PROJECTIONS OF MECHANORECEPTIVE FIELDS IN CUNEATE-GRACILE AND SPINAL TRIGEMINAL NUCLEAR REGIONS IN SHEEP

Thesis for the Degree of M. A.
MICHIGAN STATE UNIVERSITY
ROGER A. WOUDENBERG
1968

ABSTRACT

PROJECTIONS OF MECHANORECEPTIVE FIELDS IN CUNEATE-GRACILE AND SPINAL TRIGEMINAL NUCLEAR REGIONS IN SHEEP

by Roger A. Woudenberg

Neural unit discharges in response to mechanical stimulation of peripheral body tissues were mapped using tungsten microelectrodes in medullas of sheep anesthetized with Dial-urethane.

It was determined that the first order somatic sensory afferents from the sheep's body terminate in the cuneate-gracile and spinal trigeminal nuclear regions of the medulla in a somatotopic pattern that is similar to that of the receptors at the periphery but distorted in size and shape. The pattern of somatotopic organization was largely reiterative at successive rostro-caudal levels when changes in the shape and size of the nuclei were considered.

In the relatively small cuneate-gracile nuclear complex, projections from the rear half of the body were confined to a small region near the midline. Responses from the front half of the body were found over a larger, more lateral region. In this complex distal body regions were represented dorsally, and proximal body parts, ventrally. The relatively large spinal trigeminal nucleus received projections from the face with the dorsal face regions represented ventrally in the nucleus, and the ventral face parts, dorsally. Projections from the neck and ear were located between the cuneate-gracile and spinal trigeminal cellular regions.

Roger A. Woudenberg

The chief differences between the projection patterns in sheep and those in other animals studied were related to the disproportionally larger volumes of nuclear mass that receive projections from body areas with greater innervation densities. In contrast to the sheep which has a small representation of the limbs in the cuneate-gracile nuclear complex, in the alligator a large part of the volume of this complex cotains projections from limb apices. Similarly in the cat the forelimb apices have a large nuclear representation, and in the raccoon the representation of the volar hand makes up almost half of the volume of the cuneate-gracile nuclear complex. The rat like the sheep has a large representation of the face in the spinal trigeminal nucleus. However in the rat the proportionally great representation is of the nose and vibrissae, while in the sheep it is of lips and surrounding area.

In sheep the small representation of the limbs and the relatively large volume of tissue receiving projections from the lips in these medulla nuclei is analagous with the corresponding proportions of tissue receiving these cutaneous projections at thalamic and cerebral neocortical levels.

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By

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A THESIS

Submitted to
Michigan State University
in partial fulfillment of the requirements
for the degree of

MASTER OF ARTS

Department of Psychology

1968

ACKNOWLEDGEMENTS

The author wishes to express his gratitude to the chairman of this thesis committee, Dr. J. I. Johnson, whose guidance made this research possible. Special thanks are also given to Dr. G. I. Hatton and Dr. J. P. McKinney for serving on the thesis committee. The assistance of Dr. R. L. Raisler in the completion of the final draft of this thesis is also gratefully acknowledged.

To my wife and parents, who have helped me to reach this stage of my education, I dedicate this thesis.

This research was supported by NIH predoctoral fellowship MH 38130 and research grant NB 05982.

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Introduction

A number of recent electrophysiological studies have described the somatotopic organization of cutaneous input to the cuneate-gracile nuclear complex (Cu-Gr) and the spinal trigeminal nucleus (Sp Trg) of various animals including the cat (Darian-Smith, Proctor, & Ryan, 1963; Gordon, Landgren, & Seed, 1961; Gordon & Paine, 1960; Kruger & Michel, 1962; Kruger, Siminoff, & Witkovsky, 1961; Wall & Taub, 1962; Winter, 1965), the raccoon (J. I. Johnson, Welker, & Pubols, 1968; Welker, Johnson, & Pubols, 1964), the rat (McComas, 1963; Nord, 1967), and a reptile, Alligator mississippiensis (Kruger & Witkovsky, 1961). In general this research substantiates and expands the earlier physiological studies with cats (F. H. Johnson, 1952; Kuhn, 1949) and the early anatomical studies with monkeys (Chang & Ruch, 1947; Ferraro & Barrera, 1935a; Ferraro & Barrera, 1935b; Walker & Weaver, 1942).

These studies have shown that the first order somatic sensory afferents from the body terminate on the cells of Cu-Gr and Sp Trg in an orderly fashion along the longitudinal extent of these nuclei. The projections are somatotopically organized in a pattern similar to that of the receptors at the periphery although the total representation is distorted in size and shape. Generally in a cross section of the medulla, the more distal body regions are represented dorsally and the proximal regions, ventrally. In the medio-lateral dimension the more caudal parts of the body are represented near the midline and the rostral body parts, more laterally. This is conceptualized more simply by considering the representation of the animal in the nuclei as an inverted figure with the tail dorsomedial, the extremities dorsal and the face lateral. This organization exists between the nuclei as well as within them so that they may be considered together as a functional unit to which the entire body projects cutaneous input (Kruger et al., 1961).

The chief differences between the projection patterns of the different animals are related to the disproportionally larger volumes of nuclear mass that receive projections from body areas with greater innervation densities (Rose & Mountcastle, 1959). Thus half of the volume of Cu-Gr in the alligator contains projections from the apices of the limbs (Kruger & Witkovsky, 1961). Similarly in the cat the nuclear representation of the limb apices is larger than the representation of any other body part. However in the cat the representation of the forelimb and especially its digits is larger than that of the alligator and larger than the representation of the hindlimb in the cat itself (Kruger et al., 1961). In the raccoon the nuclear representation of the volar hand makes up at least 44 percent of the volume of Cu-Gr and occupies the cuneate portion of the nucleus throughout its dorso-ventral extent, whereas in the alligator and cat it is restricted to the dorsal portion of the nucleus (J. I. Johnson et al., 1968; Welker et al., 1964). In the raccoon the projections from each digit were contained in a discrete columnar subnucleus seperated by fibrous laminae from the other digit projections. In the rat which has a relatively small Cu-Gr the central representation of the vibrissae and nose fields in Sp Trg was proportionally larger than the representation of any other body part (Nord, 1967).

In sheep previous research on this afferent system in our laboratory at the cerebral neocortical level (Hatton & Rubel, 1967) and concurrent research at the thalamic level (Cabral & Johnson, 1967) has shown that a relatively large mass of these areas receives cutaneous projections from the upper and lower lips and very little input from the trunk or limbs. The purpose of the present study was to determine if an analagous somatotopic organization exists in the second-order cells of the medulla of sheep. Since the sheep does not belong to the same family as any of the other animals studied and because the relative size of its medullary tactile nuclei is different from these animals, it provides a useful comparative neurological study.

Method

Subjects

Seven adult sheep (Ovis aries) were used for microelectrode studies and one for histological study of the normal sheep brain.

Subject Preparation

The subjects were anesthetized by intraperitoneal injection of a dial urethane mixture. The initial dose was 1cc per pound (=2.2 cc/kg) of body weight. Additional injections of approximately ¼ the original dosage were given when needed (every 8-10 hours).

The body hair was clipped and the animals were suspended on two large bars to allow access to the receptive fields on the entire body surface. This is shown in Figure 1. The skull was immobilized by means of metal rods attached to it and a head holder device. The skull, atlas, and axis were held together by dental acrylic poured around screws inserted into them. The trachea was cannulated and a mechanical respirator was used when necessary. Body temperature was measured by a thermometer inserted into the muscle surrounding the scapula and was kept near 36°C by means of infra-red lamps.

In the surgical exposure of the medulla, the caudal portion of the cerebellum was aspirated and the dura and epi-pial tissue covering the dorsal surface of the medulla were removed. The exposed area was surrounded by an acrylic dam filled with mineral oil.

