MECHANOSENSORY PROJECTIONS FROM MOUTH PARTS TO VENTROBASAL THALAMUS IN OPOSSUM, SQUIRREL MONKEY, AGOUTI, CAT AND RACOON

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ABSTRACT

MECHANOSENSORY PROJECTIONS FROM MOUTH PARTS TO VENTROBASAL THALAMUS IN OPOSSUM, SQUIRREL MONKEY, AGOUTI, CAT, AND RACCOON

By

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The mechanosensory projections from mouth parts were examined in the ventrobasal complex of the thalamus in the opossum, _Didelphis marsupialis_; the squirrel monkey; _Saimiri sciureus_; the agouti, _Dasyprocta aguti_; the cat, _Felis catis_; and the raccoon, _Procyon lotor_. Microelectrode recording techniques were used in acute experiments to determine the character (_i.e._ ipsilateral or contralateral) and organization of projections from the intraoral surfaces primarily and secondarily from the perioral surfaces.

In the five species studied the perioral representation in the thalamus is primarily contralateral. It was shown that in the opossum the projections from the intraoral surfaces are essentially completely contralateral. A small ipsilateral representation was found in the thalamus of the squirrel monkey and the agouti but the projections are primarily contralateral. Both the cat and the raccoon show a large ipsilateral representation and in the case of the raccoon the contralateral component is greatly reduced. These data are compared to those of Cabral and Johnson (1971) on the sheep, _Ovis aries_. They reported a large ipsilateral representation from the perioral surfaces and an essentially completely ipsilateral representation from the intraoral surfaces.

In the contralateral projections to the ventrobasal thalamus of the opossum, agouti, and squirrel monkey the dorsal or maxillary mouth parts project dorsally to the ventral or mandibular mouth parts. In the cat the intraoral ipsilateral projections are ventromedial to the contralateral projections. In the raccoon thalamus the teeth project dorsally to the other mouth parts. No consistent organization was demonstrated within the projection pattern of the teeth themselves. Projecting below the teeth is the palate and below that either the tongue or the incisor pad, with a tendency for the tongue to project more medially and the incisor pad more laterally.

In every species studied most of the intraoral projections are from the teeth. In the agouti only the incisors were seen to project to the ventrobasal complex. Every subject species also had projections to the thalamus from the dorsal surface of the tongue. Projections were seen from the gum in the opossum; from the mucous membrane surrounding the lower incisors in the agouti; from the ventral surface of the tongue in the cat; and from the cheek, the rostral throat area and the pad just posterior to the upper incisors in the raccoon.

It is suggested that the variation in character of the projections to the ventrobasal complex reflects the major subdivisions (cohorts) of the class Mammalia as defined by Simpson (1945). An alternate hypothesis is suggested in which the variations represent specializations of groups lower than cohort.

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INTRODUCTION

The ventrobasal complex of the mammalian thalamus (vb) represents an area of second order synapses of the medial lemniscal system and displays a somatotopic organization of mechanosensory projections from the body surface (Rose and Mountcastle, 1959). The pattern of projections from body parts in vb forms a figure, often with areal distortions, which, in coronal section, depicts a lateral view of the body surface. Figure 1 demonstrates the representation pattern in the raccoon and in the sheep. The caudal body parts are represented laterally and the rostral parts are represented medially. The axial body parts are represented dorsally and the more distal parts ventrally in the thalamus. Note also the large forepaw in the schematic raccoon in Figure 1. This indicates the large amount of thalamic tissue devoted to projections from the forepaw in the raccoon. In the sheep there is a large face and intraoral projection area. In most animals studied the projections from the trunk and limbs are all from the contralateral (cl) side and the projections from the head and mouth are from either the cl side, or the ipsilateral (ips) side, or from both sides of the body. It should be noted that the above description is generalized and each animal displays some specializations.

One portion of vb which is the subject of much confusion in the literature is the most medial region, *i.e.*, that region receiving projections from the perioral and the

Figure 1. Diagrammatic representation of mechanoreceptor projections in the ventrobasal thalamus of sheep (Cabral and Johnson, 1971) and raccoons (Welker and Johnson, 1965).

Top: Diagram to show location of this region in the brains.

Center: Outline diagram of coronal section through the thalamus showing approximate locations of projections from ipsilateral and contralateral body parts.

Bottom: A pictorial representation of these projections, which for raccoons anticipates data from more caudal planes. A separate ipsilateral representation of tissues inside the mouth occurs in both animals, with tongue projections ventral-most; just dorsal to these are projections from the palate and upper teeth; .next dorsal are projections from the lower gums and teeth. In addition, in sheep there is a massive projection from the ipsilateral face, largely from the nose, ventralmost, the hairy protions of skin between the nose and lips dorsal to these, glabrous pipillae of upper and lower lips next, and dorsal-most, from hairy skin between lips and chin. (Figure and caption from Johnson, Hatton, and Rubel, 1969).

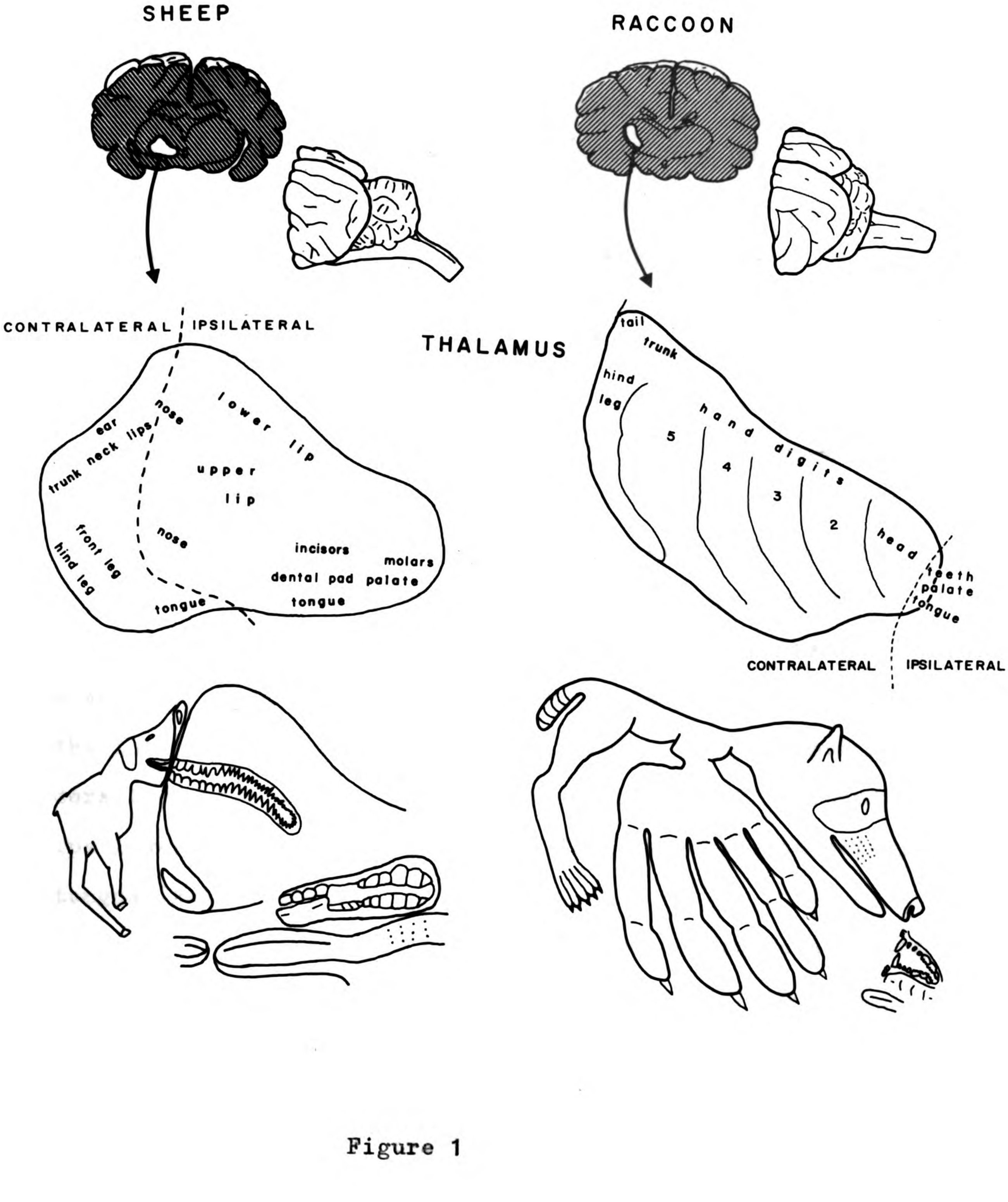
SHEEP
RACCOON
CONTRALATERAL
IPSILATERAL
THALAMUS
ear
trunk
neck
lips
nose
lower lip
upper lip
nose
front leg
hind leg
incisors
molars
dental pad
palate
tongue
tongue
tail
trunk
hind leg
hand digits
5
4
3
2
head
teeth
palate
tongue
CONTRALATERAL
IPSILATERAL

Figure 1

intraoral body surfaces. Cabral and Johnson (1971) studied the mechanoreceptive projections in vb in sheep, *Ovis aries* and discovered three particularly interesting and unusual features of this somatotopic organization:

1. There is a greatly enlarged head and face area represented in the thalamus. 2. The projections from ips body parts dominate vb in sheep to a greater extent than in any animal studied so far. 3. In the most medial areas of the thalamus, where there are projections from the ips face and intraoral regions, the somatotopic organization is quite unusual. In the cl representation in most mammals studied, as in sheep, the projections from the maxillary lips and the surrounding hairy skin are dorsal to those from the corresponding mandibular regions. In the ips projection areas of the sheep this situation is reversed. A similar situation exists with regard to projections from the interior of the mouth. Going through the thalamus in a dorsal-ventral direction Cabral and Johnson (1971) found ips lower teeth, upper teeth, and finally, most ventrally, tongue (see Figure 1).

The organization of vb was examined by Mountcastle and Henneman (1949) in the cat. They found both cl and ips responses from the face region, but the face responses were predominantly cl. The organization of the cl responses resembled that of the head itself, *i.e.*, the maxillary projections were dorsal to the mandibular. The ips face responses were few and it is unclear whether they are organized as are the cl responses or are inverted as in the sheep ips area. The responses from the interior of the mouth were primarily ips and here again it is unclear as to how they are organized. Rose and Mountcastle (1952) again studied the cat thalamus but their data do not define the organization of the ips projections from the face or mouth.

The thalamus of the macaque monkey was examined by Mountcastle and Henneman (1952). Again both ips and cl face and mouth representation was located. The somatotopic organization in the regions receiving ips projections was not examined in detail fine enough to determine exactly the pattern of organization.

In the rabbit thalamus the representation of the face and mouth is quite large (Rose and Mountcastle, 1952). The most striking information that may be inferred from the study on the rabbit is that the projections from the maxillary face are much greater than those from the mandibular face. It seems that most of the face is represented from the cl side. There is apparently considerable representation from the perioral and intraoral surfaces but the exact nature of the somatotopic organization was not described.

Emmers (1965) examined the albino rat thalamus and reported an organizational pattern which has been found in no other mammalian thalamus. He found two complete series of projections which he calls SI and SII to correspond to the SI and SII receiving areas in the cortex which have been seen in many mammals (Woolsey, 1958). Emmers found that the projections in the area he termed SI were cl and those in the area he termed SII were bilateral. His results are very unusual for two reasons: 1. The discovery of an SI and an SII thalamus is a unique finding and 2. In his SI area, which includes the most medial area of vb, he found no ips representation. In every other animal studied so far there has been at least some ips representation reported in the most medial part of the complex.

The raccoon, *Procyon lotor*, thalamus was examined by Welker and Johnson (1965) and they found some ips representation of the face, mouth, and tongue but they did not examine in detail the organization of these ips responses.

Pubols and Pubols (1966) examined the thalamus of the opossum, *Didelphis marsupialis*, and found some ips head representation. They did not, however, describe the organization of these projections. They did not find any responses from the interior of the mouth because, apparently, they didn't look for them.

