections are found, in somatotopic order, from the neck, thorax and back, finally from the abdomen, limbs and feet at the lip of the sulcus (figs. 4, 6, 8). The representation of limbs and body is confined to a 6 mm^2 area of cortical surface, which makes a detailed somatotopic analysis difficult. The only positive statements that we can make about this somatotopy are that: hind limb projections are medial and posterior to forelimb projections; and limb and abdomen projections are posterior to projections from the neck and back. At one location (animal 17, P13, posterior bank of anterior suprasylvian sulcus) projections were found from a bilateral projection field extending across the dorsal midline of the thorax to the upper forelimb on each side. This was the only representation found of any ipsilateral postcranial receptive field, and the only representation of an ipsilateral field posterior to the fundus of the anterior suprasylvian sulcus.

Latency of responses

In the main sensory region, the latencies of the initial spike of a unit cluster, responding to electrical stimulation of the receptive field, formed an orderly series related to the location of receptors on the body. Means and ranges in msec, according to location on the body, were: hind limb 31 (28–33), trunk 21.5 (18–25), forelimb 20.5 (18–23), contralateral face 13 (13), and ipsilateral face including mouth 13.7 (13–14). There were no differences related to ipsi- or contralaterality, nor between the two representations of the lower face. There is thus no basis, in latencies, for subdividing this sensory region.

Mechanosensory projections to other cortical regions

In all but two cases, the regions of cerebral cortex responsive to mechanical stimulation of the periphery were located within the dorsal portion of area praeparietalis

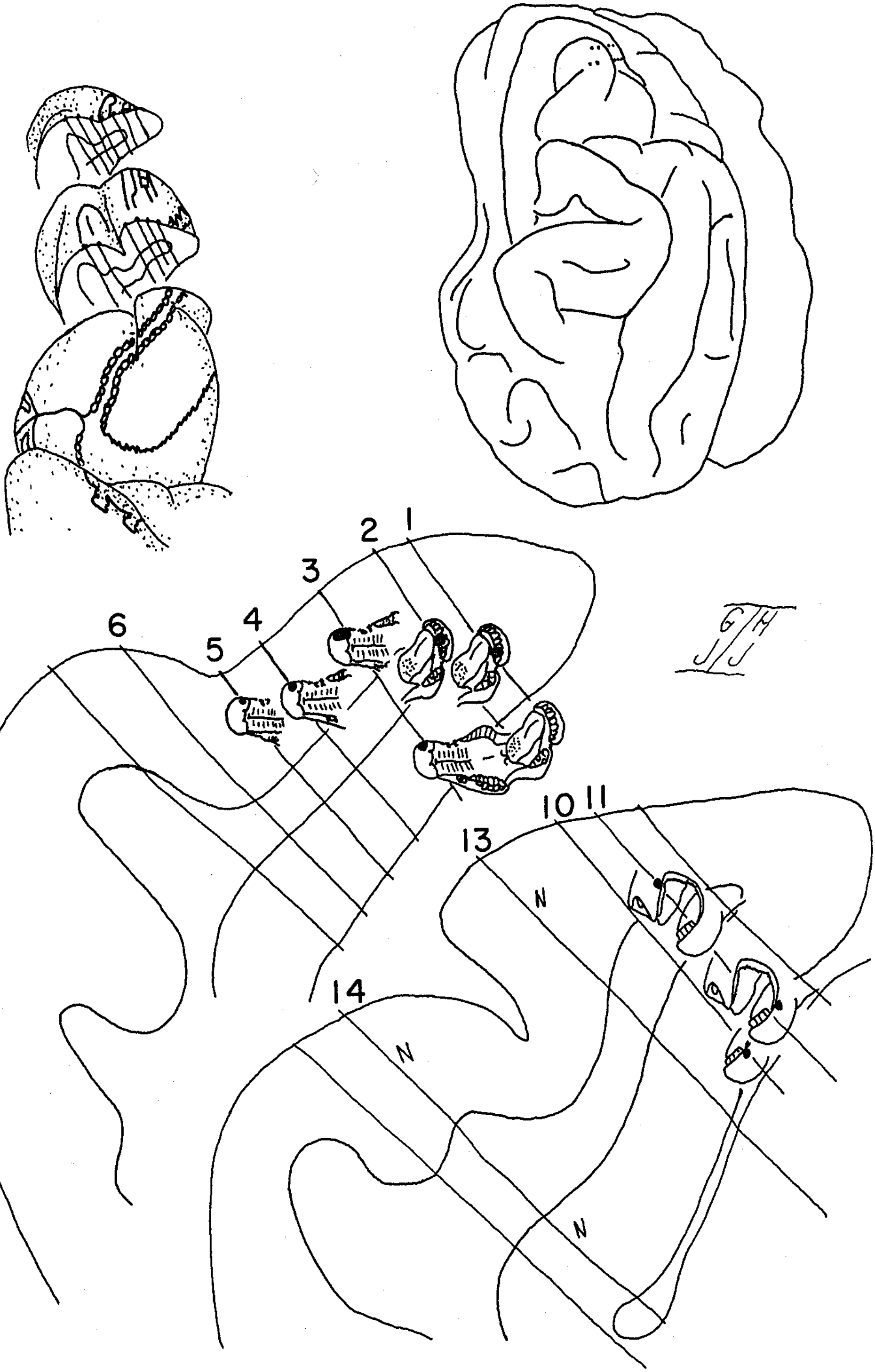

Fig. 3B Receptive fields projecting to responsive regions encountered in coronal rows of penetration in animal 29. Around the crest of the lateral bank of the anterior part of the coronal sulcus, in P 1–6 responses were to stimulation of the incisors medially, and of the dental pad laterally. In the mor posterior row of P 10 and 11, projections were from the lateral part of the lower lip medially, and th upper lip laterally. In P 13 and 14, N indicates an audible response, but not meeting our criteria of uni activity, from teeth or dental pad. No responses were encountered in unnumbered penetrations.

in the cytoarchitectural classification of Rose ('42) (fig. 10).

The first of these exceptional responsive locations was in Rose's area postcentralis and responded to stimulation of the hind leg. As pointed out by Woolsey and Fairman ('46), this region might reasonably be expected to correspond to the "primary" sensory cortex (SI) of other animals, which contains projections from the limbs and body. This small area lies largely within the anterior operculum of the ansate sulcus between the coronal sulcus and the midline. In 15 penetrations over four experiments, we found responses at only three loci in this region. The response in each case was to deep pressure into the joints or muscles of the hind limb. Two of these instances were in animal 11, anesthetized with Dial-urethane: one was a response to pressure into the lateral side of the contralateral knee, the other was a response to pressure into the cleft of the contralateral rear hoof. The third instance was in animal 31, anesthetized with methoxyflurane: the activating stimulus was pressure into the thigh muscles of either the ipsilateral or contralateral side. The motor cortex, Rose's area gigantopyramidalis, was not responsive to mechanical stimulation under the conditions of our experiments.

The second exception was a location in insular cortex, the "claustrocortex" of Sudakov et al. ('71), which Rose called area insularis. In animal 31, units at this location responded to pressure into the axillae and inguinae on both ipsilateral and contralateral sides. The latency of these responses was very long, 50 msec from the axillae and 60 msec from the inguinae. These responses were similar in many respects to those in the corresponding locus in squirrel monkeys (Sudakov et al., '71): responses were to stimulation of the ventral body surface, on either side, and had long latencies (from 30 to 300 msec in monkeys, 50 to 70 msec in sheep). These similar findings in animals of widely divergent phylogeny may indicate that this sensory input to insular cortex is a relatively basic and constant feature of mammalian brains. Testing of additional species will determine if this is true.

DISCUSSION

In sheep, the most prominent feature of the map of cortical mechanosensory projections is the relatively large ipsilateral representation of lips, nose and perioral hairy skin. Another distinctive feature is that there is only one representation (rather than the usual two) of the contralateral postcranial body, and this one is extremely small.

These features appear to be common to other artiodactyls. Similar large ipsilateral lip representations were found in goats (Adrian, '43) and llamas (Welker et al., '74). A small single postcranial body representation was found in llamas, and the hooves were the only postcranial structures whose projections to cortex were found in goats. Pigs show a large representation of the nose, with small representations of the rest of the body (Woolsey and Fairman, '46).