Recording Equipment

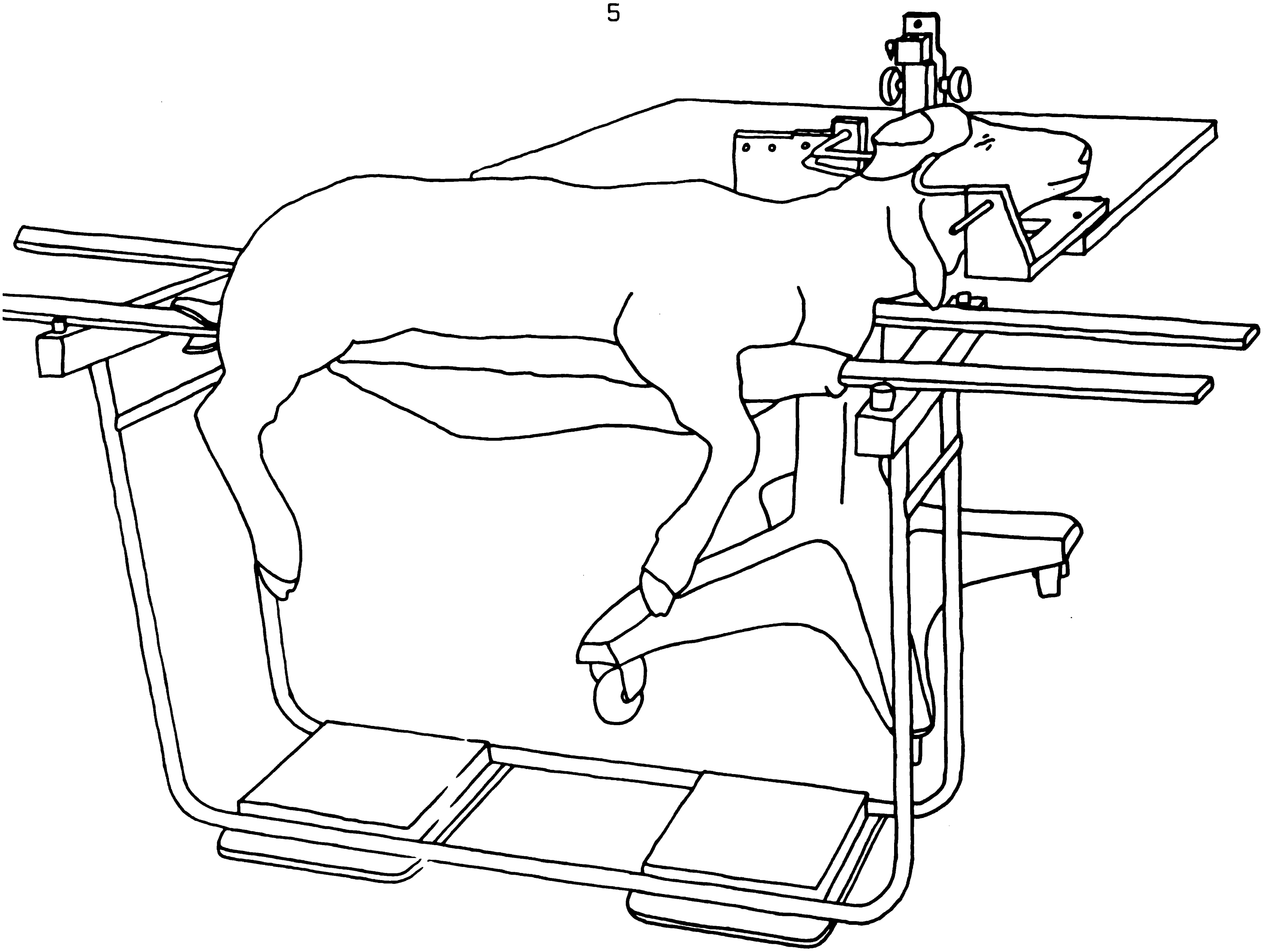


Fig. 1. Sheep suspension apparatus to allow access to the receptive fields on the body surface. The skull was immobilized by means of metal rods attached to it and a head holder device. During the experiments the head was tilted further down than shown in the drawing to allow maximum exposure of the medulla region.

Glass insulated tungsten microelectrodes were used (Baldwin, Frenk, & Lettvin, 1965; Hubel, 1957). These electrodes had shaft diameters of 40-70 microns and were insulated to within 30-80 microns of the tip. The electrodes were oriented perpendicular to the dorsal surface of the medulla and inserted in that direction. Mapping was carried out on the right side of the medulla except for several punctures on the left side near the midline.

Unit responses were led through a preamplifier and passed through low (80 Hz) and high (10 kHz) cut off filters. The output was visually displayed on an oscilloscope and audibly through an 8-inch speaker. Evoked activity and verbal description were recorded on two channels of a magnetic tape. The neural unit activity could later be reproduced using a Honeywell Visicorder. This part of the procedure is summarized in Figure 2.

Recording Procedure

The medullary regions were mapped moving the electrode in a systematic fashion while mechanically stimulating the body surface. This stimulation was done using the hands, 1/8 inch diameter wood applicators, tongue depressors, and pieces of fine polyethylene tubing. The microelectrodes were advanced vertically by a micromanipulator for lengths of approximately 200 microns and held at these points while the sheep's body was stimulated. When this mechanical stimulation evoked a neural spike or spike cluster electrical response (see below) each time it was applied, the area that activated that response