The reported face and mouth representation in the spider monkey, *Ateles*, thalamus (Pubols, 1968) is considerably less extensive than in either the macaque, *Macaca*, (Mountcastle and Henneman, 1952) or the squirrel monkey, *Saimiri sciureus*, (Blomquist, Benjamin, and Emmers, 1962). Only a few ips responses were found but the author admits that the mapping procedures used may have made the localization of ips responses unlikely.

Thus, researchers have electrophysiologically mapped the thalami of the sheep, *Ovis aries*; the cat, *Felis catus*; the albino rat, *Rattus norvegicus*; the raccoon, *Procyon lotor*; the oposssum, *Didelphis marsupialis*; the macaque monkey, *Macaca* and the spider monkey, *Ateles*. The ips projection area in the thalamus of sheep is large and its organization is inverted when compared to the organization of the cl projection areas seen in other animals studied. Cats seem to have an ips component in vb but its organization is unclear. Rabbits have a large face and mouth representation but the somatotopic organization has not been described. The data from the rat vb are very unusual and therefore of little help in the elucidation of any general organizational pattern which may exist in the mammalian vb. In both the raccoon and the opossum, ips responses were located by previous researchers but their organization was not described. Two monkeys, the macaque and the spider monkey, have been studied but in both instances the ips response area was not mapped.

From the above literature review it should be clear that little attention has been paid to the mechanosensory projections from the mouth parts to vb. It should also be clear that the relative proportions of ips vs cl projections from the mouth parts have not been adequately elucidated for the mammals which have been studied with the exception of the work on sheep (Cabral and Johnson, 1971). Again with that exception, the detailed organization of the mouth parts' projections has not been described. In this study I have analyzed by means of electrophysiological recording, and described the mechanosensory projections from the mouth parts to vb in five mammals, the common opossum, *Didelphis marsupialis*; the squirrel monkey, *Saimiri sciureus*; the agouti, *Dasyprocta aguti*; the domestic cat, *Felis catus*; and the raccoon, *Procyon lotor*.

The rationale for choosing the above animals deserves some mention. The opossum was used because it was available in the Laboratory of Comparative Neurology where this research was conducted and because it represents the infraclass Metatheria, the pouched mammals (Simpson, 1945). The other mammals studied are members of the infraclass Eutheria, the placental mammals. The squirrel monkey was chosen on the basis of its availability and represents cohort Unguiculata and order Primates. Also, it is known to have at least some ipsilateral tongue projections (Blomquist, Benjamin, and Emmers, 1962). The agouti was chosen to represent the cohort Glires, order Rodentia. Compared to common rodents it is a large animal with a large thalamus which permits more detailed mapping. The cat and the raccoon were chosen because they are common animals used in electrophysiological research and the data collected would therefore be especially valuable because they add to a growing fund of knowledge on the sensory systems of these animals. Both these animals are members of the cohort Ferungulata, superorder Ferea, and order Carnivora. It should be noted here that the sheep is a member of cohort Ferungulata, superorder Paraxonia, and order Artiodactyla.

In my final comparisons in which I include the data of Cabral and Johnson (1971) on sheep, I will compare the two infraclasses, Metatheria and Eutheria, within the subclass Theria. Within the infraclass Eutheria I will compare "representatives" of three cohorts, Unguiculata as represented by the squirrel monkey, Glires, as represented by the agouti, and Ferungulata as represented by the cat, raccoon, and sheep.

It should be noted here that comparison of animals related as distantly as even my most closely related subjects is a somewhat hazardous task. This study describes the proportions of ips versus cl projections from the mouth parts to vb in various mammals who are members of the major groups (cohorts) of mammals as defined by Simpson (1945) (see Figure 2) and presents detailed projection patterns of the mouth parts for each animal. These are compared and discussed in light of what is known of mammalian evolution. In other words this study is designed to learn how much of the mouth projections are to the ips vb versus the cl thalamus and to learn if the ips somatotopic organization seen in sheep is a specialization of sheep of is representative of a general mammalian pattern which is particularly obvious in sheep due to the large amount of thalamic tissue involved.

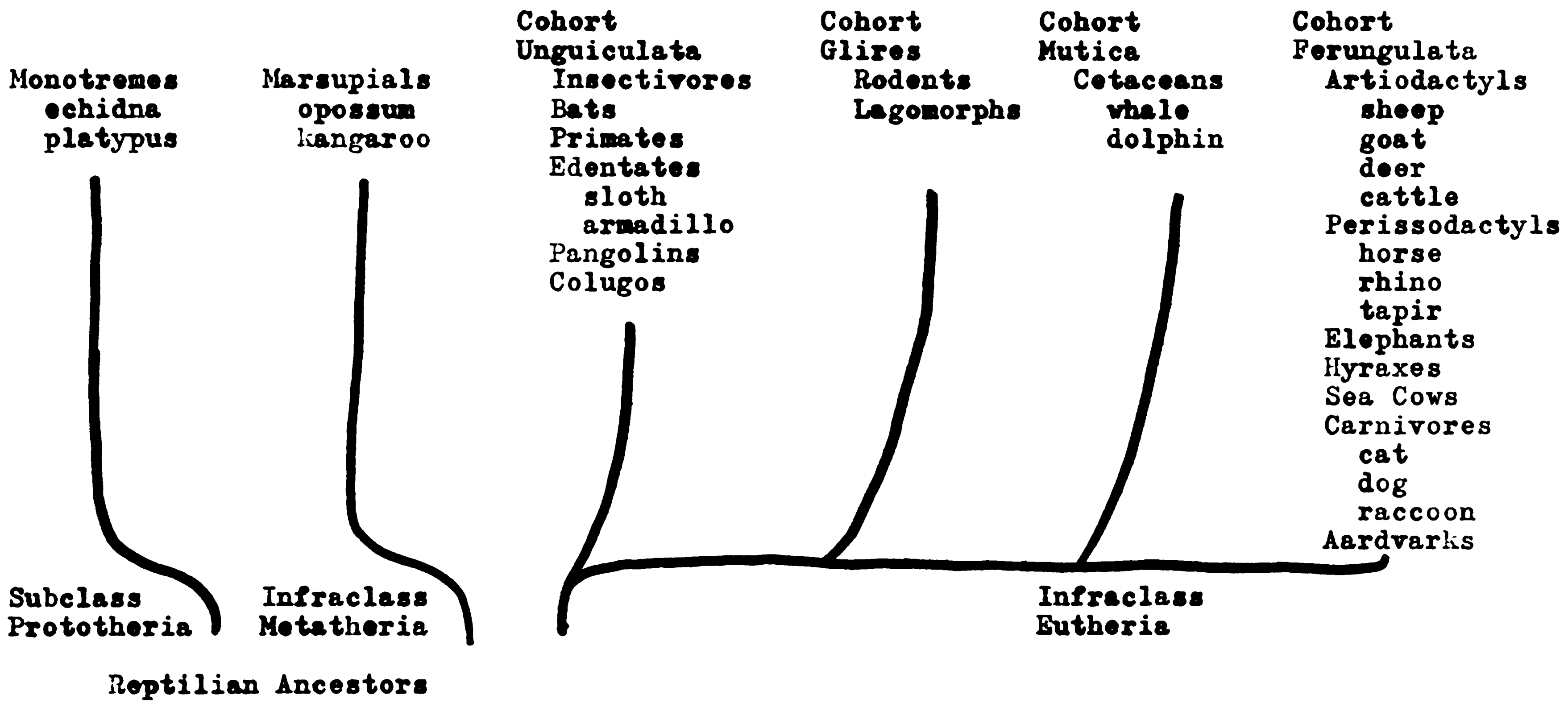

Figure 2. Major extant Mammalian groups as defined by Simpson (1945).

METHODS

Subjects and Preparation

Table 1 describes the source of each animal, number of animals used, and drugs administered to each subject species.

On the day preceding each experiment the animal was deprived of food. The anesthetized subject was shaved on the top of the head and in the throat region. The trachea was exposed, opened, and a cannula inserted to permit immediate mechanical respiratory assistance as required. The skull was exposed, cleaned of all overlying skin and muscle, and secured to a head holder by means of screws fastened to each zygomatic arch. The screws were secured to the head holder bars by means of dental acrylic. Another screw was fastened to the occipital ridge and secured to the headholder by means of another bar and dental acrylic. The brain was then exposed by removing the skull and a dam of dental acrylic was built on the skull around the brain. The dura was cut and reflected and the exposed brain protected with warmed mineral oil for the duration of the experiment. The exposed cortical surface was photographed and an enlarged print made on which the position of the electrode was noted during the experiment.

Frequently, throughout the experiment, a warmed solution of normal saline (0.9%NaCl) was applied to the buccal cavity in order to prevent the tissue from drying.

SUBJECTS AND TREATMENTS
TABLE 1

ecies	source	subject numbers	preanesth tranquil.	anesth.	atropine sulfate IP	5% dextrose in normal saline SC	other
possum idelphis arsupialis	Commerc., Maryland, U.S.A.	552 553 554 556	---	Dial-Urethan, IP,60 mg/kg diallyl-barbituric acid, 240 mg/kg urethan, init., maintenance 1/4 orig.	0.15mg/kg initial	10ml every 2-4 hours	---
uirrel nkey imiri iureus	Endocrine Research Colony, Michigan St. Univ.	562 563	---	Pentobarbital Sodium,IP, 15mg initial, 3mg maintenance	0.1mg/kg initial	7ml/2-6 hrs.	prednisolone acetate, IM, 2.5 mg initial
gouti[1] syprocta uti	Colony, Collega Universitario, Universidade Federal de Minas Gerais, Belo Horizonte, Brazil	591 593 594	Promazionan, 25mg/kg IM,30 min. before anesthetic	Dial-Urethan, IP,144mg/kg diallyl-barbituric acid, 240mg/kg urethan,init. maintenance 1/4 original	0.25mg/kg initial	---	cortisone, IM, 5mg/kg initial

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he agouti experiments were performed by Dr. J.I. Johnson,Jr. Prof. of Biophysics, Psychology, and Zoolog
.S.U. in collaboration with Dr. Gilberto Campos in the laboratories of the Depts. of Neurology and Physio
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amon Cozensa, and Peter Continho. The examination of the tissue and analysis of the data were done by
he author of the thesis and Dr. Gilberto Campos.

Table 1 (continued)

ecies	source	subject numbers	preanesth tranquil.	anesth.	atropine sulfate IP	5% dextrose in normal saline SC	other
at *elis* *atus*	Center for Laboratory Animal Research, Michigan State Univ.	557 558 559 560 561	acetopromazine, IM, 2.5mg/kg 30 minutes before anesthetic	Pentobarbital Sodium, IP, 32.4 mg/kg, init. maintenance 1/4 original	0.1–0.15 mg/kg	10ml/2-5 hrs.	---
accoon *rocyon* *otor*	Wild caught in Southern Michigan	564 565 566	---	Pentobarbital Sodium, IP, 160–195 mg, initial, maintenance, 1/5 original	0.15mg/kg	10ml/2-5 hrs.	prednisolone acetate, IM, 5mg/kg initial

Recording Apparatus

Tungsten microelectrodes were manufactured before the experiment using the method of Hubel (1957), except that they were insulated with glass as described by Baldwin, Frenk, and Lettvin (1965), and the glass on the tip of the electrode was etched with hydrofluoric acid so that 15 to 50 microns of the tip was exposed.

For recording, the microelectrode was clamped in a shielded holder, and shielded leads led from it to a Tektronix 122 preamplifier. Signals here were amplified X 1000 and fed into an audio monitor and an oscilloscope. From the oscilloscope they were fed into a Magnecord 1028 magnetic tape recorder for storage, and when appropriate for visual reproduction, they were subsequently played from the tape through the oscilloscope and were photographed.

Response Criteria

The criterion of a true response was a cluster of unit discharges which could regularly be activated by careful mechanical stimulation of localized body tissues (Figure 3). During the experiment a response was usually identifiable by the audio signal and in cases of doubt a close examination of the visual record confirmed the presence or absence of a response. Normally the units of a positive response were recorded at an amplitude of at least 50 microvolts with an average baseline amplitude of 10-30 microvolts.