A large representation of perioral tissues can be expected, reflecting the impor-

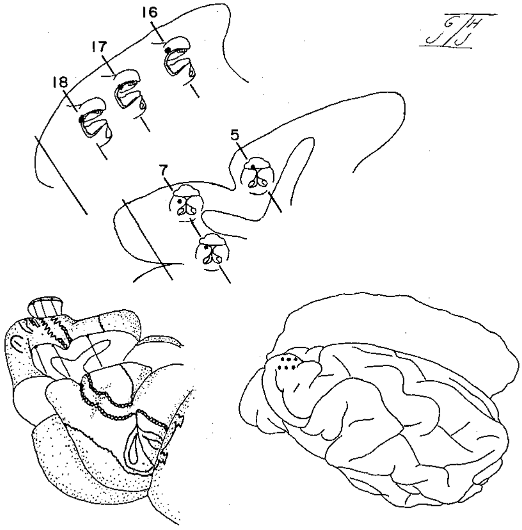

Figure 4A

Fig. 4 Location of mechanoreceptive projections found in series of parasagittal rows of electrode penetrations through the entire somatic sensory region.

A. Two rows of penetrations from sheep 10. The most medial row traversing the wall of the coronal sulcus (P 16, 17, 18), encountered projections from the long papillae of the lateral end of the ipsilateral lower lip at the corner of the mouth where it joins with the upper lip (fig. 2). The next row yielded projections from the ipsilateral lower lip nearer the midline (P5), and more anteriorly in the cortex were projections from the hairy skin above the ipsilateral upper lip (P7).

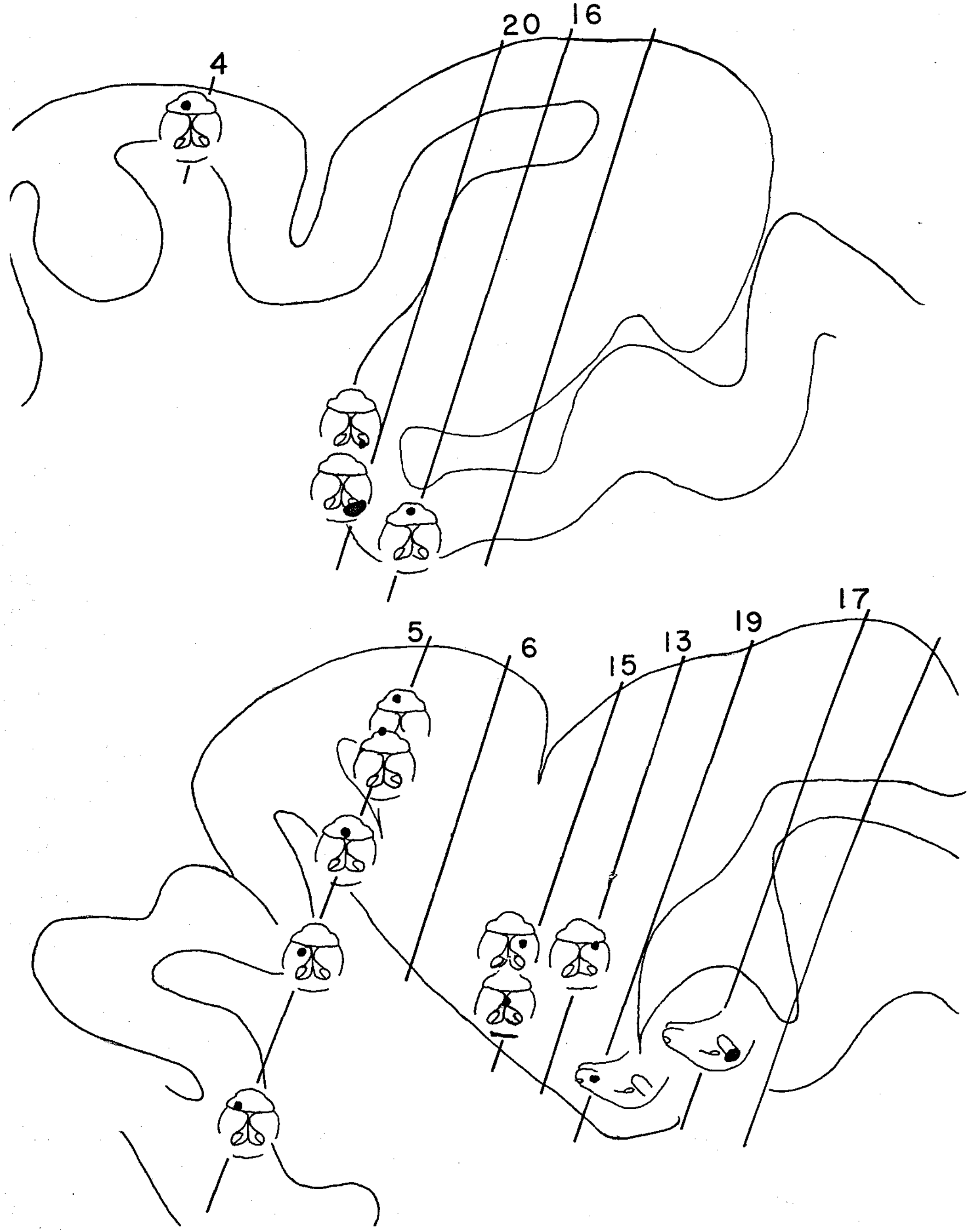

Figure 4B

Fig. 4B Two, more lateral parasagittal rows of electrode penetrations, from sheep 15. No responses were obtained from cortex lying between the lateral extension of the ansate sulcus and the anterior suprasylvian sulcus (upper portions of P 16, 20, and 15, 13, 19, and 17). This is one region where a

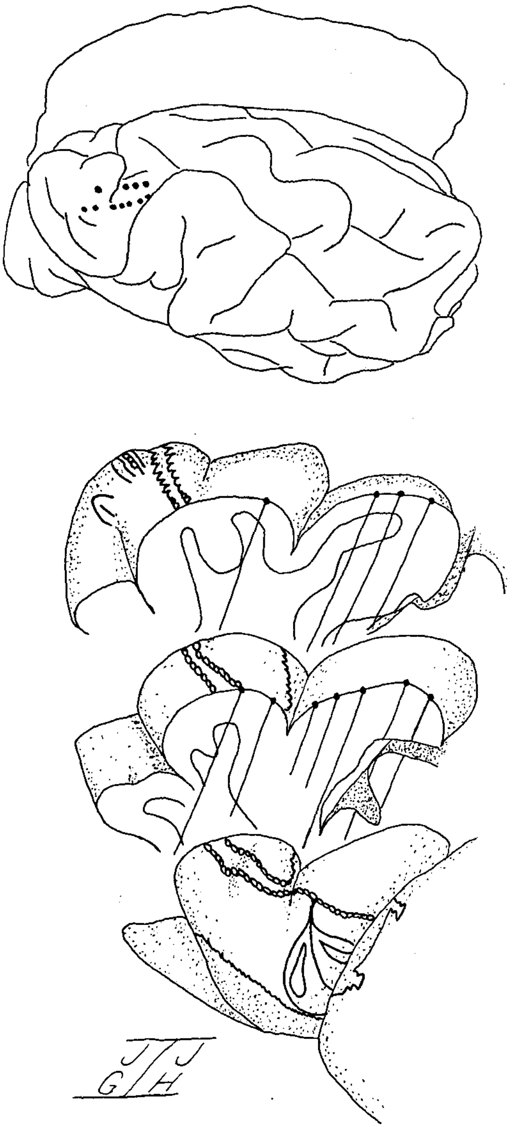

Figure 4B

representation of the body in SmI cortex might be expected from data obtained in other mammals. Anterior to the ansate sulcus, the projections found were from the ipsilateral chin and lower lip in the posterior and medial part of this region, more antero-laterally projections were from hairy skin over the ipsilateral upper lip. The response from the lower lip, ventralmost in P5, was one of seven projections encountered that were not in regular somatotopic order. In the fundus of the anterior suprasylvian sulcus we regularly found responses from the *contralateral* nose and neighboring hairy skin along with the contralateral side of the face and the pinna (lower parts of P 15, 13, 19, 17).

tance of these surfaces in the food-selecting behavior which is a major exploratory activity of grazing herbivores. Arnold ('66a, b) has demonstrated that impairment of sensory input from the muzzle affects dietary selection in sheep, and that other sensory modalities also play an important role. In this regard it is of interest that there is a special region of the retina in artiodactyls which has a high density of retinal ganglion cells; this region serves that part of the visual field that includes the muzzle (Hughes and Whitteridge, '73).

Ipsilateral projections from perioral tissues

Goats as well as sheep show a great predominance of ipsilateral over contralateral projections to neocortex from perioral tissues (Adrian, '43). However, in llamas (Welker et al., '74) the equally large perioral projections are predominantly contralateral, although the ipsilateral and contralateral components have the same topological relationship as they do in sheep. The large nose projection of pigs (Woolsey and Fairman, '46) is also predominantly contralateral.