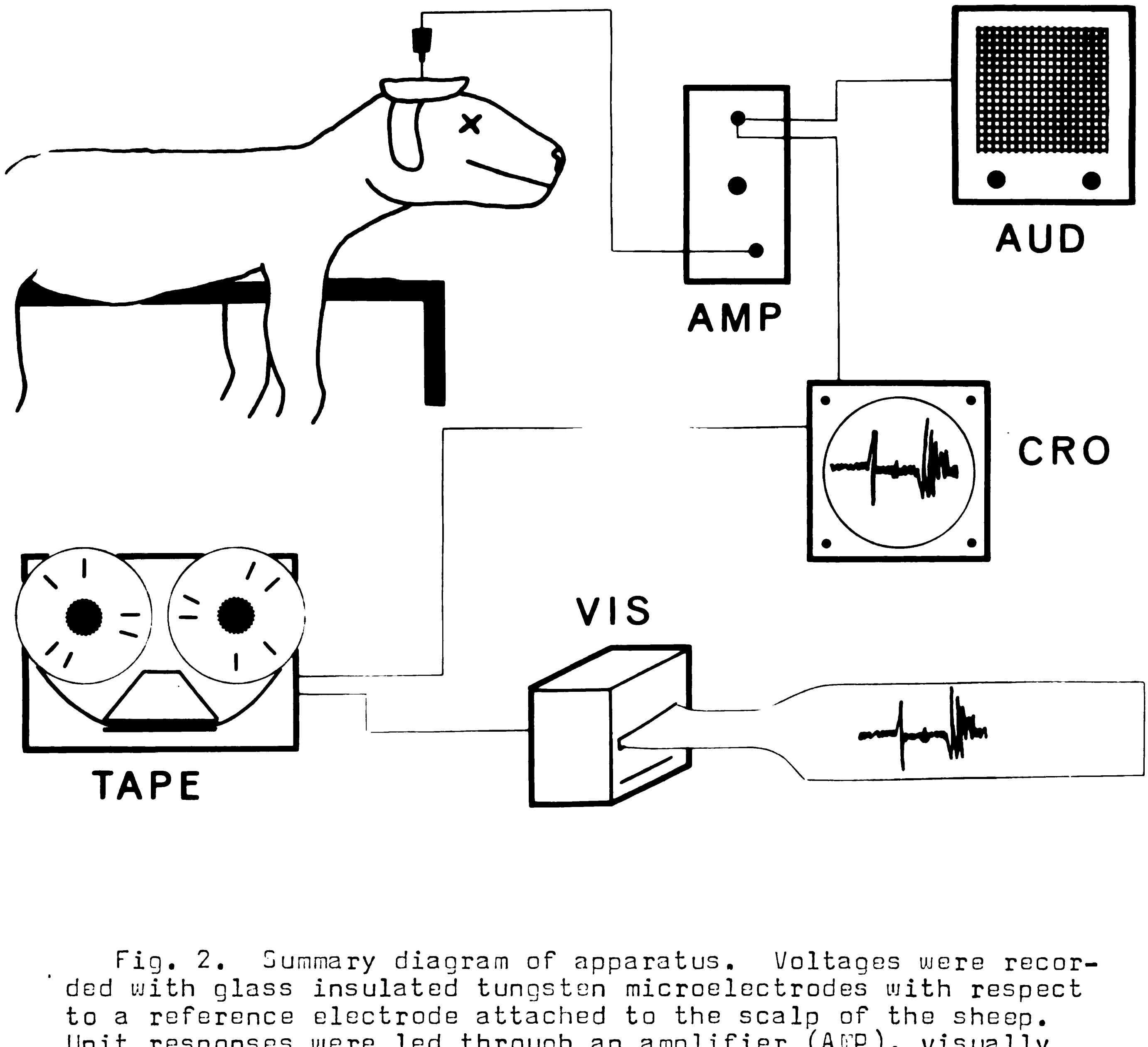


Fig. 2. Summary diagram of apparatus. Voltages were recorded with glass insulated tungsten microelectrodes with respect to a reference electrode attached to the scalp of the sheep. Unit responses were led through an amplifier (AMP), visually displayed on an oscilloscope screen (CRO), and audibly through an8-inch speaker (AUD). The output was recorded on magnetic tape (TAPE) and later reproduced when necessary with a Honeywell Visicorder (VIS).

was carefully delineated and drawn on photographs of the sheep's body. A written record describing these responsive body areas was also made. Finally it was also noted whether gentle stroking of a skin receptor or sharsh probing of deep tissue receptors evoked the neural response.

The first punctures in each experiment were in the most rostral position possible to minimize interruption of ascending dorsal column fibers. Punctures were spaced either .966 or .483 mm apart in medio-lateral rows that were 1 mm apart in the rostro-caudal dimension except where the vascular pattern made this impossible. Each placement of the electrode was measured using the coordinate system of the electrode manipulator and was recorded on a grid and on photographs of the exposed medullary region. This procedure left neat rows of punctures which could be identified histologically and related to the written, taped, and photographic records.

Response Criteria

The criteria used to differentiate the unit spike activity of Cu-Gr, Sp Trg, and other nuclear areas from the activity of neighboring fiber tracts were those of J. I. Johnson et al. (1968) as shown in Table 1. Fiber responses consisted of one or more isolated spikes that could be easily distinguished from any background activity and which were associated with a low noise level. These responses were easily lost with slight movements of the microelectrode and usually could not be retrieved. A nuclear neural unit spike discharge cluster, typical of those obtained in this experiment, is shown in Figure 3.

Table 1

Response criteria used to differentiate unit spike activity of nuclear areas from activity of fiber tracts

(Abbreviated from Table 1 in J. I. Johnson et al., 1968)

Fiber tract

1. Spikes well isolated, sharply differentiated from background; low noise level.
2. Response suddenly disappears with electrode movement, and is rarely retrieved.

Nuclear region

1. Spikes of variable amplitude, occurring in clusters with smaller spikes merging into the background; background relatively noisy.
2. Responses persist with considerable electrode movement, gradually changing in amplitude. When lost, the responses can often be retrieved by reversing the direction of electrode movement.

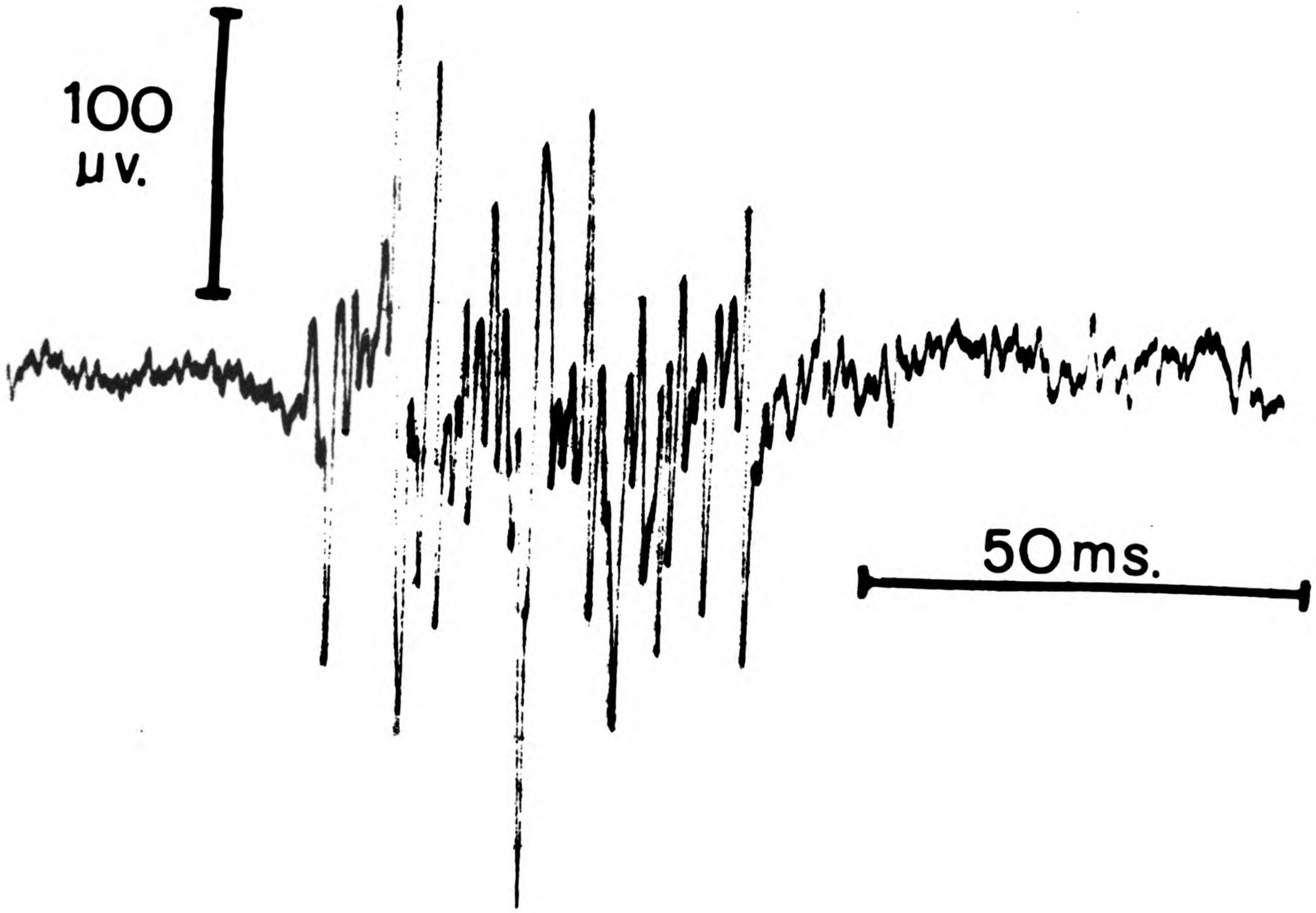


Fig. 3. Neural unit spike discharge cluster used as response criteria in medulla. This particular response was evoked by stimulation of the ipsilateral face just rostral to the eye.

These responses consisted of a cluster of spikes of variable amplitude associated with relatively noisy background activity with which the smaller spikes merged. These responses endured with considerable electrode movement so that the electrode could be manipulated in order to obtain a maximum response.