A second type of response, termed a low signal/noise response (low s/n), was recorded. A low s/n consisted of a

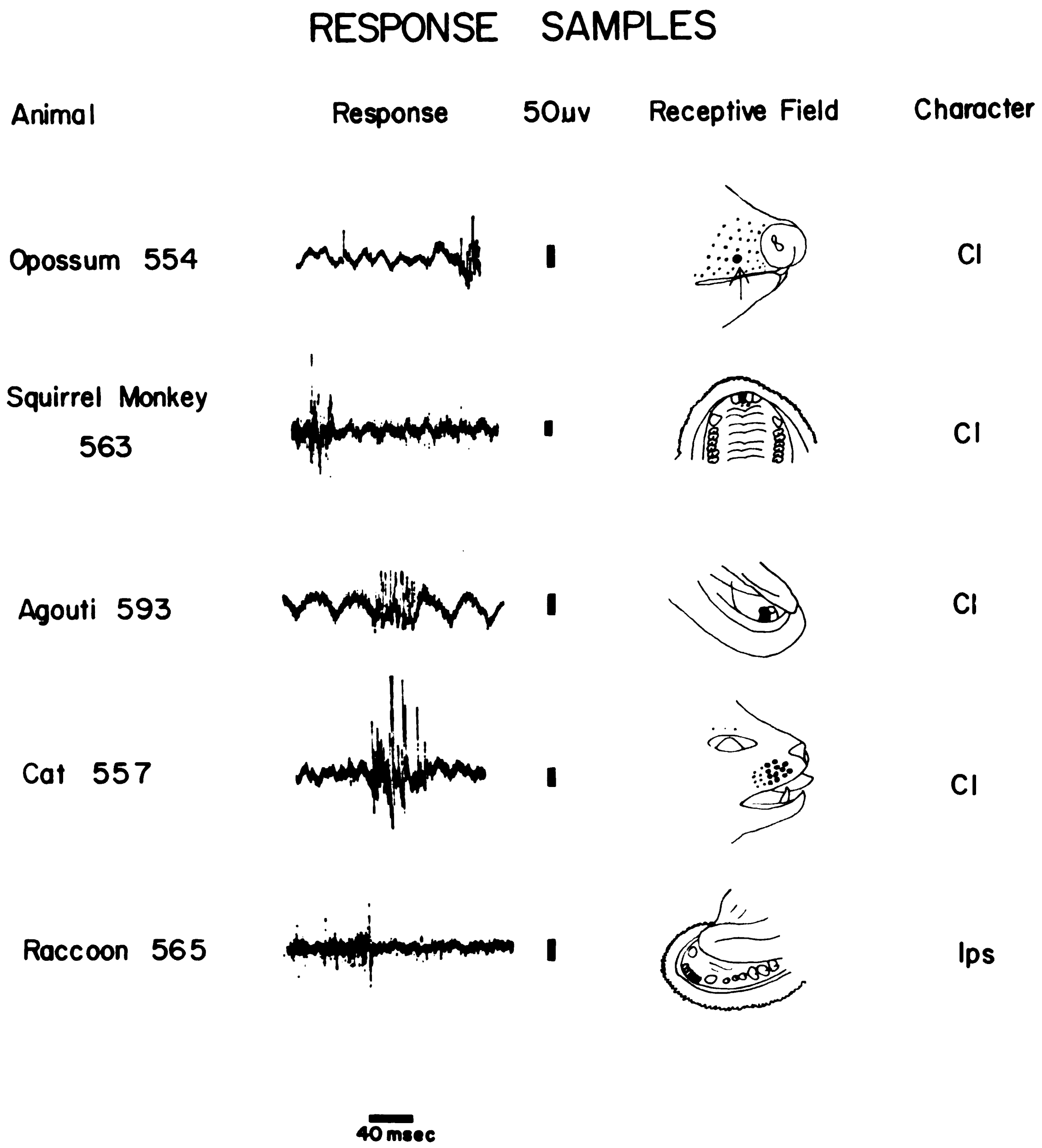


Figure 3. Samples of criterion responses, unit clusters, in the five species studied.

group of units with amplitudes less than 50 microvolts. Low s/n responses are not included in the data tabulations but in instances where it was felt they would be useful in interpretation they were included in the figures and at all times distinguished from criterion responses.

Mapping Procedures

Mapping consisted of a regular series of steps:

1. The microelectrode was introduced into the medial thalamus in a series of regularly spaced punctures, usually in rows 3/4 - 1 mm apart, with punctures within a row 1/4 to 1/2 mm apart. Because of the small amount of thalamic tissue involved it was often necessary to make several punctures before vb was located. In those cases, therefore, punctures were not always as regularly spaced as would be desired.

2. The electrode was moved quickly through the tissue overlying the thalamus and then more slowly through the thalamus itself while the body, face, and intraoral surfaces were mechanically stimulated. For gross localization the experimenter used his hand to stimulate the animal's body and for fine localization a short wooden rod or a small piece of plastic ("Intramedic") tubing was used as a stimulus. When a response was encountered the peripheral receptive field was delineated. The mouth was mapped in particularly fine detail. The experiment was continued until either the animal died, the experimenter fatigued, or no mouth responses were located anteriorly, posteriorly, medially, or laterally

to that area which did respond to stimulation of the intraoral surfaces.

3. For each response point the response activity was recorded on magnetic tape, along with a verbal description of the electrode coordinates and the minimal activating peripheral field on a synchronized second tape channel. A verbal description was also summarized in a written protocol, and the peripheral field was drawn on a photograph of the relevant part of the animal's body. A new response point or locus was recorded: a. when a receptive field was first localized; or b. when the receptive field changed significantly in size or location as the electrode was moved through the thalamus.

4. For marking the location of responding units of special interest or for help in later identification of tracks, marking microlesions were made by passing 40 microamp electric current through the recording electrode tip as anode. In those cases when the ammeter indicated that little current had passed through the electrode the polarity of the electrode was reversed and a brief pulse of current was passed through the recording electrode tip as cathode.

Tissue Preparation

At the conclusion of each experiment, the plane of electrode punctures was marked by inserting pieces of hypodermic tybing at the boundaries of the investigated area, using the electrode holder and the micromanipulator.

The animal was then perfused through the heart with normal saline followed by a mixture of 10% formalin and normal saline. After 24 hours the brain was removed and photographed, and a block of tissue containing the electrode punctures was trimmed by cutting along the plane of the inserted tubing. The tissue was dehydrated, embedded in celloidin, and sectioned at 25 microns in the plane of rows of electrode punctures. Alternate sections were stained with thionin for cell bodies, and with hematoxylin for myelinated fibers. Sections were examined microscopically to identify punctures and to localize the marking lesions.

RESULTS

Overview

In all species studied the projections from the face to vb are primarily cl (see Table 2). The intraoral projections, on the other hand, vary among the species studied in the percentages of data points which include ips responses and in the percentages of data points which include cl responses (see Table 2). The opossum intraoral projections are entirely cl while the squirrel monkey and the agouti have small ips components and large cl components. The cat and the raccoon have large ips components and in the case of the raccoon the cl component is reduced. Table 2 includes data from Cabral and Johnson (1971) which will be discussed later.

In the ventrobasal thalamus of the opossum, agouti, and squirrel monkey the projections of the maxillary mouth parts are dorsal to those of the mandibular mouth parts. In the cat the ips projections are ventromedial to the cl projections. In the raccoon thalamus the teeth projections are dorsal to those of other mouth parts. No consistent organizational pattern was demonstrated within the teeth projections themselves. Below the teeth projections are those of the palate: and below these either projections from the tongue or from the incisor pad. There is a tendency for the tongue to project more medially and incisor pad more laterally.

Following are detailed presentations of the results for individual species. The order of presentation reflects Simpson's (1945) classification of mammals (see Figure 2)

TABLE 2

SUMMARY OF CHARACTER OF RESPONSES

	No of data pts.which include face	data pts. which incl. some ips		data pts. which incl. some cl		No of data pts. which include mouth	data pts. which incl. some ips		data pts. which incl. some cl	
		#	%	#	%		#	%	#	%
possum	49	1	2%	49	100%	26	0	0%	26	100%
quirrel onkey	24	1	4%	24	100%	20	7	35%	17	85%
gouti	56	0	0%	56	100%	21	3	14%	21	100%
at	57	5	9%	53	93%	39	20	51%	27	69%
accoon	34	2	6%	33	97%	99	88	89%	30	30%
heep*	246	230	93%	33	13%	95	92	97%	4	4%

* from Cabral and Johnson (1971). Data from specimens 125 and 126

because the data will later be discussed in light of that classification.

Table 3 summarizes the intraoral structures from which positive responses were elicited in each of the animals studied. In every case most of the projections were from the teeth. The agouti was unusual in that the incisors were the only teeth from which responses were elicited. Projections from the palate were seen in all species except the agouti and the squirrel monkey. Positive responses were elicited by stimulation of the dorsal surface of the tongue in all species studied.

Opossum

In the three opossums studied five thalami were explored. In specimen 553 the punctures were done in a vertical plane. It was evident from that experiment that the most medial vertical punctures possible without either piercing or removing the superior sagittal sinus would not reach the most medial areas of vb. For that reason the electrode punctures in the subsequent opossum experiments (554 and 556) were introduced lateral to vb and directed at an angle toward the midline. One interesting result of this procedure was that in several instances the electrode crossed the midline and data were recorded in vb on the side cl to the electrode entry. It should be noted that all responses will be referred to the side from which the data were actually recorded (as determined by localization of the electrode tracks in the stained sections) and not necessarily

TABLE 3

Intraoral Structures Eliciting a Response in Vb

	No of intraoral data pts.	Data pts. which incl. teeth		Data pts. which incl. palate		Data pts. which incl. dorsal tongue		Other intraoral structures which elicited a response
		#		#		#		
Opossum	26	25	96%	2	8%	3	12%	small area of tissue between upper incisors and rhinarium, "Gum"
Squirrel Monkey	20	12	60 %	0	0 %	8	40 %	none
Agouti	21	13 incisors only	62 %	0	0 %	4	19 %	Mucous membrane surrounding lower incisors
Cat	39	36	95 %	7	19 %	4	11 %	Ventral tongue
Raccoon	99	59	60 %	11	11 %	30	30 %	Cheek; Rostral throat; pad just posterior to upper incisor, 19, 19%
Sheep*	83	17	20 %	32	39 %	28	34 %	Pad around the incisors; cheek; gums

*Data from Cabral and Johnson (1971) Data from specimens 125 and126 from the side where the electrode first pierced the brain.

A total of 46 punctures were made in the five thalami and 23 (50%) of these yielded data. Ten of these punctures included data from the body surface excluding face, 17 from the face and perioral surfaces and 11 from the intraoral surfaces. Intraoral responses were localized from the teeth, tongue and palate regions.

In the 23 punctures which included data 90 response points were localized. Sixteen of these included responses from the body surfaces, 49 from the face, jaw, and perioral surfaces, and 26 from the intraoral surfaces.

Of the 26 intraoral responses 25 (96%) included teeth, and 3 (12%) included responses from the palate. There was also one point which responded to stimulation of the very small area of tissue between the upper incisors and the rhinarium. This area may best be termed gum.

Of the 25 data points responding to stimulation of the teeth 5 (20%) responded to stimulation of the upper teeth to the exclusion of the lower, 9 (36%) responded to stimulation of the lower teeth to the exclusion of the upper and 11 (44%) responded at the same locus to stimulation of both the upper and lower teeth.

The character of the projections to vb in opossums is evident from this study. Of the 90 data points observed 89 (90%) were completely cl. At one locus a bilateral response from both the cl and ips anterior lower lip was obtained.

The somatotopic organization of the medial parts of vb is also evident. Both the perioral and intraoral projections are organized in much the same way as are the cl body projections to the thalamus in other animals studied, including the opossum (Pubols and Pubols, 1966). In other words the more dorsal body elements are represented dorsally in the thalamus and the more ventral body elements are represented in the ventral region of the complex. Also, the most medial areas of the complex are devoted to representation from the interior of the mouth. These details are best seen in Figures 4 and 5.