Thus the peculiar feature of a predominantly ipsilateral sensory projection to cerebral cortex may be confined to the family Bovidae or their suborder Ruminantia. Sheep and goats are closely related Bovids, but llamas are of the family Camelidae in the suborder Tylopoda, and pigs belong to the remaining artiodactyl suborder, the Suiformes (Simpson, '45). Investigations of the sensory projections in deer, from another family of Ruminantia, the Cervidae, will help to delimit the phylogenetic extent of the unusual ipsilateral predominance, whether it is limited to the Bovid family or is common to the rest of the suborder Ruminantia.

Thalamo-cortical relationships

The predominance of ipsilateral projections to the cortical sensory representation of sheep is a faithful reflection of the representation formed by projections to the ventrobasal thalamus (fig. 9). The cortical representation differs from the thalamic in only two respects. In the thalamic representation of intraoral tissues, the projections from the posterior portions of the

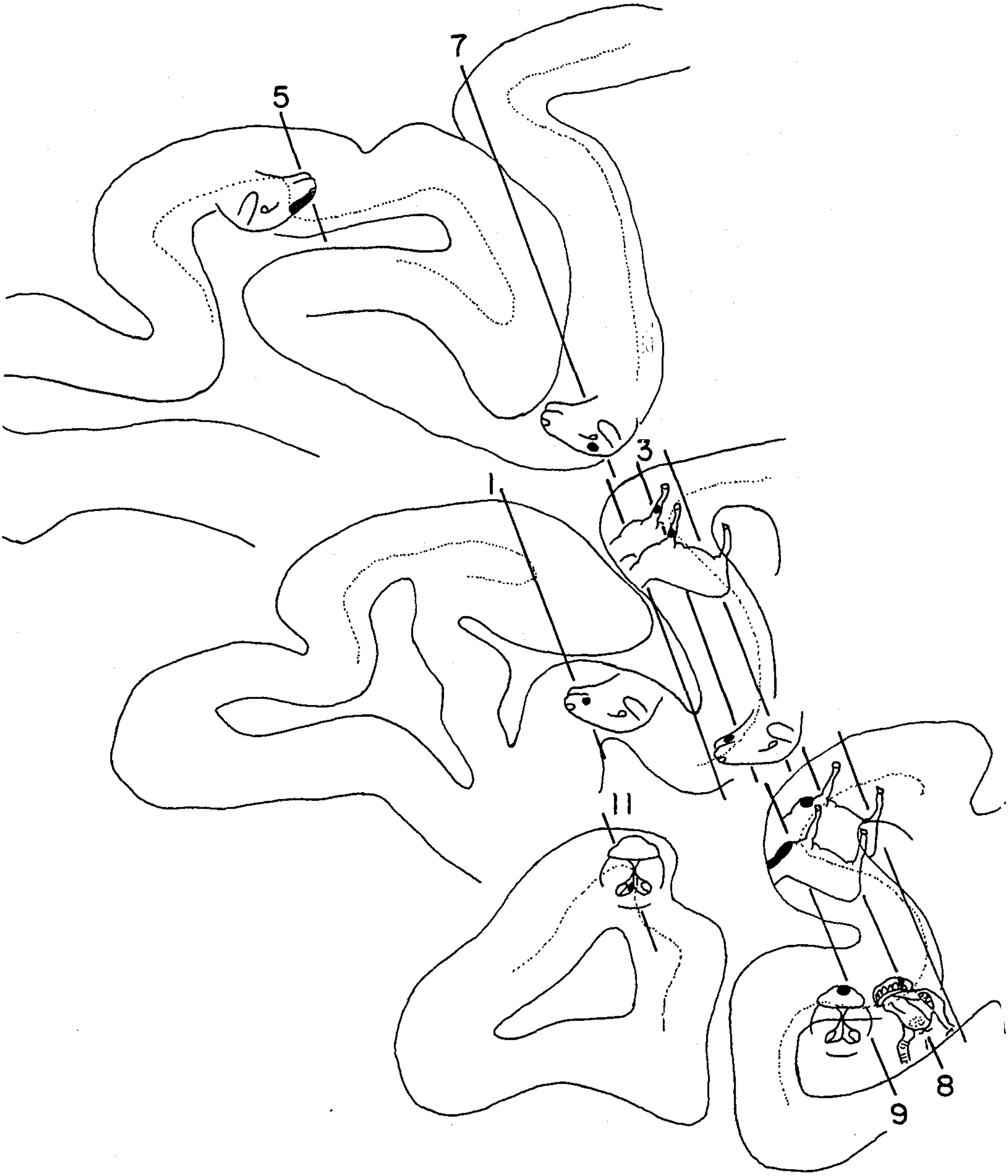

Figure 4C

Fig. 4C Data from three rows of penetrations in sheep 30, through the most lateral part of the sensory region. Projections anterior to the anterior suprasylvian sulcus (P 5 and 11) are from ipsilateral fields on the upper face and rhinarium. Projecting to the fundus of the sulcus P 7, 1, lower portion of P3, 8, 9) are fields on the contralateral face, with mandibular fields projecting more laterally. This represents a "second" mandibular projection; the first is more medial, as shown in figure 4B. Projections from the contralateral body and limbs are found in the posterior bank of the sulcus (upper parts of P3, 8, 9).