Only those electrical responses which met the criteria of the nuclear neural unit spike discharge cluster were included in the data except for two fiber responses from the solitary tract (see below).

Histological procedures

At the completion of each experiment, the brain was fixed by intracardial perfusion of the anesthetized animals with 0.9% NaCl solution followed by a mixture of 10% formalin and 0.9% NaCl. The part of the medulla containing the electrode tracks was cut from the brain and photographed. In order to insure that the medulla was sliced from the brain in the coronal plane of the electrodes, it was cut along the line of reference electrodes placed in the tissue with the micromanipulator before perfusion.

The medullas were dehydrated, embedded in celloidin, and sectioned approximately every 25 microns. Alternate sections were stained to show cell bodies with thionin (Nissl method) or myelinated fibers with hematoxylin (Weil and Heidenhain stains). These sections were compared with similar sections of a sheep medulla that did not undergo microelectrode recording. All sections were studied by projection through a light magnifying device.

The final localization of recording sites was determined from the following data:

Dorso-ventral dimension:

1. Recorded micromanipulator readings.
2. Microelectrode tracks identified and drawn from brain sections. Data from electrode tracks not histologically identified were not included in the results.
3. Identification of microlesions created during the course of the experiments by sending current through the electrode tip (50 μA, 5 sec., Anodal).

Rostro-caudal and medio-lateral dimensions:

1. Correlation of identified electrode tracks with the marks made on photographs of the exposed medulla and on coordinate grids.
2. Comparison between and within experiments of electrode tracks on the basis of three-dimensional plexiglass reconstructions of tracks and nuclear regions.

All data regarding the activating receptive fields and activated neural sites were combined and organized to show the somatotopic organization within and between Cu-Gr and Sp Trg.

Results

The data with regard to the somatotopic organization within Cu-Gr and Sp Trg of projections of the peripheral mechanoreceptive fields reveal that these nuclei exhibit a relatively high degree of somatotopic organization within themselves and with reference to each other. In general the sheep is represented in a cross section of these nuclei as an inverted figure with the tail and rump ventromedial, the extremities dorsal and the face lateral. In the main the somatotopic organization is reiterated at successive rostro-caudal levels of these nuclei. However there are some changes in the organization associated with variations in the position and shape of the nuclei along the rostro-caudal axis. This will be discussed in more detail below.

A total of 251 electrode punctures were made. Approximately 40% (102) of these punctures yielded no data. In the other 60%, 229 responsive nuclear loci were identified. These responsive loci and the peripheral mechanoreceptive fields projecting to them are summarized diagramatically in six coronal sections along the rostro-caudal extent of Cu-Gr in Figures 5, 9, and 12. Figures 6-8, 10-11, and 13-16 supplement these with diagrams of actual responses obtained and photomicrographs of cell and fiber stained coronal sections showing the tracks of the electrode when these responses were obtained. Table 2 lists the abbreviations used in these figures.

The relevant medulla region and its location within the sheep brain are shown in Figure 4. Figures 5 through 16 show

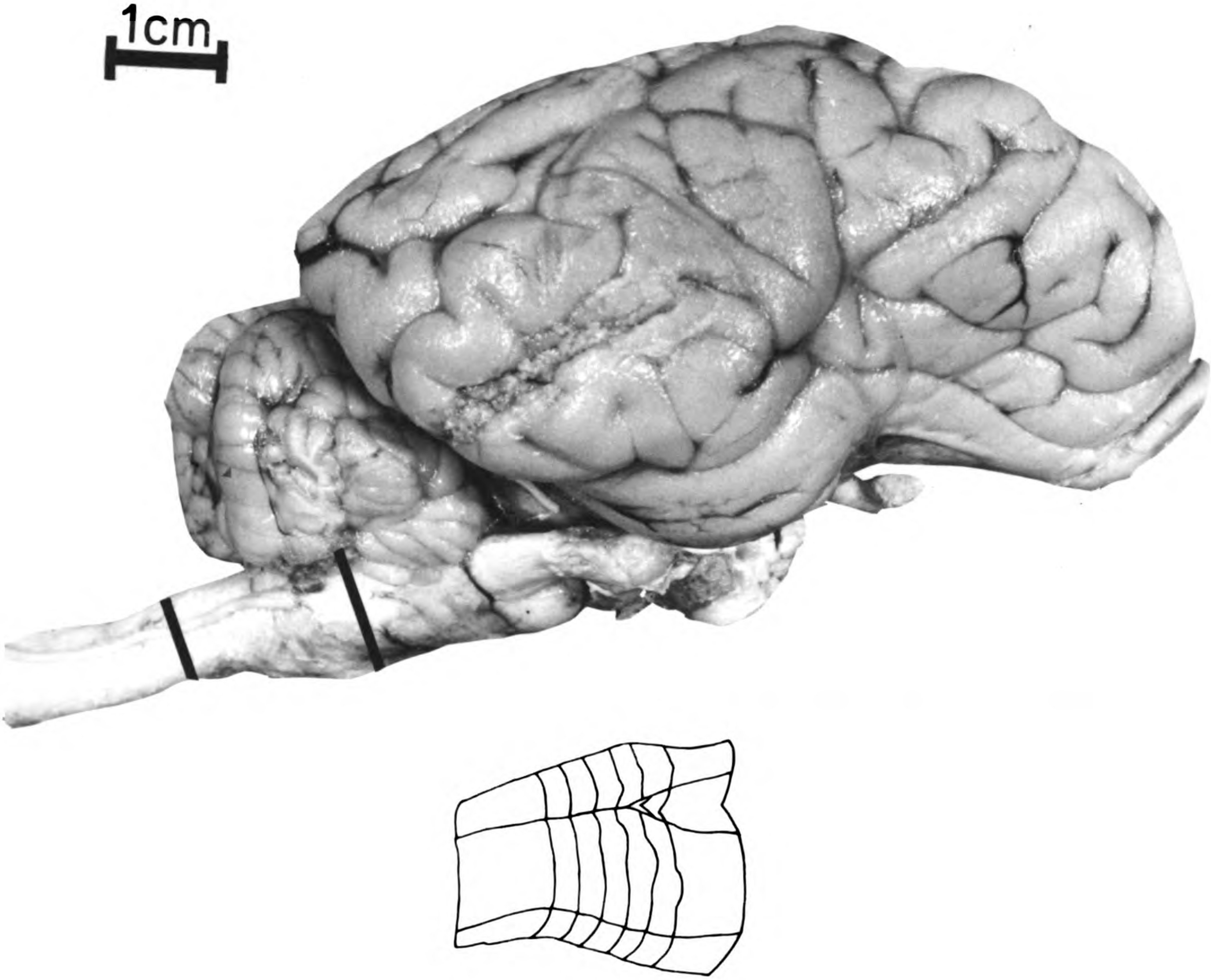


Fig. 4. Photograph of entire sheep brain (lateral view) showing the location of the relevant medulla region. The corresponding drawing of the medulla (dorso-lateral view) is the same as that shown in Figures 5, 9, and 12.

caudal portion. The external cuneate nucleus is now directly lateral to Cu-Gr in the area occupied more caudally by Sp Trg. The boundary between Cu-Gr and Sp Trg is less definite than more caudally and this is complicated by the fact that all three nuclei meet each other in the same region.

Consistent with what has been said above about the organization more caudally, Cu-Gr receives projections from the body up to and partially including the neck. The neck and pinna are represented in the region where the three nuclear groups are contiguous (Figure 9). However, projections from the pinna are located more directly between Cu-Gr and Sp Trg as they were more caudally. Figures 9, 10, and 11 show that the area directly between Cu-Gr and Sp Trg receives projections from the neck, throat, and cheek.