The data collected demonstrate that there are projections from the intraoral surfaces which include teeth, tongue, and palate, and from the perioral surfaces. The overwhelming majority of the projections are from the cl side and these are organized in much the same way the cl projections from the body surfaces project to the dorsal area of the complex and ventral surfaces project to the ventral area of the complex. It is also seen that the most medial projections are from the mouth parts.

Squirrel Monkey

In the two squirrel monkeys studied three thalami were explored. The electrode was moved in a vertical plane, *i.e.* not tilted, during both experiments.

Thirty-six punctures were made and fifteen (42%) of these yielded data. Four punctures included responses from

Table 4

LIST OF ABBREVIATIONS

A.. Abbreviations used in Figures 4-13. Abbreviations of brain structures after Oswaldo-Cruz and Rocha-Miranda (1968).

A	anterior
cha	commissura habenulae
ci	capsula interna
fx	(c olumna)fornicis
GLD	nucleus corporis geniculati lateralis dorsalis
GLV	nucleus corporis geniculati lateralis ventralis
GM	nucleus corporis geniculati medialis
HM	nucleus medialis habenulae
IMD	nucleus intermedialis dorsalis
L	lateral
M	medial
Mm	nucleus mamillaris; pars medialis
mm	millimeter
mth	fasciculus mamillothalamicus
nIII	nervus oculomotorius
P	posterior
ped	pedunculus cerebri
rfl	fasciculus retroflexus
Rt	nucleus reticularis thalami
SN	substantia nigra
STh	nucleus subthalamicus
tro	tractus opticus
VM	nucleus ventralis thalami medialis
xVB	nuclei ventralis thalami basalis
ZI	zona incerta

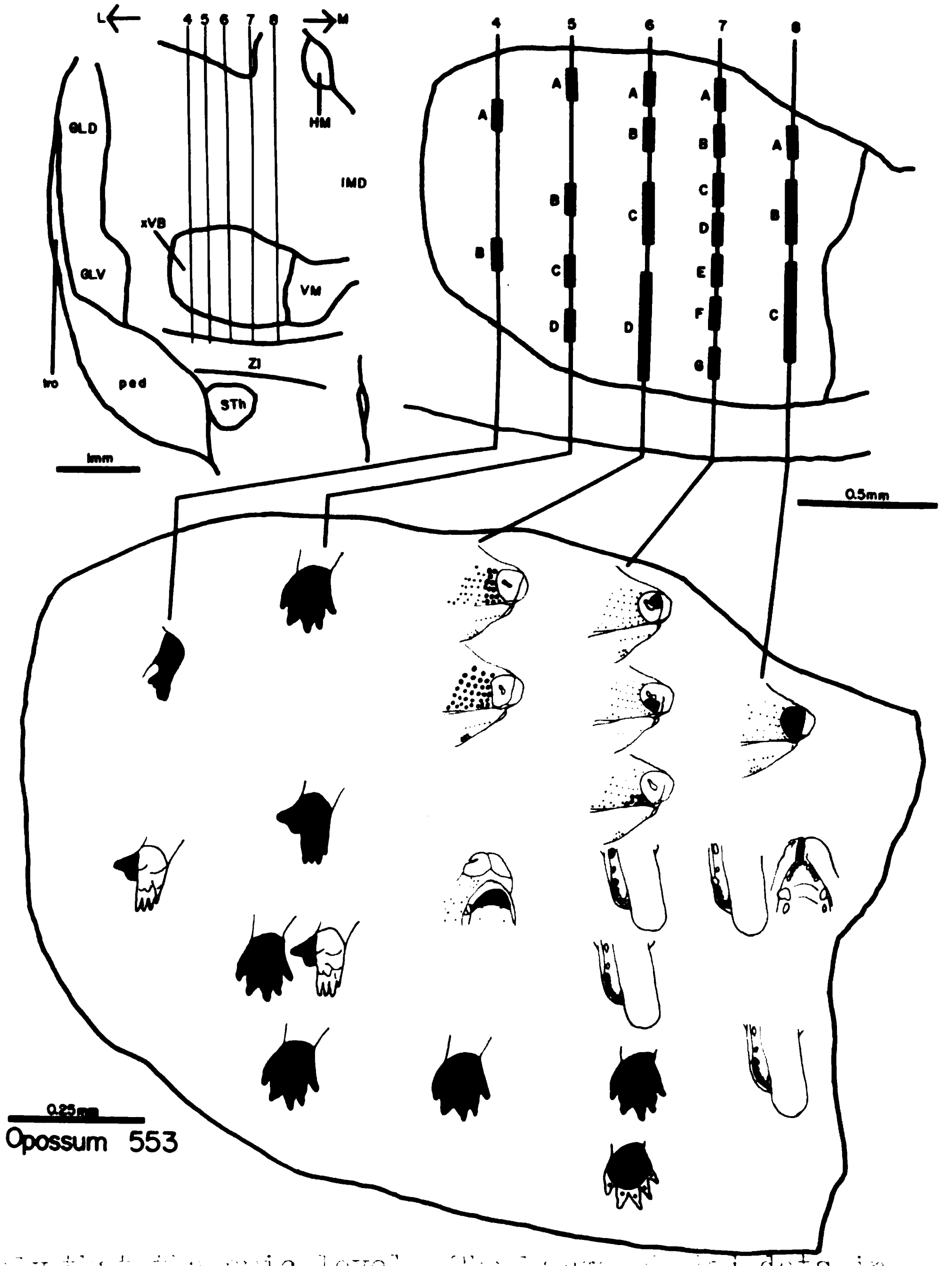
B. Abbreviations used in the body of the thesis.

cl	contralateral
ips	ipsilateral
vb	ventrobasal complex of the thalamus

Figure 4. Projection pattern in a coronal row of punctures in opossum 333.

See Table 1 for abbreviations.

Right: A line drawing whose format is similar to that found in Figures 4-13. At the top right portion of the drawing is a section of thalamus from which responses were elicited (in this case section 76). In this figure and in Figures 5-11 and Figure 13, coronal planes are depicted. In Figure 12 a parasagittal plane is depicted. By convention, the left thalamus is shown in all figures although in many instances the right thalamus was explored. Solid lines are used to define nuclear boundaries when those boundaries were evident. Dotted lines are used when nuclear boundaries were unclear. The lines which are numbered at the top represent the electrode tracks at this level. To the right of the thalamus is an enlargement of vb with the approximate location of responses indicated by dark horizontal bars and labeled A,B, etc. Circles labled A,B, etc., indicate [illegible] responses. At the bottom of the figure is a further enlargement of vb with figurines of various body parts. The darkly shaded areas (receptive fields) [illegible] the areas which, when stimulated, elicited a response at



[illegible] approximately that thalamic level. The large shaded dots in [illegible] of some figures indicate vibrissae [illegible], when stimulated, elicited a response. The receptive fields are arranged [illegible] and the convention that all data are assumed to have been recorded from [illegible] left thalamus. In other words all receptive fields [illegible] the right side of the body.

In this figure note that the intraoral projections [illegible]. [illegible] puncture 8 [illegible] the mandibular teeth projection [illegible] beyond the [illegible] teeth. No punctures were made medial to 8 because [illegible] ended after puncture 8.

Right: Photomicrograph of section [illegible] stained for myelinated fibers, [illegible] approximately the level indicated [illegible] the right. Magnification [illegible].

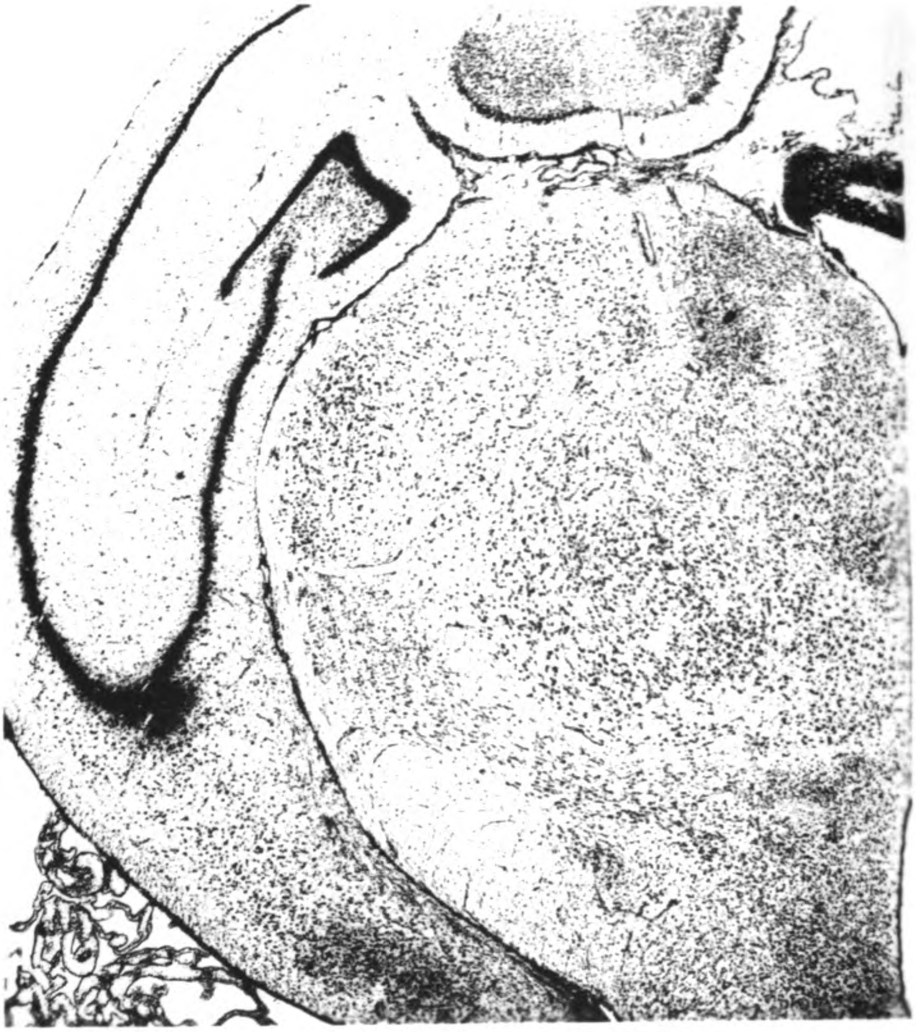


Figure 5. Projection pattern in a coronal row of punctures in opossum 556.

See Table 4 for abbreviations.

See Figure 4 for the explanation of the format of this figure.
Right: Section 46 is depicted. In punctures 11 and 13 note the details of the organization of the intraoral responses.
In puncture 11 note the orderly progression of receptive fields from the maxillary face to the nose to the upper teeth and finally to the lower teeth and tongue.

Above: A photomicrograph of section 50 stained for cell bodies at approximately the level described on the opposite page.
Magnification = 22X.

the body surface excluding face, eight included responses from the face, jaw, and perioral surfaces, and six included responses from the interior of the mouth. The only intraoral surfaces from which responses were elicited in the squirrel monkey were the teeth and the dorsal surface of the tongue.

In the fifteen punctures which included data 57 data points were localized. Thirteen of these included responses from the body parts excluding face, 24 included responses from the face, jaw, and perioral surfaces, and 20 responded to stimulation of the intraoral surfaces.

Twelve (60%) of the 20 mouth data points responded to stimulation of the teeth and 8 (40%) responded to stimulation of the tongue. In these experiments there were no data loci which responded to both teeth and tongue.

Of the 12 data points responding to stimulation of the teeth 7 responded to stimulation of the upper teeth to the exclusion of the lower teeth and five responded to stimulation of the lower teeth to the exclusion of the upper. There were no data points responding to both upper and lower teeth simultaneously.

In the squirrel monkey, as in the cat, both cl and ips projections are seen in vb. All of the thirteen body responses were cl and all of the 24 data points from the face included projections from the cl surfaces. One of these data points responded to stimulation of a small area on the middle of the rostral nose and therefore must be said to include both a cl and an ips component. Of the 20 data points responding to stimulation of the intraoral surfaces 17 (85%) included responses from the cl surfaces and 7 (35%) included responses from the ips surfaces. Included in the ips responses were the tip of the tongue, the incisors, the canine, and the molars.