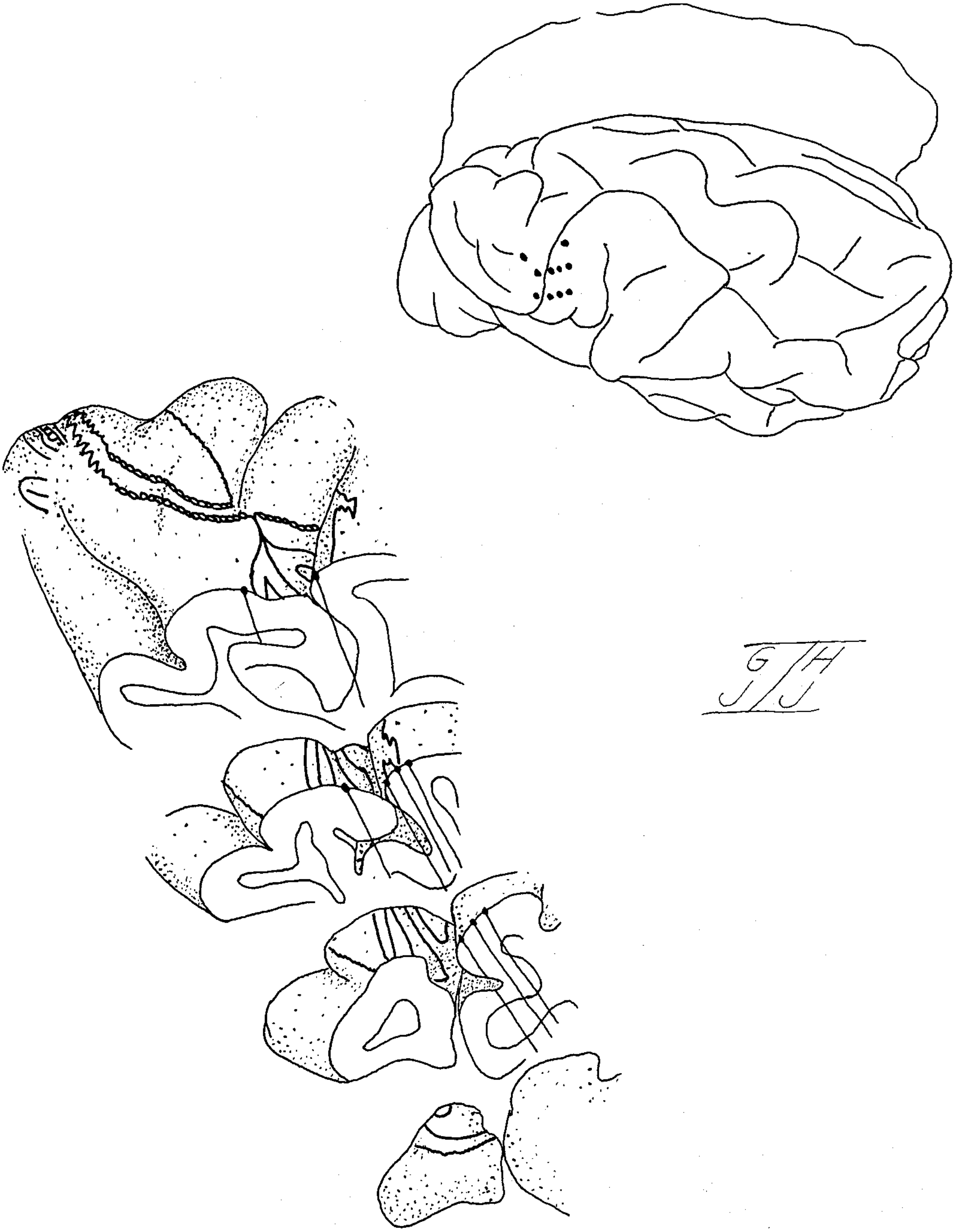

Figure 4C

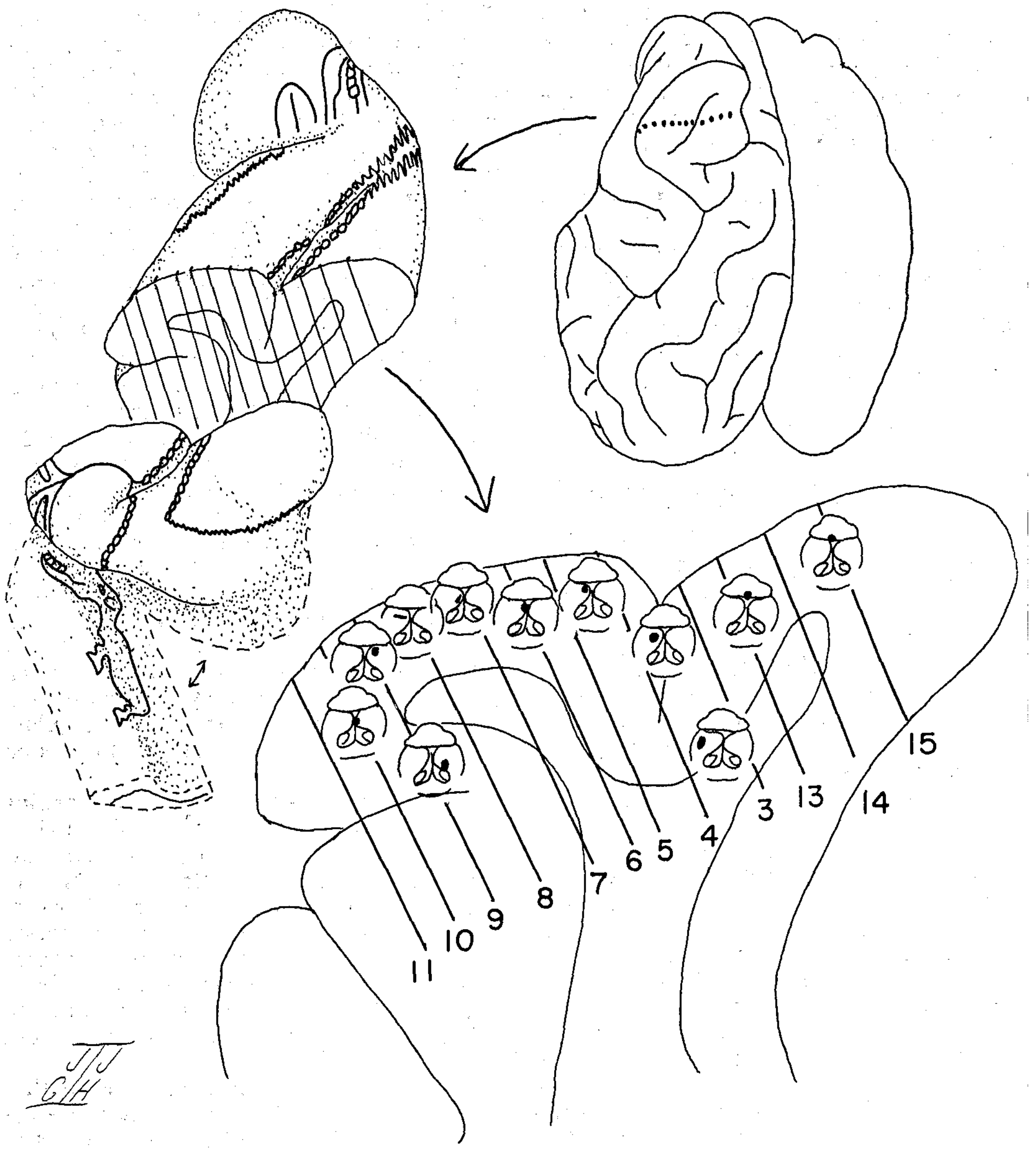

Fig. 5 Location of responsive regions found in a coronal row of penetrations in sheep 31. The most medial locations respond to stimulation of the ipsilateral lower lip near the midline. More laterally were projections from the hairy skin above the ipsilateral upper lip and most laterally, around the curve of the gyrus, were projections from the contralateral nose and neighboring hairy skin. These penetrations were spaced 0.5 mm apart.

tongue and teeth are adjacent to the projections from the corner of the mouth, and those from anterior tongue and teeth are near those from the nose and anterior parts of lips. In the cortex, however, projections from the anterior tongue extend rostrally on the cortex, away from rather than towards the lip and nose projections. Since in cortex we found projections only from the most anterior portions of the teeth and dental pad, it is not possible to judge the anterior-posterior sequence of these representations. It appears that tongue projections from the thalamus "unfold" to point the projections of the tip of the tongue away from, rather than towards, the representation of the face. This also contrasts with the tongue representation in primates, where projections from the tip lie caudal to those from the base (Pubols and Pubols, '71).

The second difference between cortical and thalamic maps is in the representation of the postcranial body and limbs. In thalamus the limb projections are between those of the posterior trunk and those of the face; while cortical projections of the posterior trunk are between those of the limbs and those of the face (fig. 9).

Body and limb projections as SII cortex

This position of limb projections posterior and ventral to all other sensory projections is contrary to the situation found in the "primary" sensory cortex (SI or SmI, Woolsey, '58) of any other mammal. An explanation of this discrepancy is provided by the findings of Haight ('72). In his fine-grain mapping of the second sensory area (SII) in cats, he found the limb representations ventral and lateral to the trunk projections in SII (fig. 9). Furthermore, the SII trunk representation in cats extends into the anterior suprasylvian sulcus. Although the naming of the sulcus was fortuitous, the trunk projections in sheep, llamas, and very probably goats, also lie in their "anterior suprasylvian" sulcus. Welker et al. ('74) believed the body representation in llamas to belong to SII on other grounds: the presence of bilateral projections and propinquity to the auditory cortex. Similar criteria led Woolsey and Fairman to suggest that the anterior suprasylvian projections from body and limbs in pigs represented SII. The SII body representation in agouti has recently been found to conform to the pattern seen in cats, with limbs represented postero-laterally (F. Pimentel de Sousa, personal communication). Collectively these data yield a strong argument that the body representation found in the postero-lateral sensory cortex of artiodactyls corresponds to the "secondary" (SII) sensory cortex of other mammals.

Absence of SI postcranial representation

A "primary" SI cortical representation of the body and limbs is apparently absent (or smaller than 1 mm^2 of the cortical surface) in sheep. In the normal mammalian pattern, it would be expected dorsal and medial to the SII and facial SI regions. We thoroughly explored this cortical region in several sheep (e.g., fig. 4B); the only sensory responses we found were those three from the muscles of the hind limbs medial to the coronal sulcus in the anterior wall of the ansate sulcus, the area postcentralis of Rose ('42).

The hind limb responses we found in the area postcentralis, in the ansate sulcus, may represent some vestigial trace of what corresponds to the SI representation of body and limbs. They were, however, in marked contrast to SI responses in the face representation of sheep or in any SI representation in other animals. For example, they were scarce in number and were surrounded by unresponsive tissue; SI cortex is characterized by multitudes of responding cells completely occupying a band of cortical tissue. They responded only to strong and deep pressure into muscles or joints; in SI cortex this type of response is outnumbered by units responding regularly and vigorously to delicate cutaneous stimulation.

Woolsey and Fairman ('46) and Sanides ('72) have suggested that the SII cortical regions may be phylogenetically more ancient, due to their location between the rhinencephalon and the more differentiated SI regions. Since all animals studied thus far have an SII, the apparent absence of a typical SI body representation in sheep suggests that the SI cortex, but not the SII, can be dispensed with where it is not needed.