Projections from the rear part of the body are again located near the midline with projections from the front part of the body ventrolateral to them as shown in Figures 9, 10, and 11. This change from lateral to ventrolateral organization is consistent with the change in position of the nuclei. The proximal body portions were always represented ventral to the distal body part (Figure 9) reiterating the more caudal organization.

The somatotopic organization of Sp Trg at this central level of the rostro-caudal extent of Cu-Gr also reiterates the organization shown more caudally, but the data at this level provide more detail. A large portion of Sp Trg receives projections from the upper and lower lips and the immediate surrounding area including the buccal cavity (Figures 9 and 10). The ventral aspects of the face (lower lip, chin) are represented dorsally and the dorsal aspects (upper lip, snout, and ophthalmic region) are represented ventrally. This is illustrated clearly in the two series of face responses shown in Figure 10 where the receptive fields of cells lying from dorsal to ventral in Sp Trg show the following progression: chin, lower lip, lower incisors, upper palate, upper lip, nose, snout. The buccal cavity responses that are shown in Figure 10 were the most laterally located responses that were obtained from that peripheral area in Sp Trg. Figure 11 shows that some exceptions were found in the boundary region between Cu-Gr and Sp Trg where projections from the upper lip were sometimes dorsal to projections from the lower lip. However it is also possible that these electrical discharges were recorded from the nucleus of the solitary tract rather than from Sp Trg.

Rostral Region

In the rostral portion of the rostro-caudal extent of Cu-Gr the Sp Trg lies ventrolateral to Cu-Gr, and in the extreem rostral portions of Cu-Gr the Sp Trg is almost directly ventral to it (Figures 12-16).

In general the more caudal body portions were represented dorsal to the rostral body parts in Cu-Gr at this level. This is shown in Figure 14 where when moving from dorsal to ventral in Cu-Gr, the successive projections are from the rump and back, then only from the back above the middle of the body and finally from the shoulder. The decision that these and similarly located

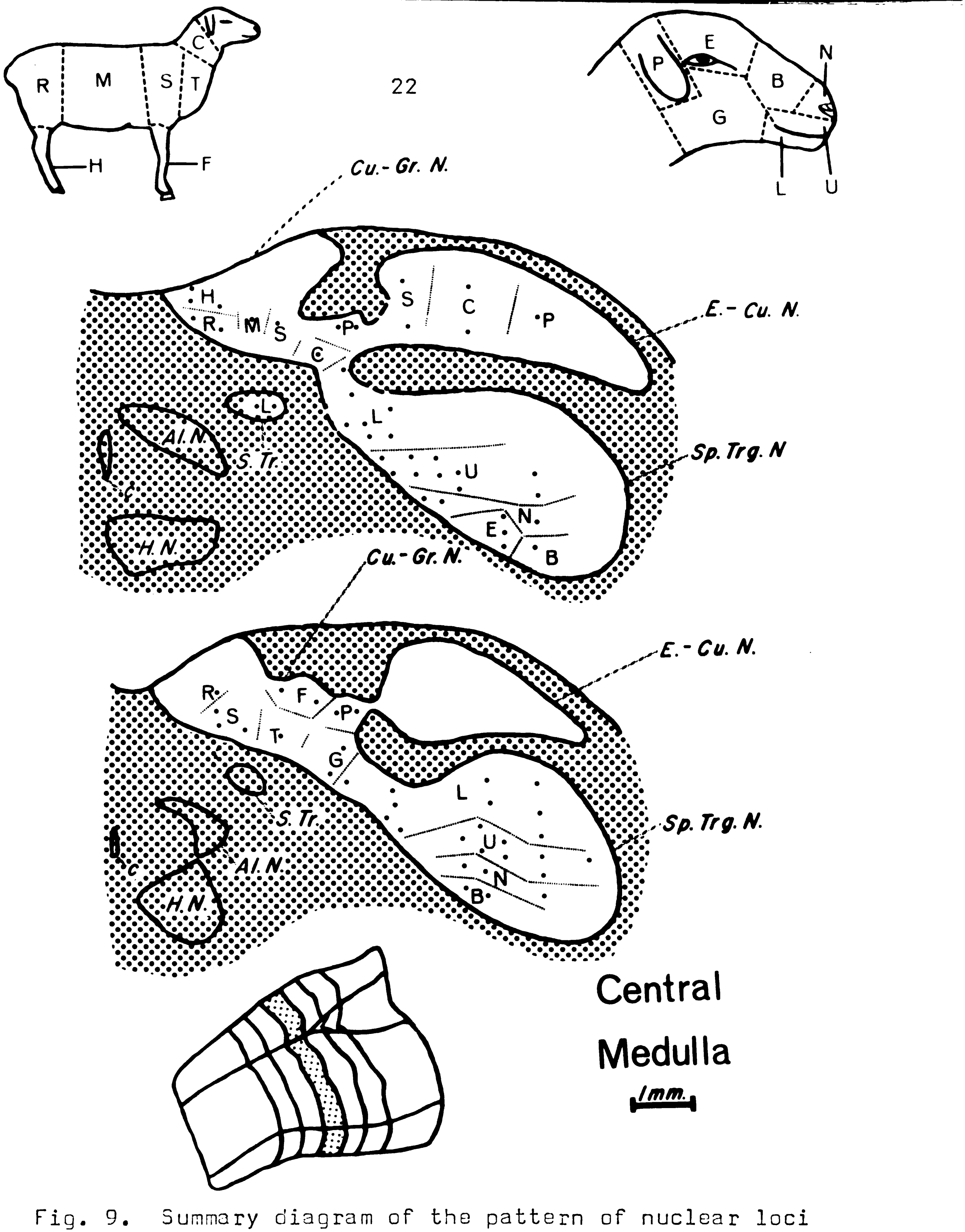


Fig. 9. Summary diagram of the pattern of nuclear loci responding to mechanical stimulation of peripheral body receptive fields at two coronal levels in the central portion of the rostro-caudal extent of the Cu-Gr. The bottom section is most caudal and both are located by the darker lines surrounding the shaded area on the bottom diagram of a section of medulla. Dots in the unshaded nuclear areas represent actual responding loci identified in similar histological coronal sections. The letters designate areas of the body within which the receptive field was located or which the receptive field included as its main portion.