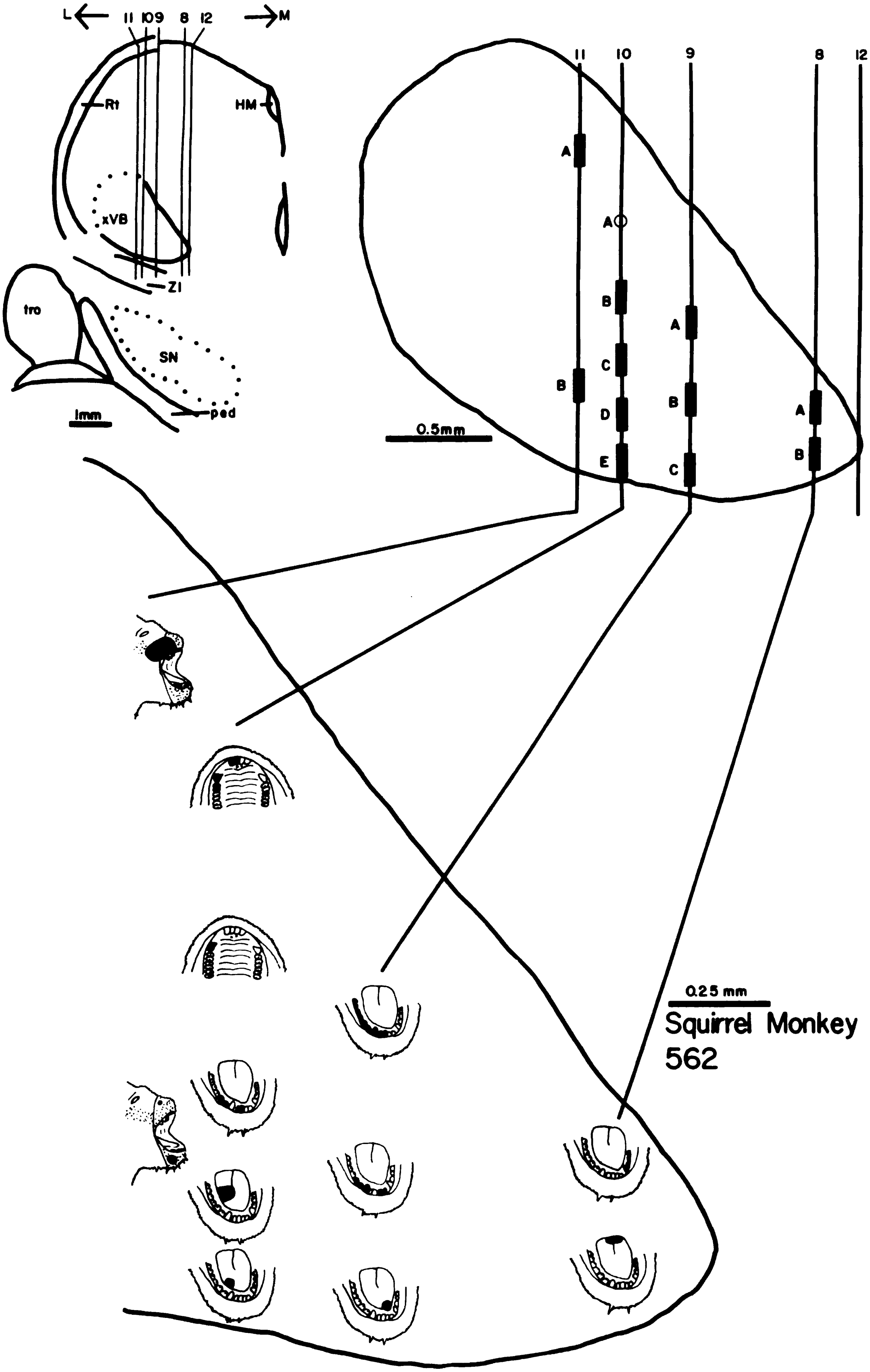
The cl intraoral projections are seen in the lateral edge of the mouth projection area (Figure 5). The most dorsal of these projections are from the maxillary teeth, followed ventrally by projections from the mandibular teeth and finally most ventrally are the projections from the tongue. More medially in the complex are found the ips and bilateral loci (Figure 6). In this very small medial mouth projection area the teeth, both cl and ips, project dorsally and the tongue, which again may include ips and/or cl components, projects ventrally (Figures 6 and 7).

In these squirrel monkey experiments the face projected almost exclusively to the cl thalamus while the interior of the mouth projected to both the cl and ips sides. The cl mouth projections are organized as are most cl projections to the thalamus. The dorsal body parts project to the dorsal part of the complex and the ventral parts project to the ventral part of the complex. In the most medial projection area both cl and bilateral responses are seen and in this area the teeth project dorsally to the tongue. There are too few responses in this region to define an organizational pattern among them.

Figure 6. Projection pattern in a coronal row of punctures in squirrel monkey 562.

See Table 4 for abbreviations.

See Figure 4 for the explanation of the format of this figure.
[illegible]: Section 112 is depicted. In this figure note the cl responses whic project dorsally and laterally to the ips responses. Also note the progression in puncture 10 from maxillary to mandibular cl intraoral responses as the electrode is moved down through the thalamus.
[illegible]: A photomicrograph of section 112 stained for cell bodies at the level described on the opposite page. Electrode tracks 11, 10, 9 and 8 are visible in this section. Magnification = 12X.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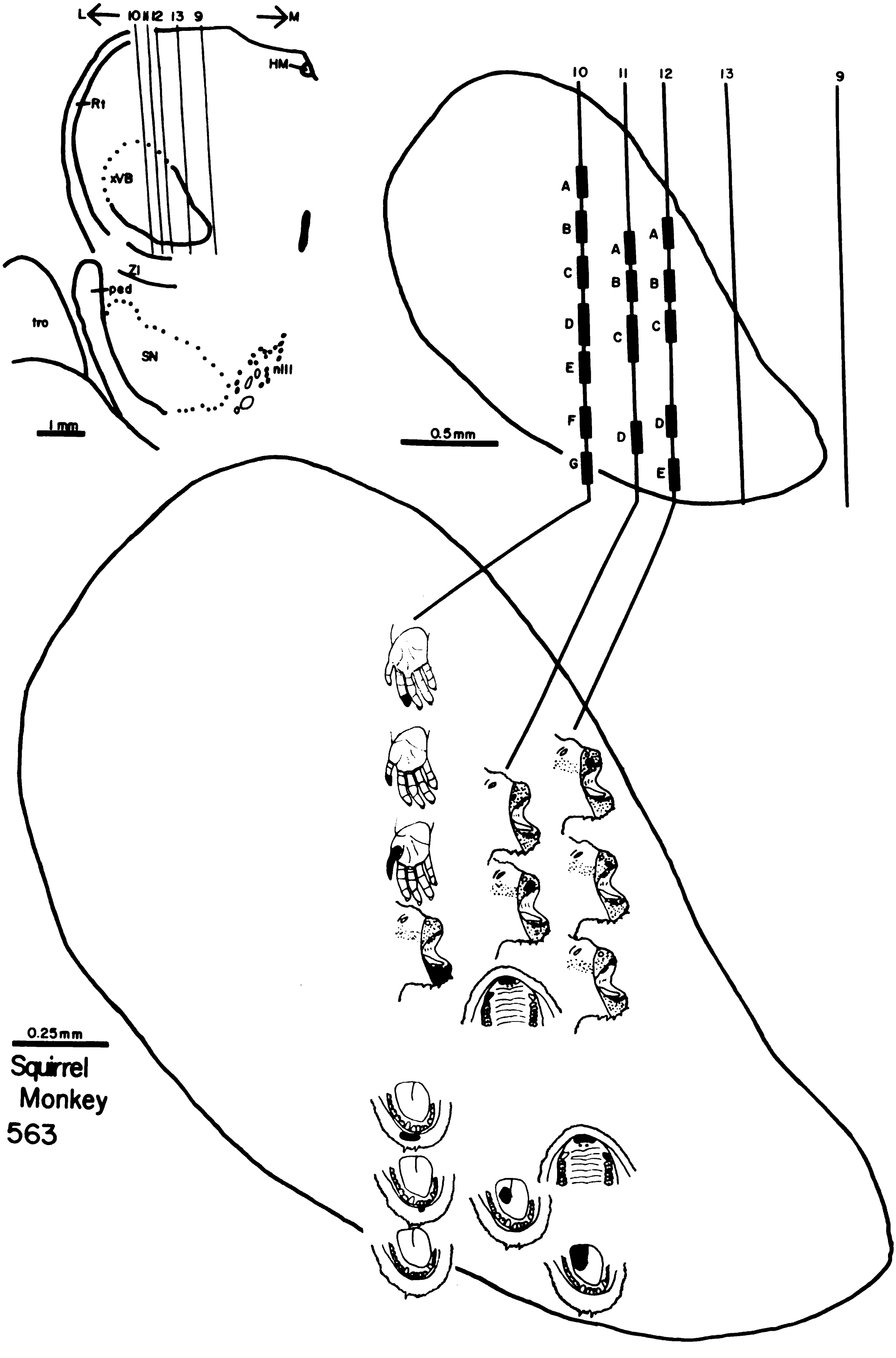
Squirrel Monkey
562

Figure 7. Projection pattern in a coronal row of punctures in squirrel monkey 563.

See Table 4 for abbreviations.

See Figure 4 for the explanation of the format of this figure.
Right: Section 136 is depicted. In punctures 11 and 12 note the progression of responses from the maxillary face, to the maxillary tooth, which in both punctures includes both cl and ips components, and finally to the cl tongue. Locus 11C includes only one ips tooth, the most medial ips incisor. Stimulation of this tooth may have stimulated the cl incisors because they are close. In 12D, however, several ips teeth are included.
Above: A photomicrograph of section 136 stained for cell bodies at the level described on the opposite page. Electrode tracks 10,11,12 13 and 9 are visible in this section. Magnification = 13.75X.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Squirrel
Monkey
563

Agouti

Six thalami were explored in four agoutis but only the data from three thalami in three agoutis will be examined here. In one subject, 592, all electrode tracks were seen, upon examination of the prepared sections, to be lateral to the thalamus in the region of the reticular nucleus and the internal capsule. In specimen 593 the one data point that was found in the left thalamus was also localized lateral to vb. The above mentioned data may have been recorded from post-synaptic fibers but will not be included in the tabulations. In all experiments the electrode was moved in a vertical plane, i.e. not tilted.

A total of 60 punctures were made and 37 (62%) yielded data. Eleven punctures included data from the body surface excluding face. Twenty-five puncutres included data from the face, jaw, and perioral surfaces, and eleven included intraoral responses. In the agouti there are two folds of hairy skin which extend down from the face, fold into the mouth, and meet each other. The responses from the external surface of this hairy skin are considered perioral. Intraoral responses were elicited from the incisors, the tongue, the mucous membrane around the lower incisors, and from the inside of the lip.

Ninety-nine data points were localized and examined of which 23 included responses from the body surface excluding the face, 56 included responses from the face, jaw, and perioral surfaces, and 21 included responses from intraoral surfaces.

Thirteen (62%) of the 21 intraoral data points included incisor responses, 4 (19%) included responses from the dorsal surface of the tongue, 3 (14%) included responses from the inside of the lip, and 2 (10%) included responses from the intraoral surfaces.

Four (31%) of the 13 incisor data points responded to stimulation of the upper incisors to the exclusion of the lower, 8 (62%) responded to stimulation of the lower incisors to the exclusion of the upper and 1 (8%) responded to stimulation of both upper and lower incisors.

The agouti experiments demonstrated an almost entirely cl representation in vb. All of the responses from the body and the face which were recorded in the nucleus were entirely cl. In the left thalamus of 593, however, the one response mentioned earlier was an ips response from the hairy skin which folds inside the mouth. This response was localized outside the nucleus. Its significance is unclear. All 21 of the intraoral responses included a cl component and 3 (14%) of these also included an ips component. In those cases both incisors responded together and it was impossible to determine if the ips tooth was responding directly or merely stimulating the cl tooth.

These data demonstrate a clear organizational pattern for both the intraoral and perioral responses. The body projections are lateral to the projections from the face, jaw, and perioral surfaces which are, in turn, lateral to the projections from the intraoral surfaces (Figures 8 and 9).