Sanides ('72), for example, suggests that the "primary" or SI sensory cortex has developed as a region with a focus of dense thalamic input and refined relationship with peripheral receptors. Such a region related to face and mouth receptors is obviously useful to grazing sheep; such discriminatory capabilities in body and limbs may not be sufficiently important, given the ecology and behavior of sheep, to warrant the survival of the SI cortex. Additional examples, wherein a portion of SI is entirely absent, have not, to our knowledge, been reported. Our speculative conclusions can be tested through a deliberate search

Fig. 6 Responses obtained along a penetration which closely followed the outer stripe of Baillarger down the posterior bank of the anterior suprasylvian sulcus in sheep 9. In the photomicrograph (section 586) at left, the arrow shows the location of the electrode track. The corresponding locations in the other sections (from sections 510 to 606) show the track remaining in close proximity to the stripe (dashed line). The receptive fields of responding units, at progressively deeper locations, are indicated by the blackened areas on the figurines of the sheep body at the right. Progressively deeper units responded to stimulation of progressively more dorsal and anterior receptive fields. There was much overlap between these successive receptive fields.

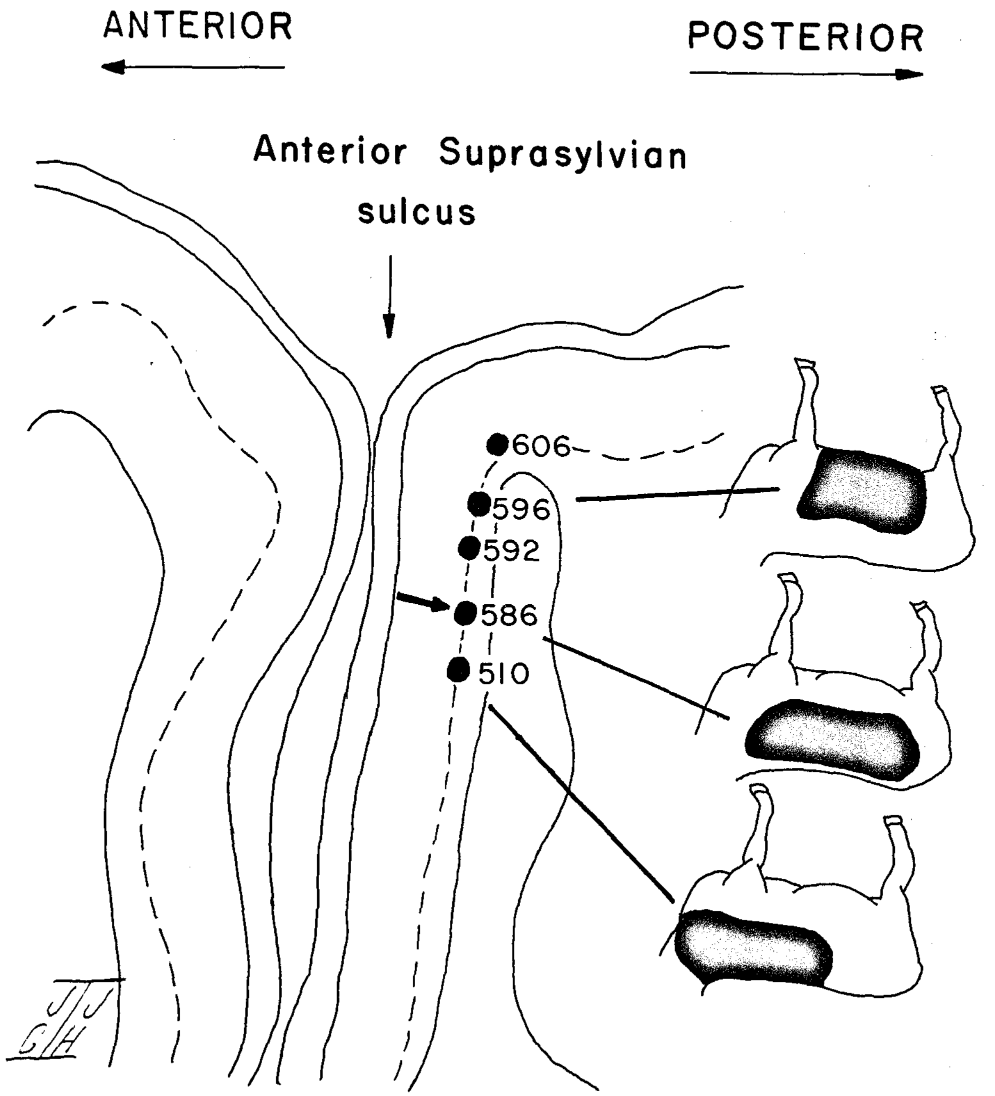

Figure 6

for such additional cases. The Perissodactyla (horses, tapirs, etc.) for example, may be a likely group in which to search: like the Artiodactyla, they are specialized cursorial herbivores and their cortices have not been adequately mapped.

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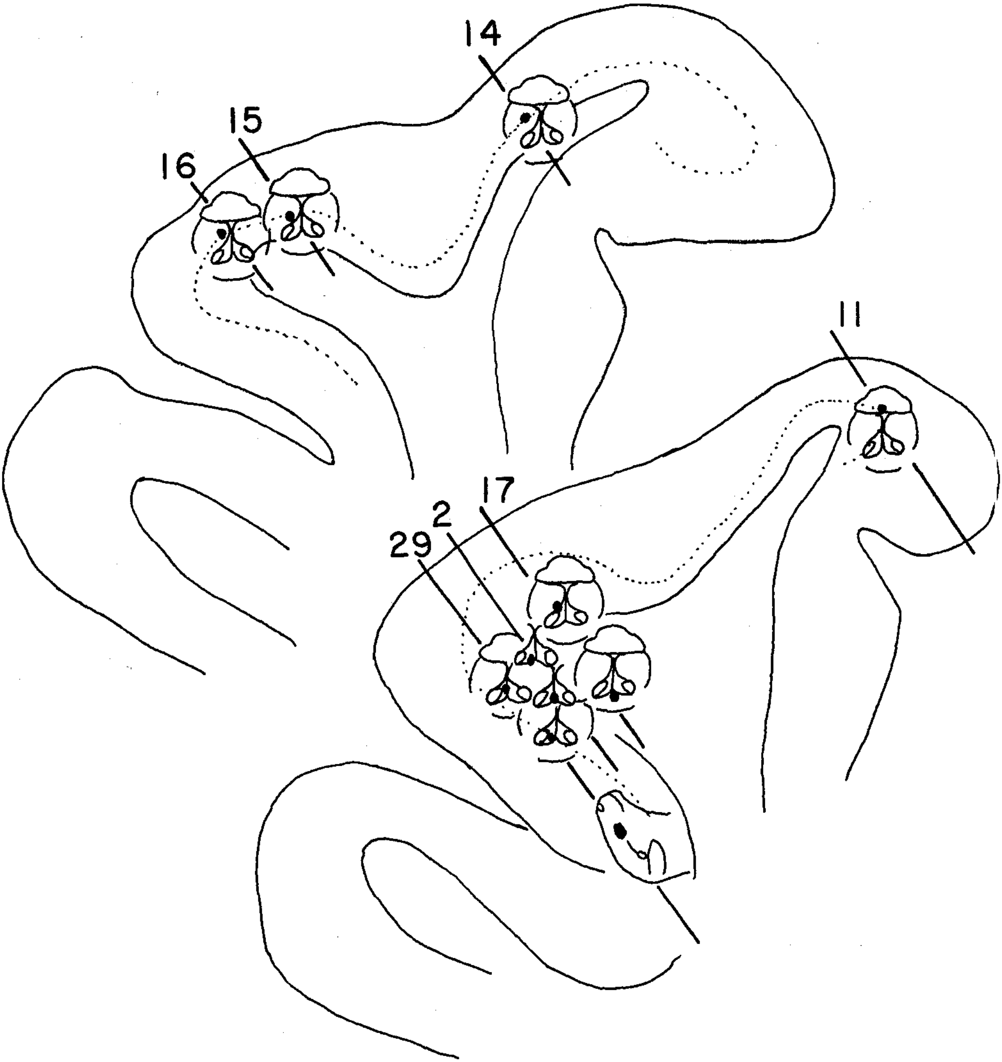

Fig. 7 Projections from receptors of the rhinarium and neighboring regions, encountered in coronal rows of penetrations in animal 14. These projections lie in the ventral part of the sensory field, where, in this case, the anterior suprasylvian sulcus merges with the diagonal sulcus. As the electrode advanced down the bank of the sulcus, the projections were from progressively more dorsal receptive fields, changing from ipsilateral to contralateral. Near the fundus of the sulcus, the deepest projection, in P 29, was from a field well around on the contralateral side of the face near the eye. As in other penetrations near the postero-medial border of sensory region, the response in P 11 was from the lower lip at the midline.