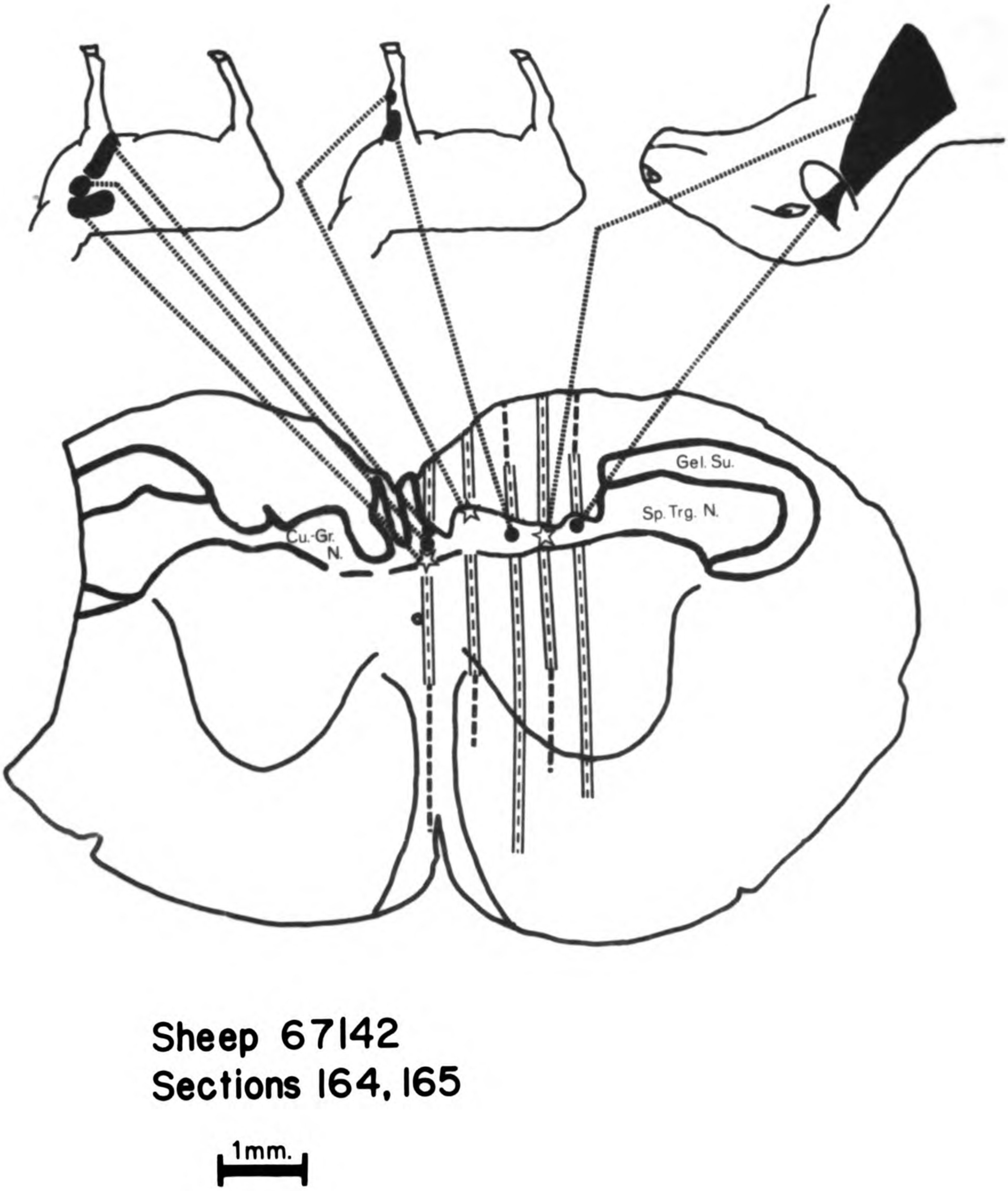
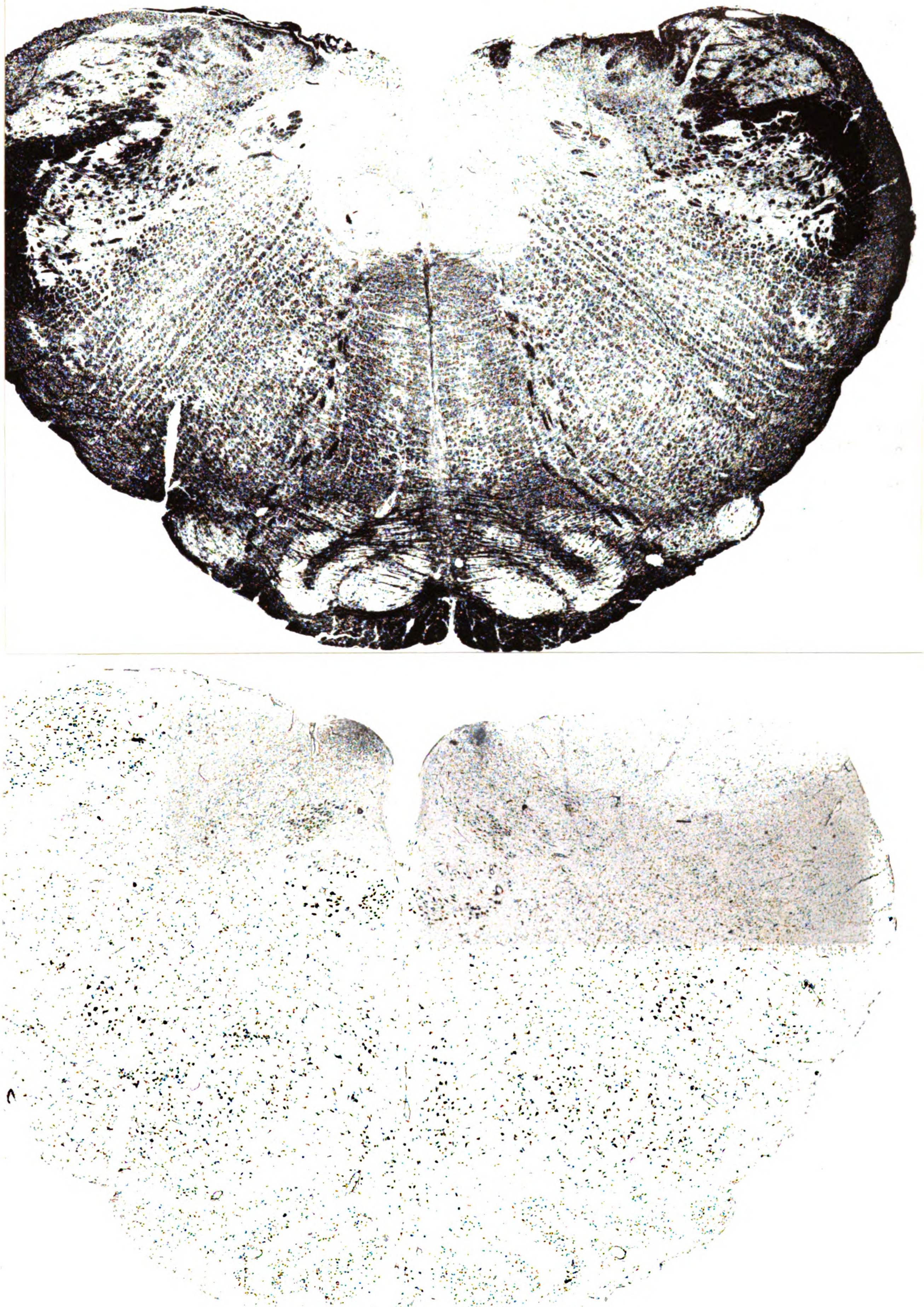


Fig. 6. Figurines and diagram showing actual receptive fields (shaded black) and the nuclear location of responding loci (dots and stars) and photomicrographs of cell and fiber stained coronal sections showing parts of the electrode tracks. This section is at the level of Figure 5: Caudal medulla, and shows the most caudal responses obtained from the Cu-Gr and Sp Trg. The electrode tracks that are visible in the photomicrographs are drawn on the diagram as single dashed lines. Black dots represent the location of the responsive nuclear loci. White stars represent microlesions made at responsive loci but which are not visible in the photomicrographs.



responses were recorded from Cu-Gr and not from the nearby external cuneate nucleus is based on the assumption that these nuclei in the sheep are similar to those in the raccoon in certain anatomical and physiological ways. More specifically it is assumed that the external cuneate nucleus can be distinguished from Cu-Gr by its relatively larger cells and by the fact that harsher tactile stimulation is required to activate the deep muscle receptors that project to it (J. I. Johnson et al., 1968).

In the caudal portions of Cu-Gr the rostral body projection was lateral to the caudal body projection, and in the central Cu-Gr the rostral projections were ventrolateral to the caudal body projections. At this rostral portion of Cu-Gr the rostral body projections are almost directly ventral to the caudal body projections. This is consistent with the changes in shape and position of the nuclei. However Figure 13 shows a response that was obtained in the dorsomedial corner of Cu-Gr following stimulation of the forelimb, a rostral body part; and which was marked by a microlesion. This is inconsistent with the rostro-caudal body projection pattern as just described. This was also the only distal body area whose receptive field projected to the rostral portion of Cu-Gr. Therefore any differences in representation of distal and proximal body areas at this level of the rostro-caudal extent of Cu-Gr have not been determined.