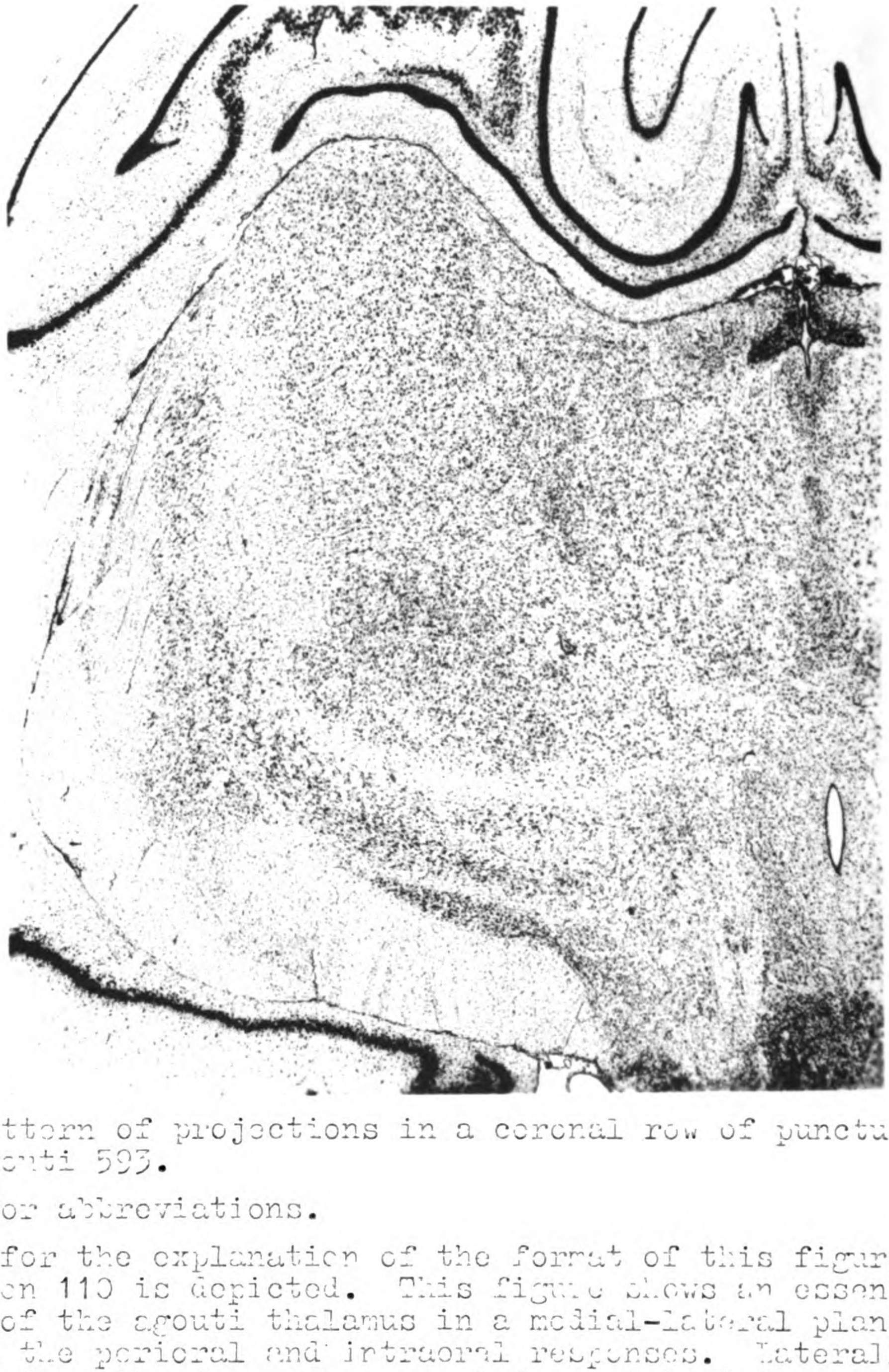
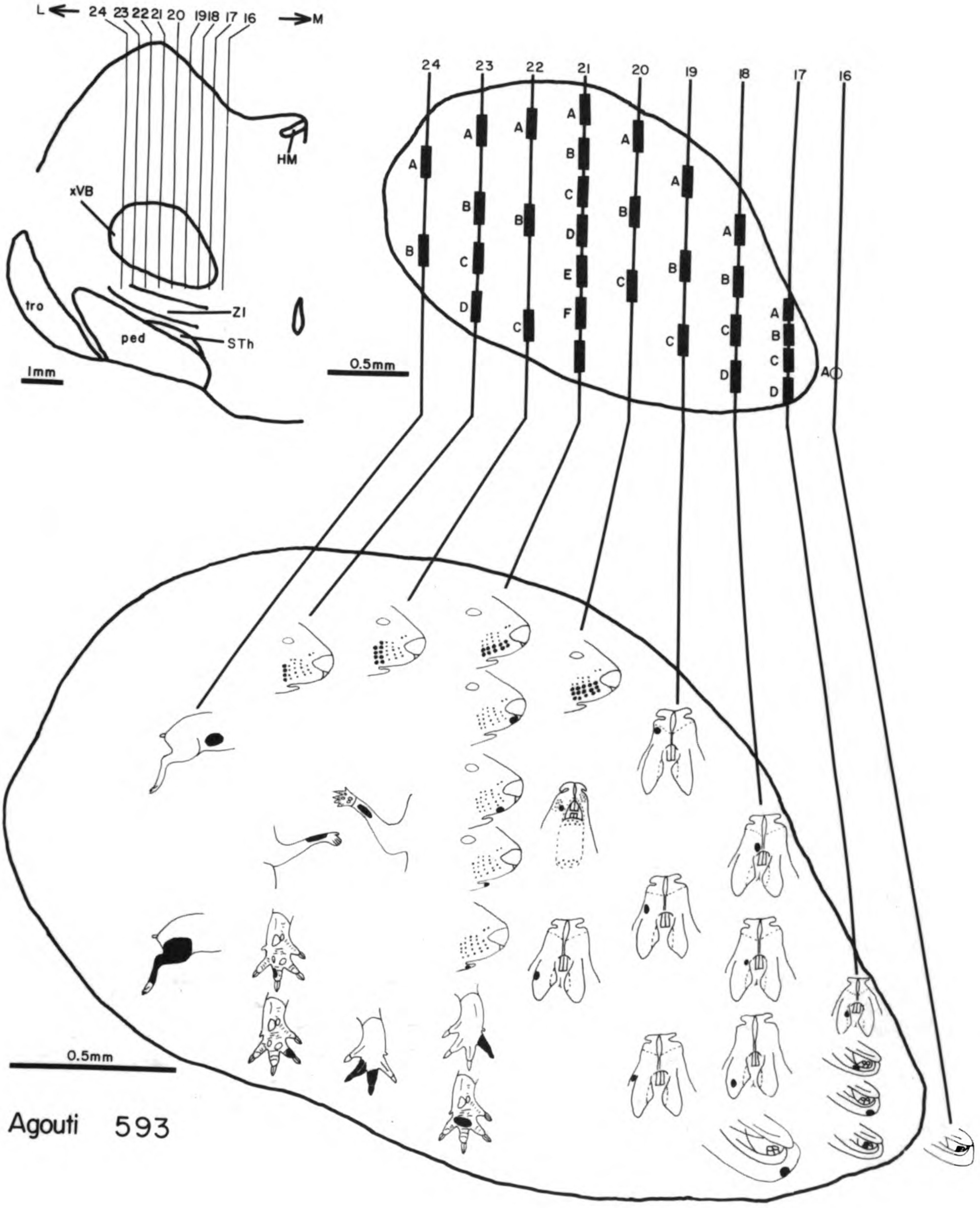


Figure 8. Pattern of projections in a coronal row of punctures in agouti 593.

See Table 4 for abbreviations.

See Figure 4 for the explanation of the format of this figure.
Right: Section 110 is depicted. This figure shows an essentially complete map of the agouti thalamus in a medial-lateral plane. Medially note the perioral and intraoral responses. Laterally there are responses from the face, forepaw, body, and hind leg.
Above: A photomicrograph of section 104 stained for cell bodies at approximately the level described on the opposite page.
Magnification = 14.2X.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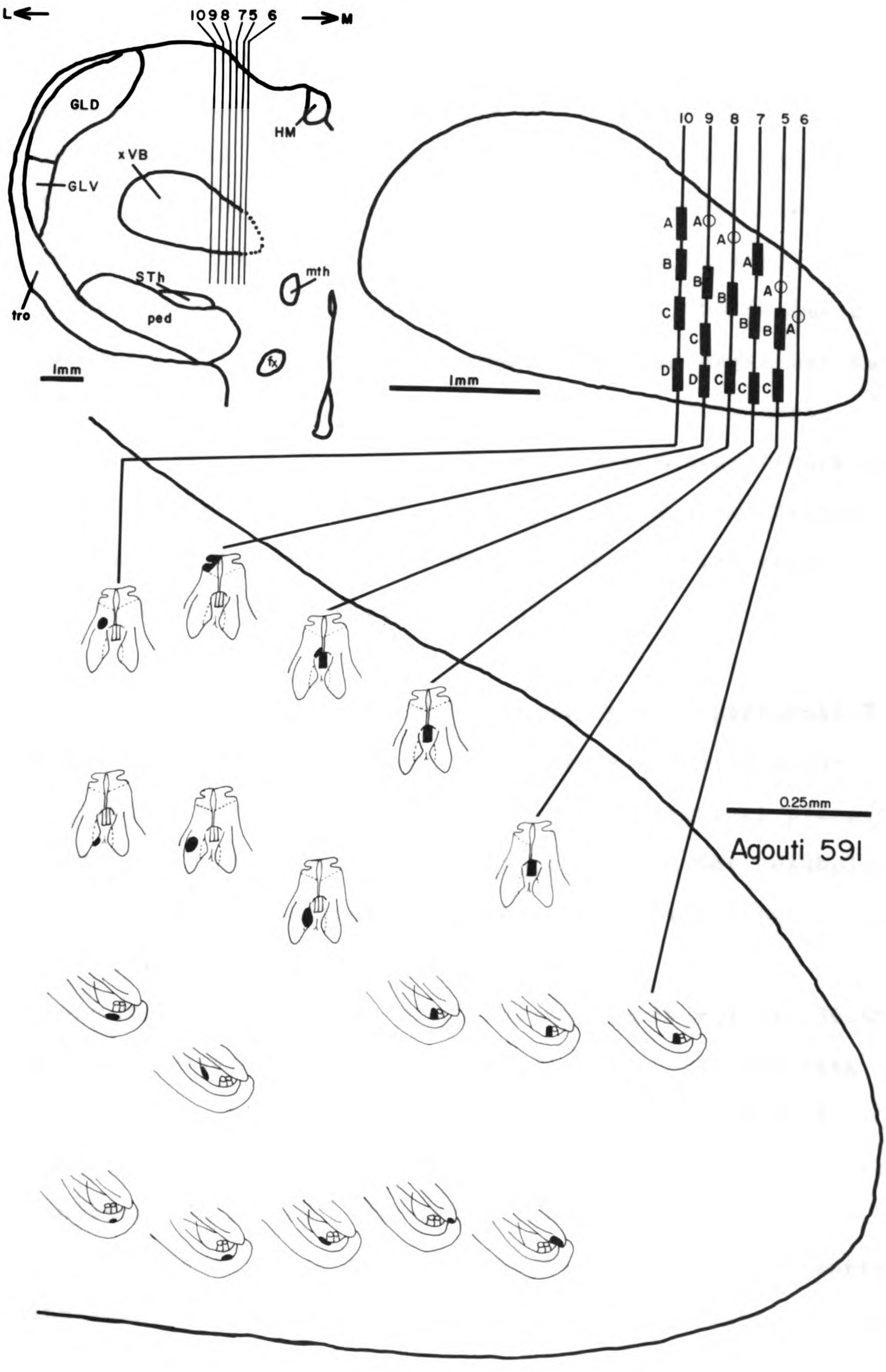
Agouti 593

Figure 9. Pattern of projections in a coronal row of punctures in agouti 591.