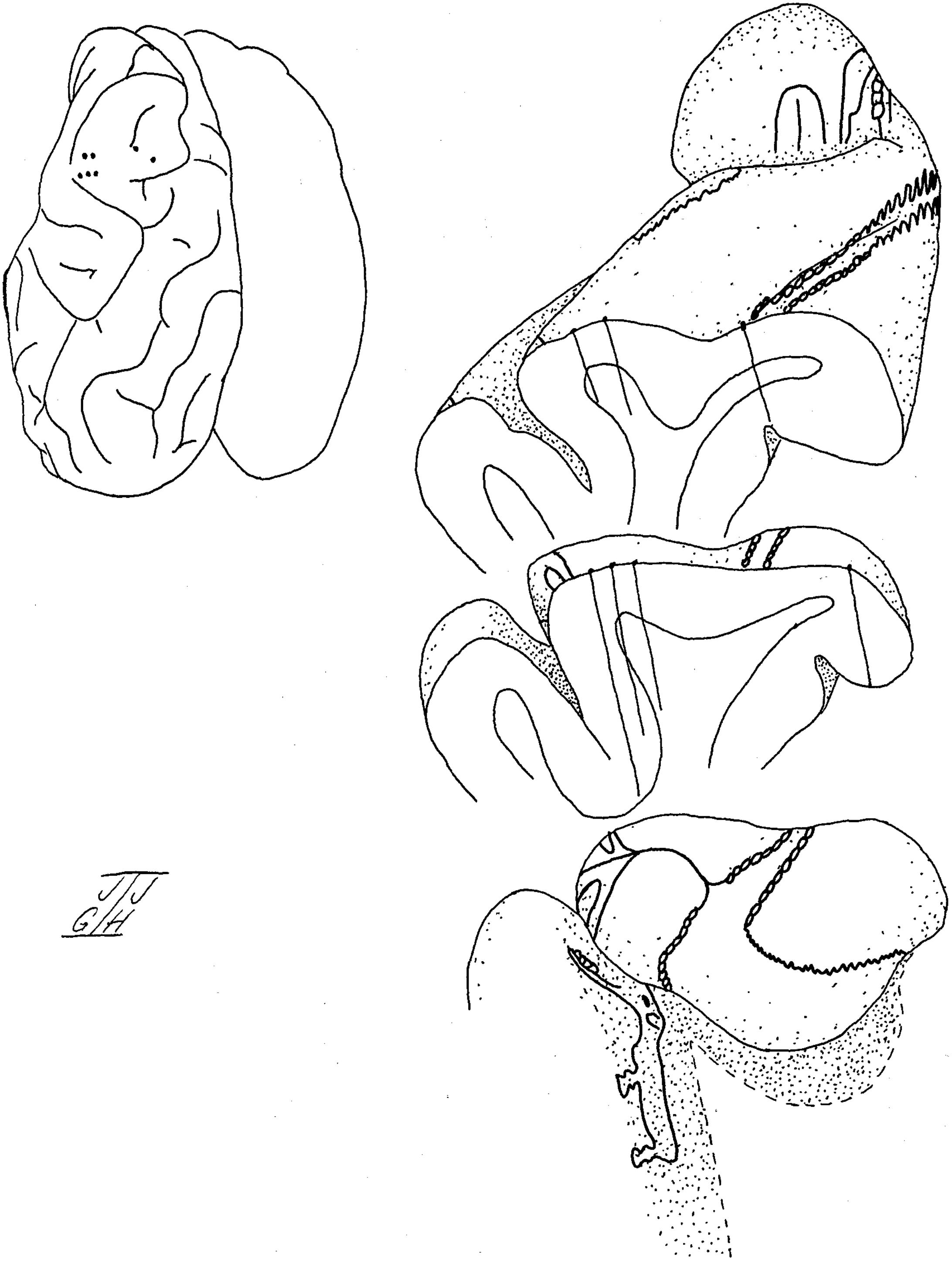

Figure 7

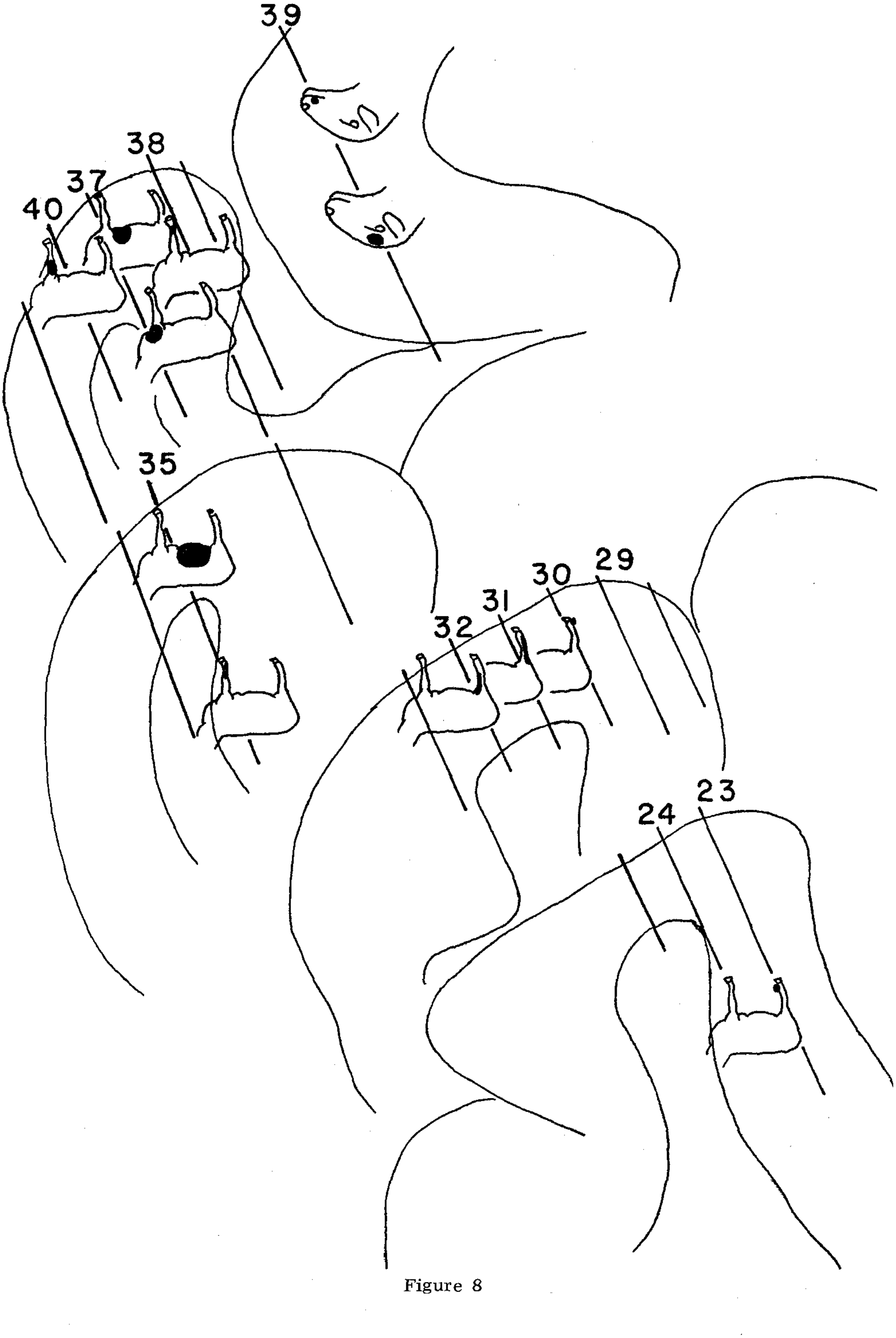

Figure 8

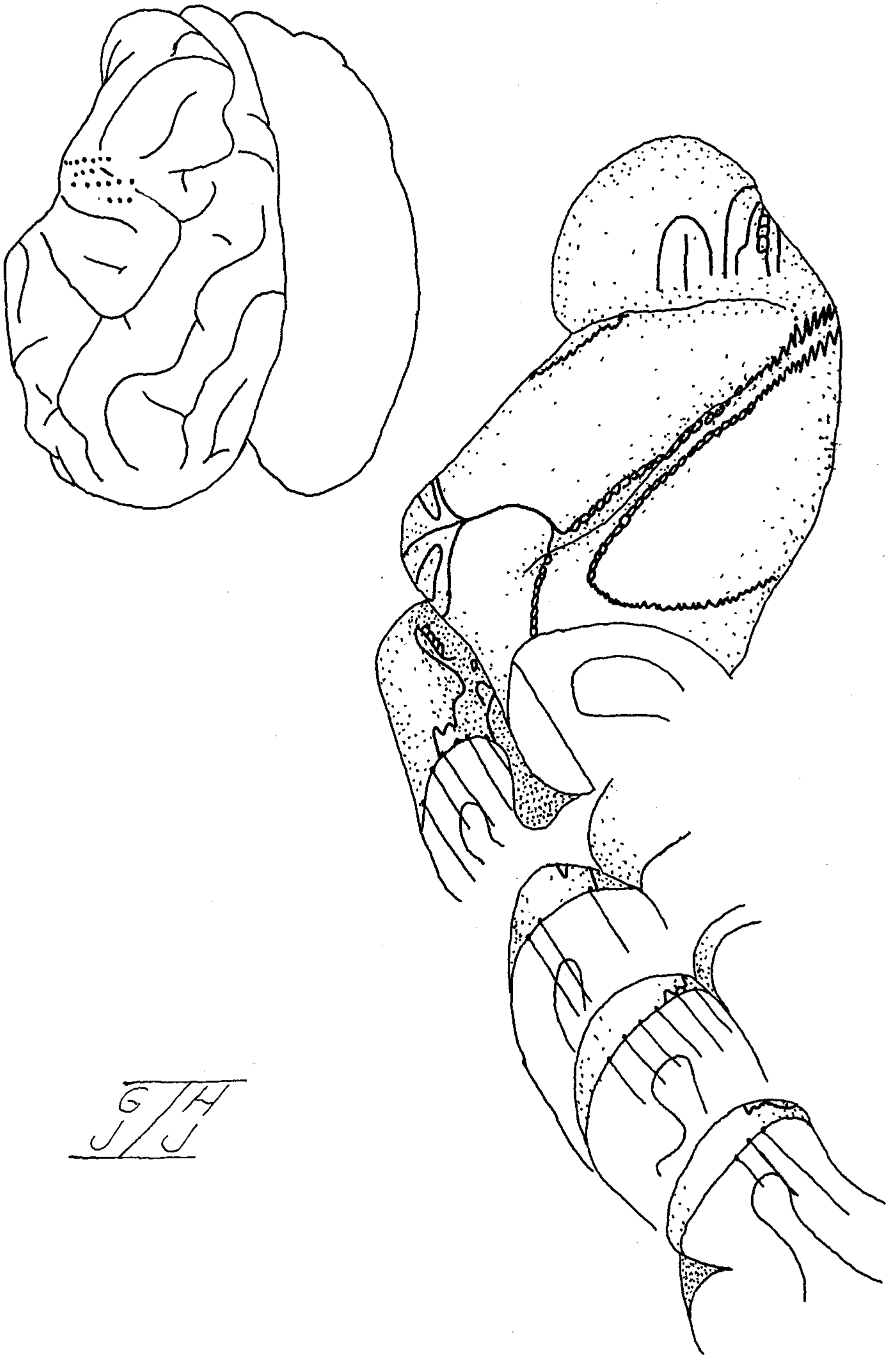

Fig. 8 Projections from contralateral face and body found in coronal rows of penetrations along the anterior suprasylvian sulcus in animal 31. In the anteriormost row (P 37–40) responses were from the side of the face in the antero-medial bank of this sulcus (P 37), and from the forelimb and neighboring trunk in the postero-lateral bank of this sulcus (P 35, 37, 38, 40). More postero-medially in the walls this sulcus (P 23, 29–32) were projections from the hind limb. Penetration 35 was another case (fig. 4B, P5) where the usual somatotopic order seen in other penetrations and experiments was not found; in all other cases, projections from distal limbs were near the lip of the sulcus, and those from the trunk were deeper in the sulcal bank (figs. 4C, 6).

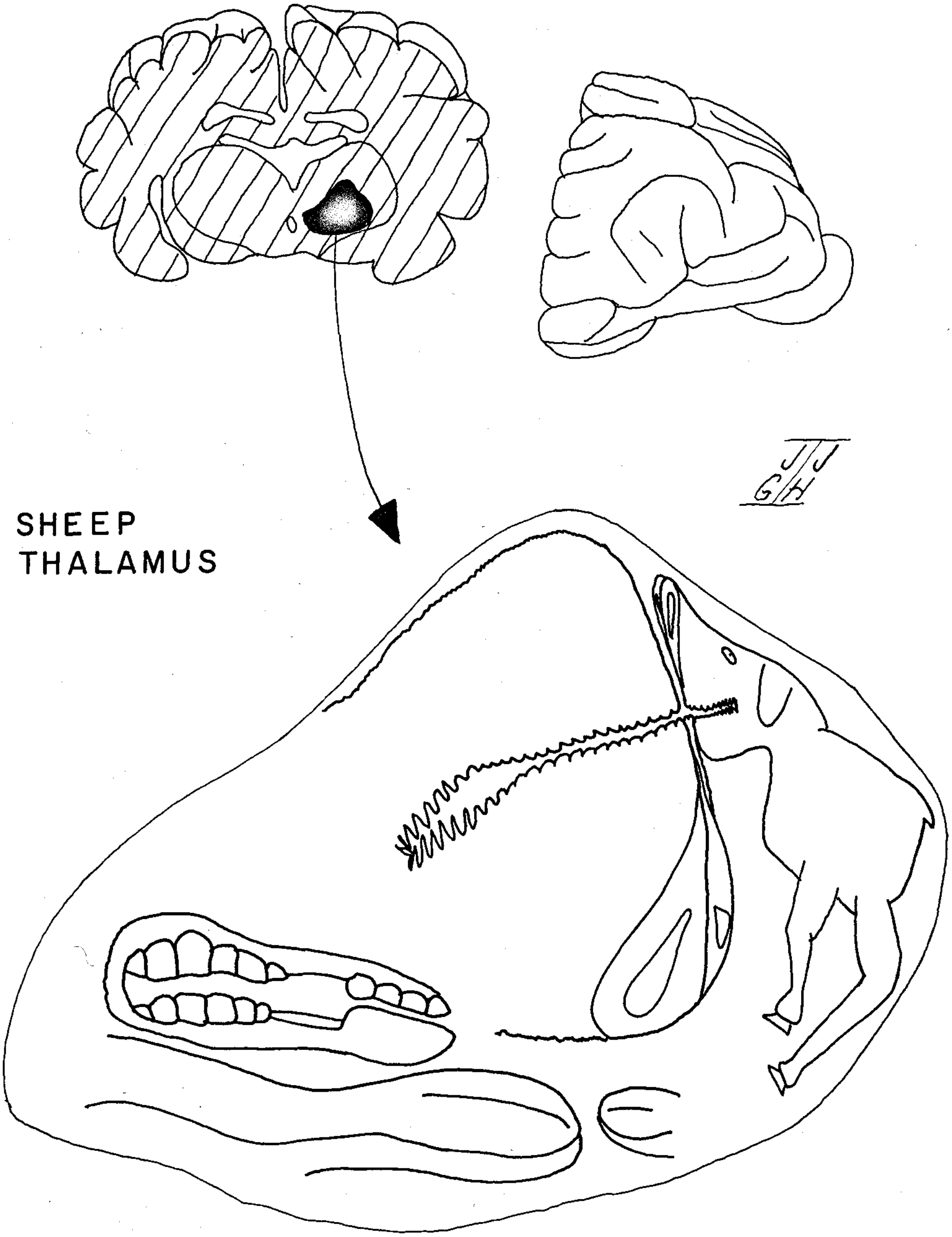

Fig. 9 Organization of mechanosensory projections in sensory cortex of sheep (lower right) compared with that seen in thalamus of sheep (left) and in sensory cortex of cats (upper right). In sheep thalamus (at left) the pattern of projections is depicted as it appears in a coronal plane through the forebrain (above). Mechanosensory projections lie in the ventrobasal nuclear complex (indicated in black) and are detailed in the enlarged drawing (below). Most projections are from the ipsilateral lips, nose and surrounding hairy skin, with the lower lip represented dorsal to the upper lip and nose; there is a small representation of the contralateral body and face, the contralateral face representation is inverted compared to the ipsilateral one; and separate representations of the teeth, dental pad and tongue are found in the ventromedial part of the sensory region (Cabral and Johnson, '71). In the sensory cortex of sheep (lower right) the projections from the ipsilateral nose and mouth faithfully reflect the thalamic representation, except that the cortical representation of the tongue has its tip pointing away from the other representations unlike its thalamic counterpart. In cat cortex (upper right) there are two body representations, one a mirror image of the other. The larger representation is the so-called "primary" sensory cortex (SI) (Rubel, '71); the smaller represents the "secondary"