Projections from the pinna, throat, and cheek lie in the boundary region between the Cu-Gr, Sp Trg, and external cuneate nucleus (Figures 12 and 15).

The somatotopic organization within Sp Trg at this level of the Cu-Gr reiterates that shown at more caudal regions of the nucleus. The ventral parts of the face are represented dorsally in Sp Trg and the dorsal parts, ventrally (Figures 14 and 15). Figure 16 shows a series of responses that were obtained in a single electrode puncture through Sp Trg at a level where Cu-Gr is no longer present. Moving from dorsal to ventral in this puncture, the successive projections begin from the chin, then move from the lower lip around to the more dorsal upper lip.

All but two of the electrical discharges obtained in Cu-Gr and Sp Trg occured in response to mechanical stimulation of the ipsilateral body. The two exceptions which are shown in Figure 10 occured in the same electrode puncture into Sp Trg and followed stimulation of ipsilateral and contralateral upper and lower lips.

In general the peripheral receptive fields activating cells in Sp Trg were larger than those activating Cu-Gr cells. A typical receptive field that activated Sp Trg cells would cover an area of a few square centimeters and in some cases, involving the lips, only a few hairs. The receptive fields activating Cu-Gr cells typically included large body areas (eg. entire shoulder or rump). The smallest Cu-Gr receptive fields were located on the limbs and always included several square inches or more.

In terms of the type of stimulation required to evoke a neural response (gentle stroking of a skin receptor vs. harsh probing of deep tissue receptors), light tactile stimulation of hairs and skin produced unit discharges in both Cu-Gr and Sp Trg, although occasionally deep pressure was required to produce electrical discharges in Cu-Gr. In general units in Sp Trg responded to more delicate stimulation than that required to activate responses in Cu-Gr.

Evoked electrical responses were also obtained from the external cuneate nucleus and from the solitary tract and its surrounding nucleus following tactile stimulation of certain body areas. The data with regard to the external cuneate nucleus, shown in Figures 9 and 12, although generally consistent with studies of other animals, are too scanty to be conclusive. Only two responses were identified within the solitary tract (Figure 11) and one within its surrounding nucleus (Figure 13).

In general every part of the sheep's body was represented within Cu-Gr and Sp Trg. These projections of peripheral body receptive fields exhibited a high degree of somatotopic organization which was largely reiterative along the rostro-caudal axis when changes in the shape and position of the nuclei were considered.

Discussion

The somatotopic organization that exists in the Cu-Gr and Sp Trg of the sheep is consistent with the gross organization described for other animals. In general the sheep may be considered as being represented in a cross section of these nuclei as an inverted figure with the hindlimb dorsomedial in the gracile portion of the nucleus and forelimb represented dorsally in the cuneate portion of the nucleus. The proximal body parts are located ventrally in Cu-Gr. The representation of the neck, cheek, and pinna are located between Cu-Gr and Sp Trg which receives projections from the face. Thus the projections to the boundary area between the nuclei are from peripherally adjacent body areas demonstrating that the somatotopic organization exists between the nuclei as well as within them.

Cu-Gr

In an early anatomical study Chang and Ruch (1947) found a seperate mass (pars dorsomedialis of nucleus gracilis) in the medulla for the relay of tactile impulses from the tail of the spider monkey. In a more recent physiological study with raccoons (J. I. Johnson et al., 1968) the tail representation was found always to lie in the dorsomedial aspect of Cu-Gr, and at more caudal levels this representation was located in a cell column that straddled the midline which in some animals became completely seperated from the rest of Cu-Gr. The authors identified this cell column as Bischoff's (1899) "median accessory nucleus," although Chang and Ruch claimed that they had not found Bischoff's "tail nucleus." In the raccoon the ventral portion of this cell column contained the representation of the hindlimb. In the sheep the dorsomedial portion of the gracile nucleus contained the representation of the hindlimb. The tail on the other hand sent projections to the cells in the ventromedial portion of the gracile nucleus and was usually part of a larger receptive field including the rump. This is probably related to the fact that relative to the other animals mentioned, the sheep has a very small tail.

Although the representation of the tail and rump is less conspicuous in the medio-lateral and dorso-ventral dimensions than in other animals, it seems to be represented throughout a greater rostro-caudal extent than that reported for other animals. Responses from the rostral portions of the longitudinal extent of Cu-Gr have been obtained in other animals only from stimulation of the forelimb and forequarters since the gracile portion of the Cu-Gr is no longer present at this level (J. I. Johnson et al., 1968). In the rat Nord (1967) found that the tail was observed only in the caudal 60% of the hindquarter representation. It would seem from this that the gracile portion of the Cu-Gr complex in sheep is present throughout the extent of the complex, and that the tail representation is usually included within a larger receptive field including at least part of the hindquarters so that it is represented as far rostrally as the hindquarters.

Sp Trg

Within the Sp Trg the ventral face areas were represented dorsally in the nucleus, and the dorsal face areas, ventrally. A great deal of the nuclear volume of Sp Trg, which is large relative to Cu-Gr and relative to Sp Trg of most other animals studied, receives projections from the upper and lower lips and the immediately surrounding area including the buccal cavity. This is consistent with the results obtained at the cerebral neocortical (Hatton & Rubel, 1967) and thalamic levels (Cabral & Johnson, 1967) of the sheep. The relatively small size of Cu-Gr and the concomitant small representation of trunk and limb parts is also consistent with the results at the other levels of this afferent system.

The representation of the buccal cavity of sheep is located in approximately the medial two-thirds of Sp Trg between the projections from the upper and lower lips. The fact that this representation extends more laterally than in other animals reported (Kruger & Michel, 1962; Nord, 1967) is probably related to the relatively extensive representation of the lips and surrounding areas in sheep. This might also explain the fact that the buccal cavity was represented in Sp Trg at least throughout the length of Cu-Gr in sheep, although Nord reports that in the rat the representation does not occur caudal to the obex. Kruger and Michel (1962) report that in the cat the buccal cavity representation extends to the caudal extreem of Sp Trg which seems more congruent with the sheep data.

Relative Size of Nuclear Formations

The general somatotopic organization and relative size of Cu-Gr and Sp Trg of the sheep is most similar to that described for the rat (Nord, 1967). In both animals Sp Trg is large relative to Cu-Gr and to Sp Trg of other animals studied, and both animals have a proportionally large central representation of a specific face area. However in the sheep the relatively large representation is from the lips and immediate surrounding area and in the rat it is from the vibrissae and nose. The alligator, cat, and raccoon, which have relatively and successively larger Cu-Gr, have proportionally greater central representations of specific limb regions (J. I. Johnson et al., 1968; Kruger et al., 1961; Kruger & Witkovsky,1961). These larger central representations correspond to a greater density of peripheral receptors in the area represented. It is usually inferred that these densely innervated peripheral areas with large central representations are the areas most discriminatively used by the animal in activities requiring tactile sensation.

There has been some controversy with regard to the presence or absence of rostro-caudal variations in general somatotopic organization and peripheral field sizes. The general somatotopic organization that exists in medio-lateral and dorso-ventral dimensions in the sheep was seen to be reiterative along that part of the rostro-caudal axis that was sampled in this study when changes in the position and shape of the nuclei were considered. That is, stimulation of any particular part of the body led to electrical discharges in similarly located cells throughout the length of the nuclei so that most of the body projected to every rostro-caudal level. It has been suggested on the basis of similar results with other animals that the cells receiving projections from particular body regions extend as columns along the rostro-caudal extent of the nuclei (Gordon et al., 1961; J. I. Johnson et al., 1968; Kruger & Michel, 1962; Kruger et al., 1961; Kruger & Witkovsky, 1961).