See Table 4 for abbreviations.

See Figure 4 for the explanation of the format of this figure.
Right: Section 42 is depicted. In this figure note the detailed pattern of intraoral and perioral responses. Note the organization in the dorsal-ventral direction. The maxillary teeth project dorsally to the mandibular teeth which in turn project dorsally to the tongue. A similar situation exists with the perioral responses seen in the lateral punctures.
Above: A photomicrograph of section 42 stained for cell bodies at the level described on the opposite page.
Magnification = 14X.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Agouti 591

In the dorsal-ventral direction the organization of the projections is as would be expected in any cl thalamic projection pattern. The dorsal or maxillary face or teeth project dorsally to the corresponding ventral or mandibular surfaces (Figure 9). In those punctures which included tongue the tongue projected most ventrally (Figure 9).

These experiments have demonstrated that the thalmaic projections in the agouti are primarily cl and organized as other cl projection patterns are; i.e. dorsal body parts projecting dorsally, ventral body parts projecting ventrally, and rostral parts projecting medially. One unusual feature of the representation is that the only teeth which were found to project to vb were the incisors.

Cat

In the five cats on which experiments were performed 7 thalami were explored. In all experiments except one the electrode was moved down to the thalamus in vertical plane. In animal 561 the subject's head was tilted in the headholder and therefore the electrode was introduced lateral to vb and moved at an angle toward the midline.

One hundred and forty punctures were made and 51 (36.4%) of these yielded data. Twenty-two punctures included data from the body surfaces excluding face, 22 yielded data from the face, jaw, and perioral regions, and 19 yielded data from the intraoral surfaces. The intraoral surfaces from which responses were elicited included teeth, palate, dorsal surface of the tongue, and the ventral surface of the tongue and its attachment to the floor of the mouth.

In the 51 punctures which included data 125 response points were localised. Forty-three included responses from the body surface, 57 included responses from the face, jaw, and perioral surfaces, and 39 included responses from the intraoral surfaces.

Of the 39 intraoral response loci 36 (95%) responded to stimulation of the teeth, 7 (19%) responded to stimulation of the palate, 4 (11%) responded to stimulation of the dorsal surface of the tongue and 2(5%) responded to stimulation of the tissues on the ventral surface of the tongue and the floor of the mouth.

Of the 36 loci responding to stimulation of the teeth 10 (27%) responded to stimulation of the upper teeth to the exclusion of the lower: 13(36%) responded to stimulation of both upper and lower teeth.

In the cat both cl and ips projections are seen in vb. All 43 data points responding to stimulation of the general body surface were, as expected, cl, while of the 57 data points responding to stimulation of the face, jaw, and perioral surfaces 53 (93%) included responses from the cl side and 5 (9%) included responses from the ips side. Of the 39 loci responding to stimulation of the intraoral surfaces 27 (69%) included responses from the cl side and 20 (51%) included responses from the ips side.

Because of the small size of vb receiving projections from inside the mouth it is impossible to state, with one

exception, exactly what the somatotopic organization is. In some instances the lower teeth project ventrally in the thalamus, while in other instances the upper teeth are seen to lie ventral to the lower teeth. One pattern which does appear is for the ips responses to be located ventro-medially to the cl responses (Figures 10 and 11).

These experiments demonstrate that the cat has both cl and ips projections from the face and mouth to vb and that the ips projections are ventromedial to the cl projections. These experiments have not, however, demonstrated the somatotopic organization of the projections to the medial areas of vb.

Raccoon

Three thalami were explored in three raccoons. In all experiments the electrode was moved in a vertical plane, *i.e.* not tilted.

Sixty-eight punctures were made and 48 (71%) of these yielded data. Two punctures included data from the body surface excluding the face, 21 included data from the face, jaw, and perioral surfaces and 40 included data from the interior of the mouth. The intraoral surfaces from which responses were elicited were the teeth, the dorsal surface of the tongue, the pad just posterior to the upper incisors, the palate, the cheek, and the rostral throat area.

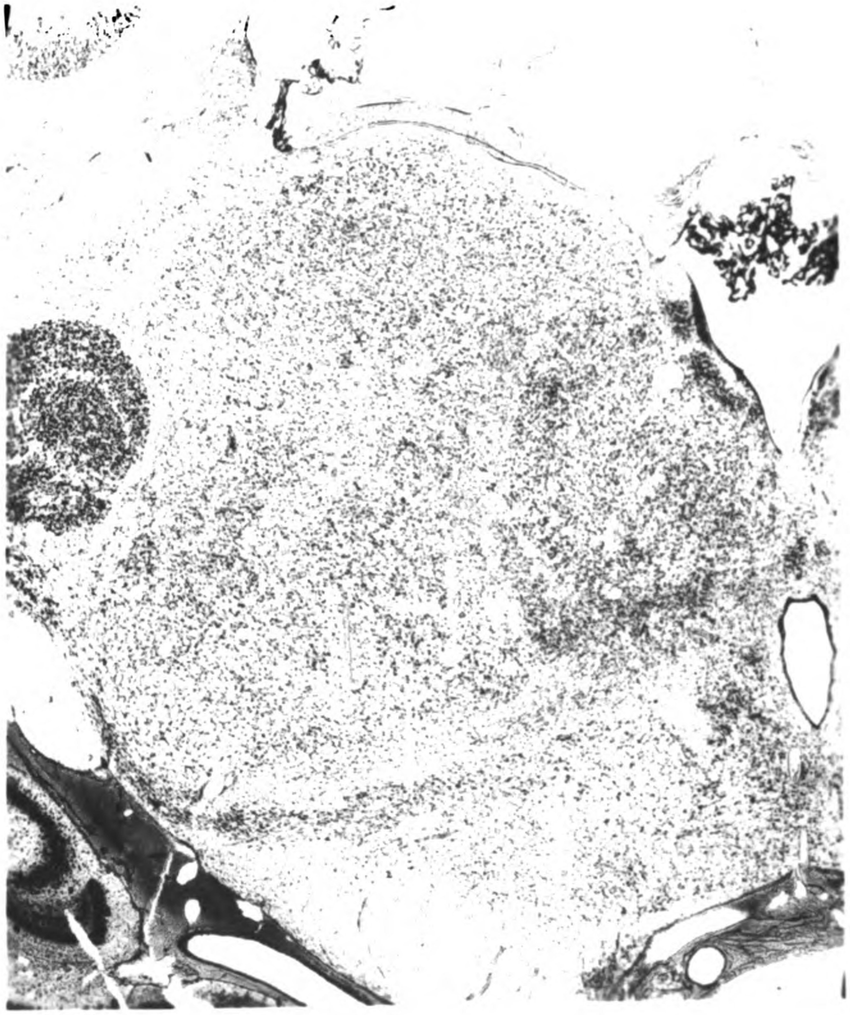


Figure 10. Pattern of projections in a coronal row of punctures in cat 560.

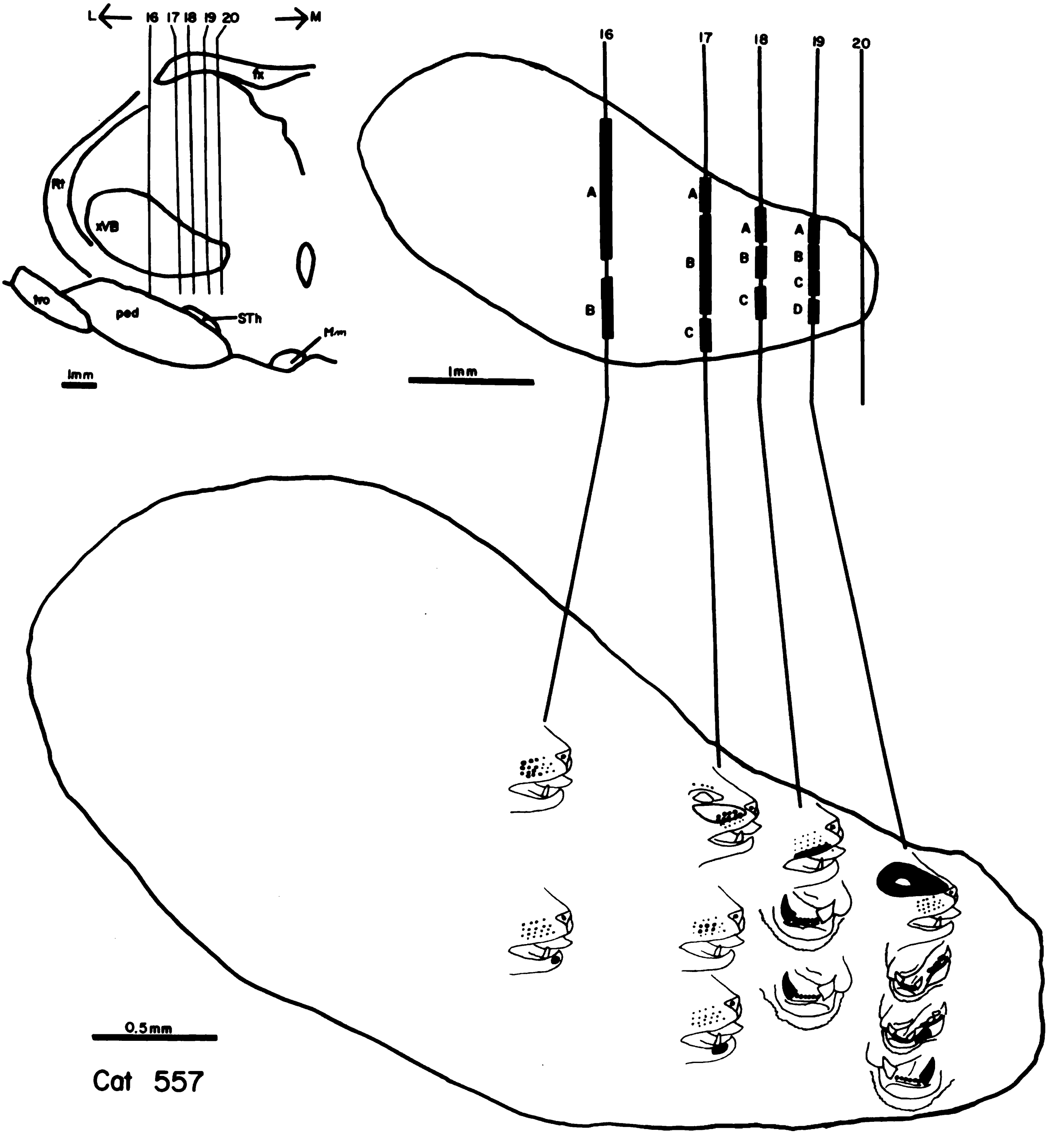
See Table 4 for abbreviations.

See Figure 4 for explanation of the format of this figure.
Right: Section 176 is depicted. Note that all responses in puncture 38 and two of those in puncture 37 are of the low s/n type. The ventromedial responses, 38D and 37C are from the ips tongue.
Above: A photomicrograph of section 172 stained for cell bodies at approximately the level described on the opposite page. Electrode tracks 35,36, and 37 are visible in this section.
Magnification is 12.75X.

Figure 11. Pattern of projections in a coronal row of punctures in [illegible].

See Table 4 for abbreviations.

See Figure 4 for explanation of the format of this figure.
Right: Section 175 is depicted. In this figure note again the tendency for the responses to project to the ventromedial portion of [illegible]. This is seen in 180 and 187, [illegible].
Left: A photomicrograph of section 175 stained for cell bodies [illegible] on the opposite side. Electrode tracks 16,17,18,19, and 20 are visible in this section.
Magnification 12.5X.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Cat 557

In the 48 punctures which included data, 119 data points were localized. Only 2 of these included responses from the body excluding the face. Thirty-four included responses from the face, jaw, and perioral surfaces and 99 included responses from the intraoral surfaces.

Fifty-nine (60%) of the 99 intraoral data points responded to stimulation of the teeth. Thirty (30%) responded to stimulation of the tongue, nineteen (19%) responded to stimulation of the pad just posterior to the upper incosors. Eleven (11%) responded to stimulation of the palate. In addition two data points responded to stimulation of the cheek and one responded to stimulation of the rostral throat area.