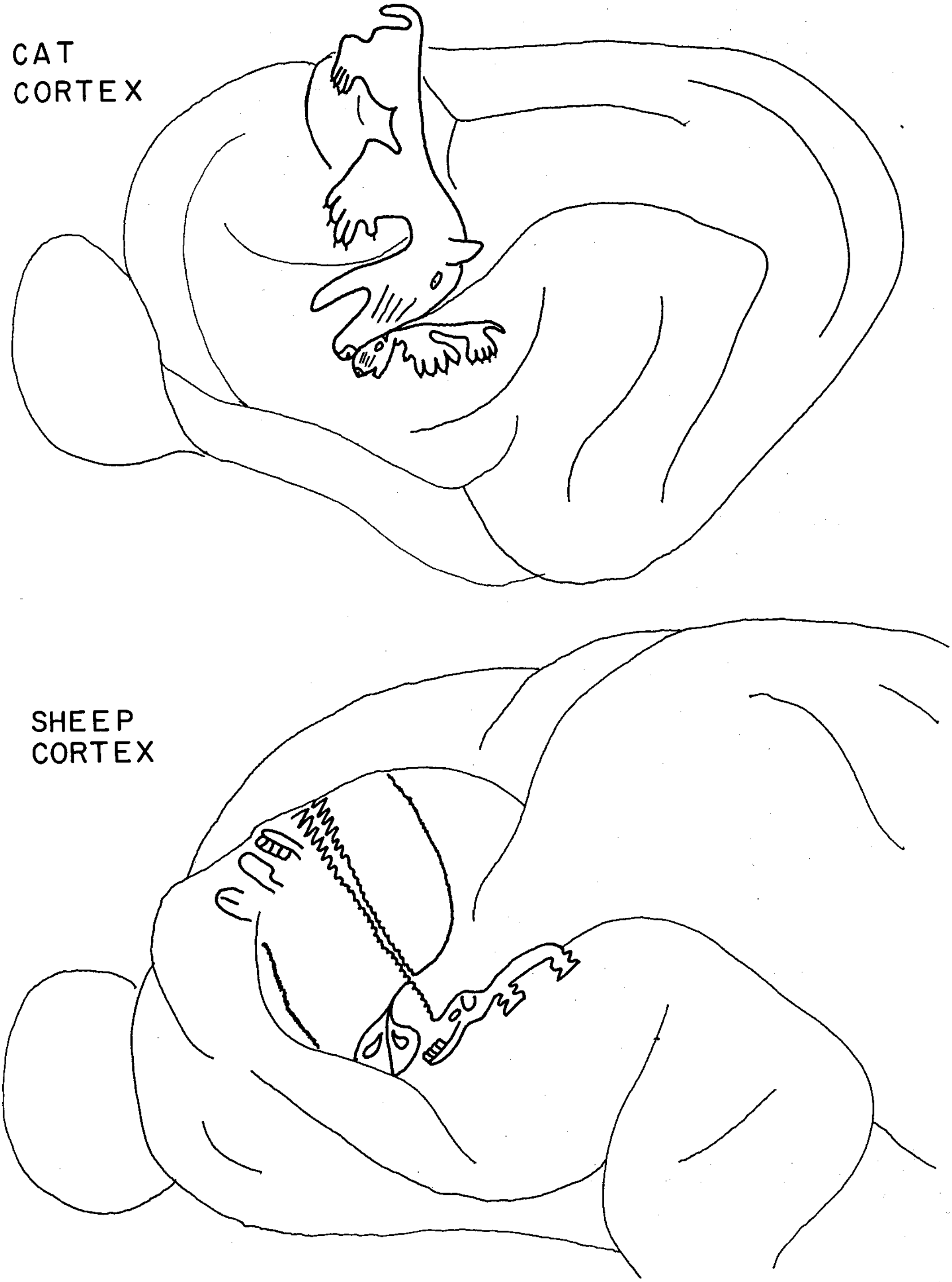

Figure 9

sensory region (SII) (Haight, '72). The cat SII representation is positioned as is the body representation in sheep, and in both animals the region lies along the ventro-posterior bank of the anterior suprasylvian sulcus, with trunk projections closer to the depth of the sulcus and limb projections closer to the gyral crown. This indicates that the body representation in sheep corresponds to the SII projections in cats and other mammals.

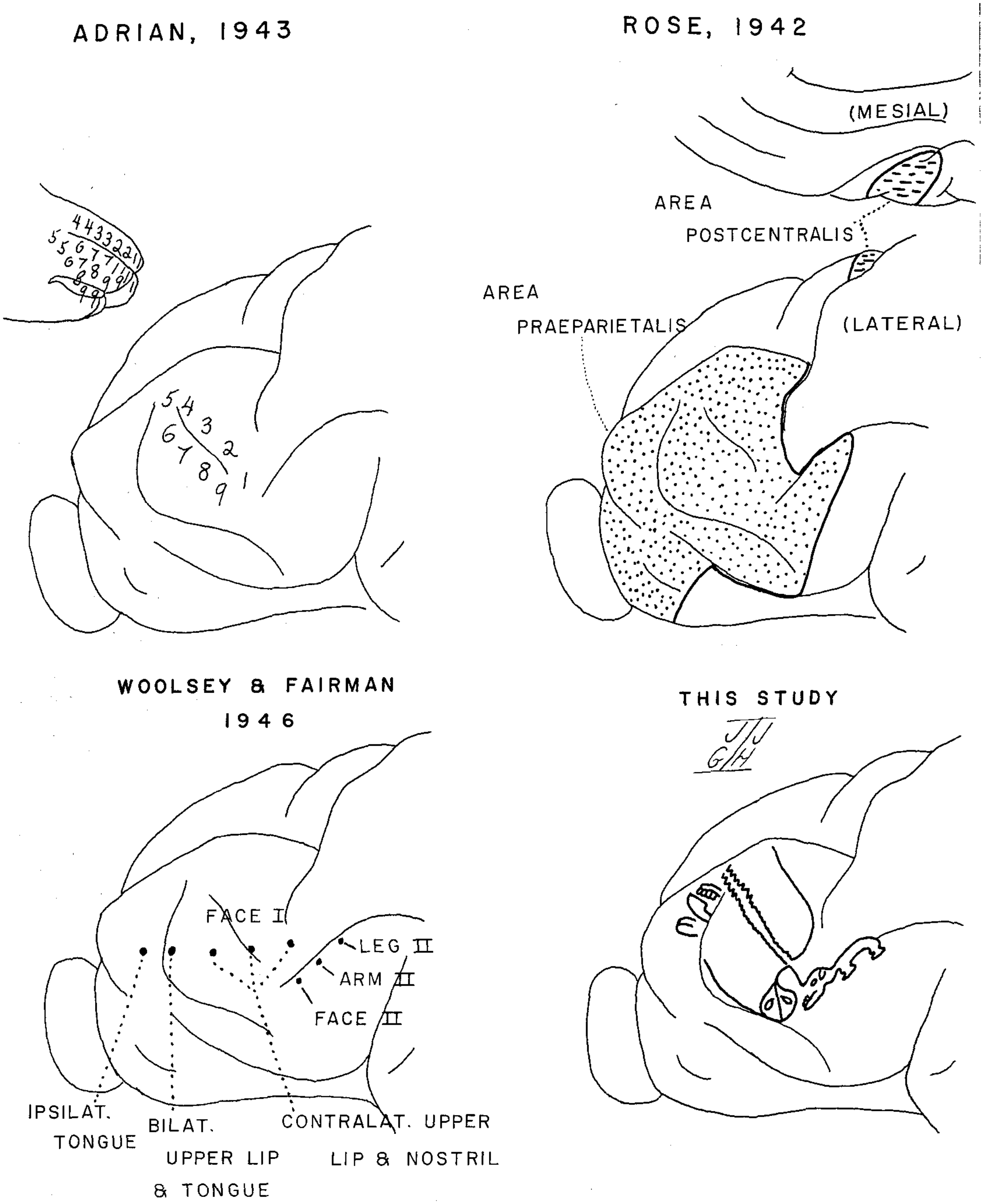

Fig. 10 Comparison of results from four studies of somatosensory cortex in sheep. In the partial map of Adrian, numbers on the diagram of the cortical surface correspond to receptive fields on the diagram representing the muzzle (with chin uppermost). The location of two of the cytoarchitectural areas described by Rose are illustrated; these contained regions where we found somatosensory projections. The diagram shows medial and lateral surfaces at this part of the hemisphere. The data from Woolsey and Fairman show the location of electrode placements on the cortical surface and the receptive fields projecting to these loci. I and II denote their belief that these regions represent the "primary" (SI) and "secondary" (SII) sensory regions; this opinion is supported by our findings.

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