Receptive Fields

Although no exact quantitative records were kept in this study with regard to receptive field size, there seemed to be no systematic variance in field size along the rostro-caudal axis of either Cu-Gr or Sp Trg in sheep. However the contrary has been suggested by some authors with regard to other animals (Darian-Smith et al., 1963; Gordon & Paine, 1960; McComas, 1963; Wall & Taub, 1962). The only factor that seemed to be related to peripheral receptive field size in sheep was the relative proportion of central nuclear volume containing the representation of a given body part. Thus the smallest receptive fields were found on the upper and lower lip of sheep which were the peripheral body areas that had the greatest representation in the large Sp Trg. The trunk and limbs on the other hand which were represented centrally with a proportionally smaller nuclear volume had large receptive fields. Similar results can be found for other animals (J. I. Johnson et al., 1968; Kruger et al., 1961; Nord, 1967).

Other studies have shown that receptive fields of a given size and of a specific body area project uniformly throughout the rostro-caudal extent of the nuclei (J. I. Johnson et al., 1968; Kruger & Michel, 1962; Kruger et al., 1961; Nord, 1967; Winter, 1965). Most of these authors conclude that the major determinant of receptive field size is the peripheral location of the fields. Here as in the controversy with regard to rostro-caudal variation in somatotopic organization, it seems important to take into account the changes in shape and position of the nuclei along the rostro-caudal axis in order to be sure that homologous portions of the somatotopic pattern are being sampled at the different rostro-caudal levels. J. I. Johnson et al. (1968) have made a similar point with regard to differences in size, shape, and length of the columns of subnuclei and emphasize the importance of knowing the exact location of the electrode tip within their three dimensional organization.

Possible Inhibitory Interactions

There is one other factor which seems to be pertinent to both controversies--spatial inhibition. It has been reported that tactile stimulation outside of a receptive field can inhibit the firing of the cells within the receptive field (Gordon et al., 1961; Gordon & Paine, 1960). Since all animals must be suspended by some means during the experiments to allow access to most body parts, there is always some form of tactile stimulation in similar areas across experiments. This means that some receptive fields might be inhibited in the experiments which would lead to different conclusions about the somatotopic organization and possibly about receptive field size than those that might have been arrived at if this unwanted stimulation were not present. The fact that different animals were suspended by different means complicates this even further.

All of the electrical discharges obtained in Cu-Gr were in response to stimulation of the ipsilateral body. In Sp Trg only two responses included part of the contralateral face within their receptive fields. The two exceptions which occured in the same electrode puncture involved the upper and lower lips, the body areas with the largest central representation. Similarly, Kruger et al. (1961) reported a few contralateral peri-oral responses in the cat. In general this is consistent with all other studies of these nuclei.

Further Studies Needed

There are a number of areas within Cu-Gr and Sp Trg where the relationship between nuclear morphology and somatotopic organization has not been completely described by this study.

The somatotopic organization of the lateral portion of Sp Trg has not been thoroughly determined. Thus the somatotopic pattern in this nucleus along the medio-lateral dimension including the full extent of the buccal cavity representation is not clear. There is also some question with regard to the organization of projections from the eye, cheek, and nostril.

The somatotopic pattern within Cu-Gr in its rostral portion requires more extensive mapping and confirmation of present results. Accepting the results thus far, there still remains the question as to how the proximal vs. distal body parts project to Cu-Gr at this level. The essential problem at this level of the medulla, however, is the means by which to differentiate Cu-Gr and external cuneate nucleus responses.

Ultimately this will require electrophysiological mapping experiments of the external cuneate nucleus as well as a more extensive study of this portion of Cu-Gr. Similarly microelectrode mapping in the region of the solitary tract and its nucleus would help clarify the somatotopic organization and boundary of the medial portion of Sp Trg.

References

Baldwin, H. A., Frenk, S., & Lettwin, J. Y. Glass-coated tungsten microelectrodes. *Science*, 1965, 148, 1462-1464.

Bischoff, E. Zur anatomie der Hinter-strangkerne bei saugetheiren. *Jahrbucher fur Psychiat. Neurol.*, 1889, 18, 371-384.

Cabral, R. J. & Johnson, J. I. Somatic sensory projections in thalamus of sheep. *Amer. Zool.*, 7: in press (Abstract)

Chang, H. -T. & Ruch, T. C. Organization of the dorsal columns of the spinal cord and their nuclei in the spider monkey. *J. Anat.*, 1947, 81, 150-164.

Darian-Smith, I., Proctor, R. & Ryan, R. D. A single-neurone investigation of somatotopic organization within the cat's trigeminal brain-stem nuclei. *J. Physiol.*, 1963, 168, 147-157.

Ferraro, A. & Barrera, S. E. The nuclei of the posterior funiculi in Macacus rhesus. *Arch. Neurol. Psychiat.*, 1935a, 33, 262-275.

Ferraro, A. & Barrera, S. E. Posterior cokumn fibers and their termination in Macacus rhesus. *J. Comp. Neur.*, 1935b, 62, 507-530.

Gordon, G., Landgren, S. & Seed, W. A. The functional characteristics of single cells in the caudal part of the spinal nucleus of the trigeminal nerve of the cat. *J. Physiol.*, 1961, 158, 544-559.

Gordon, G. & Paine, C. H. Functional organization in the nucleus gracilis of the cat. *J. Physiol.*, 1960, 153, 331-349.

Hatton, G. I. & Rubel, E. W. Somatic sensory projections in cerebral cortex of sheep. *Anat. Rec.*, 1967, 157, 256. (Abstract)

Johnson, F. H. Microelectrode studies on the cuneate and gracile nuclei of the cat. *Am. J. Physiol.*, 1952, 171, 737.

Johnson, J. I. Jr., Welker, W. I. & Pubols, B. H. Jr. Somatotopic organization of raccoon dorsal column nuclei. *J. Comp. Neur.*, 1968, 132, 1-42.

Kruger, L. & Michel, F. A single neuron analysis of buccal cavity representation of the sensory trigeminal complex of the cat. *Arch. oral Biol.*, 1962, 7, 491-503.

Kruger, L., Liminoff, R., & Witkovsky, P. Single neuron analysis of dorsal column nuclei and spinal nucleus of trigeminal in cat. *J. Neurophysiol.*, 1961, 24, 333-349.

Kruger, L. & Witkovsky, P. A functional analysis of neurons in the dorsal column nuclei and spinal nucleus of the trigeminal in the reptile (Alligator mississippiensis). *J. Comp. Neur.*, 1961, 117, 97-106.

Kuhn, R. A. Topographical pattern of cutaneous sensibility in the dorsal column nuclei of the cat. *Trans. Amer. Neurol. Soc.*, 1949, 74, 227-230.

McComas, A. J. Responses of the rat dorsal column system to mechanical stimulation of the hind paw. *J. Physiol.*, 1963, 166, 435-448.

Nord, S. G. Somatotopic organization in the spinal trigeminal nucleus, the dorsal column nuclei and related structures in the rat. *J. Comp. Neur.*, 1967, 130, 343-355.

Rose, J. E. & Mountcastle, V. B. Touch and kinesthesis. In J. Field, H. W. Magoun, & V. E. Hall (Eds.), *Handbook of Physiology*. *Section I*, *Neurophysiology*. Vol. 1. Wahington, D. C.: Am. Physiol. Soc., 1959.

Walker, E. A. & Weaver, T. A. Jr. The topical organization and termination of the fibers of the posterior columns in Macaca mulatta. *J. Comp. Neur.*, 1942, 76, 145-158.

Wall, P. D. & Taub, A. Four aspects of trigeminal nucleus and a paradox. *J. Neurophysiol.*, 1962, 25, 110-126.

Welker, W. I., Johnson, J. I. Jr., & Pubols, B. H. Jr. Some morphological and physiological characteristics of the somatic sensory system in raccoons. *Amer. Zool.*, 1964, 4, 75-96.

Winter, D. L. Nucleus gracilis of cat. Functional organization and corticofugal effects. *J. Neurophysiol.*, 1965, 28, 48-70.

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