Of the 59 data points responding to stimulation of the teeth 30 (51%) responded to stimulation of the upper teeth to the exclusion of the lower teeth, 20 (34%) responded to stimulation of the lower teeth to the exclusion of the upper teeth and 9 (15%) responded to stimulation of both upper and lower teeth.

Again in the raccoon both cl and ips projections are seen in vb. Both data points which responded to stimulation of the body were from the cl side. Thirty-three (97%) of the 34 face data points included responses from the cl side and 2 (6%) included responses from the ips side. Thirty (30%) of the 99 mouth data points included responses from the cl side and 88 (89%) responded to stimulation of the ips side.

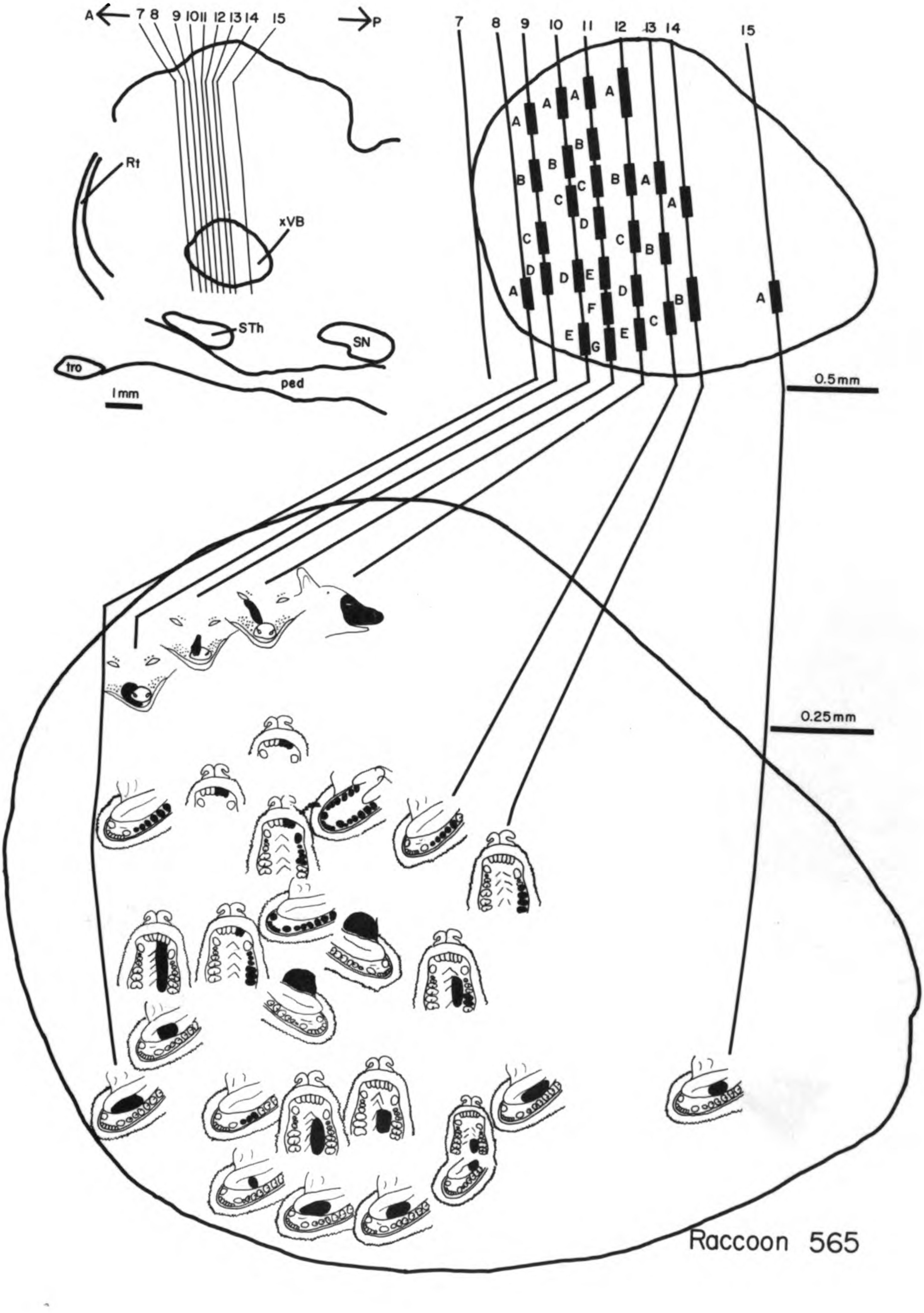
The organisation of the projections from the interior of the mouth in the raccoon is so complex that only the few tendencies which are most obvious will be noted. The cl projections are scattered among the ips projections and consist mainly of teeth projections. They are often associated with ips projections and in those cases the ips responses were generally stronger. In several instances all lower teeth, both ips and cl, responded at one data locus (see locus 12B Figure 12). The cl teeth responses were too scattered to demonstrate a clear organisational pattern. The ips responses from the teeth did not demonstrate a consistent dorsal-ventral organisational pattern within themselves but did consistently project dorsally to the other mouth components which were primarily tongue, palate, and incisor pad (Figure 12). There were too few punctures in which upper and lower teeth were represented sequentially, and these punctures showed too much variability to make a conclusion about dorsal-ventral organization. Represented below the teeth was the palate and below that either the tongue or the incisor pad. There is a tendency for the tongue to project more medially and the incisor pad more laterally. (see Figures 12 and 13).

The raccoon vb receives both cl and ips projections from the body parts. The body and face are represented almost entirely on the cl side and the mouth is represented on both the cl and ips sides with the ips projections dominant. The organization of the intraoral projections is complex and unclear except for the tendencies mentioned earlier.

Figure 12. Pattern of projections in a parasagittal row of punctures in raccoon T65.

See Table 4 for abbreviations.

See Figure 4 for explanation of the format of this figure.
Right: Section 91 is depicted. The complexity of this figure demonstrates the difficulty in defining an organization pattern of intraoral responses in the raccoon. All intraoral responses in this figure are completely ips except 12P. The most ventral projections are from the tongue and the palate.
Left: A photomicrograph of section 91 stained for myelinated fibers at the level described on the opposite page. Electrode tracks 7 and 12 are visible in this section. Magnification = 12X.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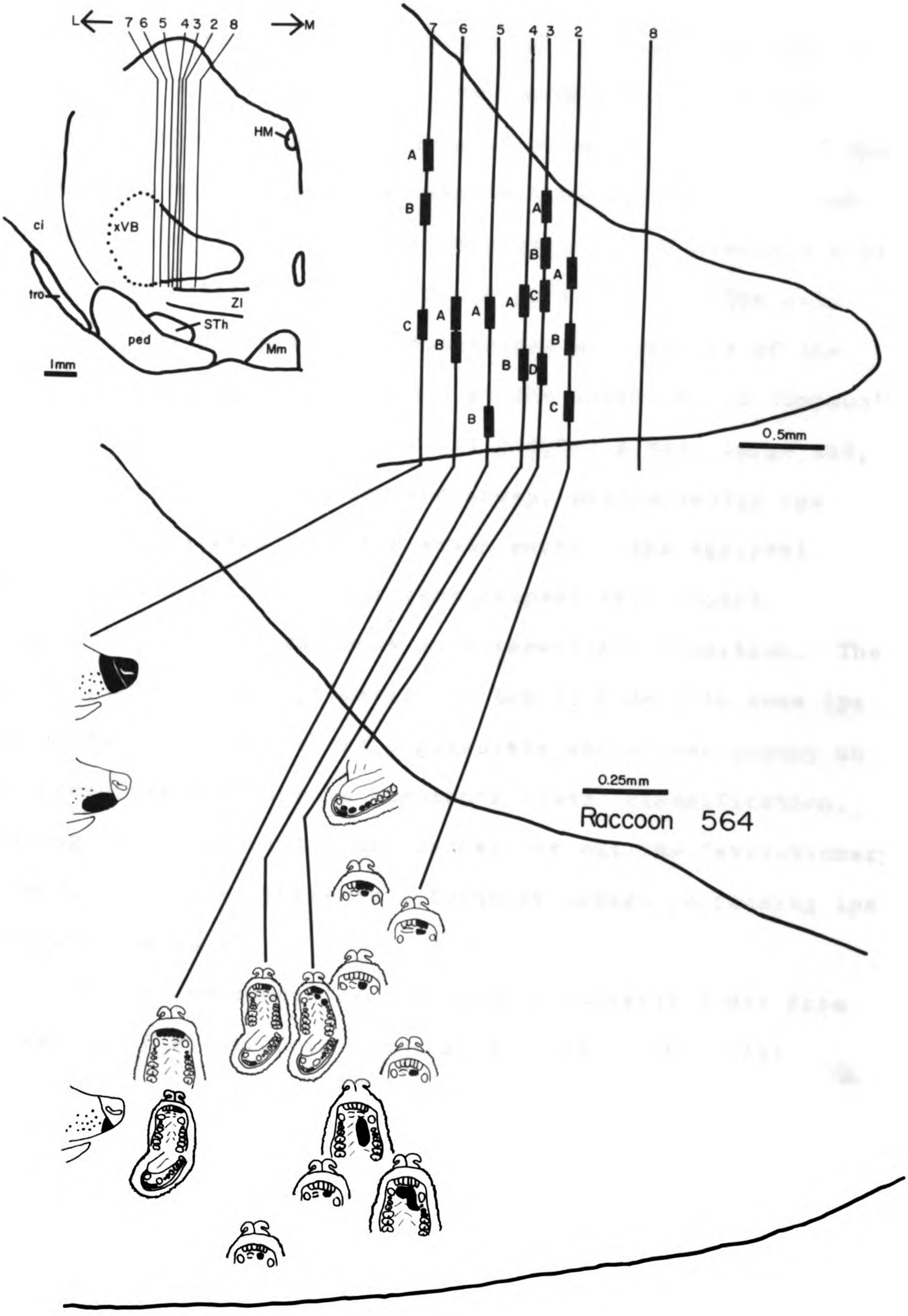
Raccoon 565

[illegible] 15. Pattern of projections in a coronal row of punctures in Raccoon [illegible].

Table 4 for abbreviations.

[illegible] Figure 4 for explanation of the format of this figure.
[illegible] 22 is bilateral. In this figure all intraoral responses [illegible] groups for [illegible] is bilateral.
[illegible]: A photomicrograph of a section [illegible] stained for cell bodies at [illegible] described on the opposite page. [illegible] tracks 2 and 3 [illegible] in this section.
[illegible] = 15X.



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Raccoon 564

DISCUSSION

The differences in character of intraoral projections (see Table 2) are systematic when examined in light of Simpson's (1945) classification of mammals (Figure 2). The opossum, a member of infraclass Metatheria, is at one end of Simpson's (1945) "evolutionary scale". It displays a cl projection pattern from the mouth parts to vb. The cat, raccoon, and sheep are all eutherians and members of the cohort Ferungulata which ranks at the other end of Simpson's (1945) classification. They all display a very large and, in the case of the raccoon and sheep, predominantly ips projection pattern from the mouth parts. The squirrel monkey and agouti who represent respectively cohort Unguiculata and Glires show an intermediate condition. The mouth parts project primarily to the cl side with some ips projections. Both cohort Unguiculata and Glires occupy an intermediate position in Simpson's (1945) classification. Moving "up the evolutionary ladder" or out the "evolutionary limb", therefore, there is a tendency toward increasing ips projections to vb.

Further evidence for the above hypothesis comes from a series of electrophysiological studies on the first somatic sensory area (SI) of the cortex. Efferent projections from vb have been shown to project to S1 (Clark and Powell, 1953, Pubols, 1968, and Welker and Johnson, 1965). It is, therefore, reasonable to infer information about the

projections to vb by examining the projections upon the cortex. Electrophysiological mapping studies of the cerebral cortex support the hypothesis that variation in the character of projections to vb is systematic.

Lende (1964) studied the echidna (*Tachyglossus aculeatus*) and found considerable head and tongue projections to the cortex which were all cl. The echidna is a member of subclass Protheria, order Monotremata (Figure 2). Lende and Sadler (1967) studied the hedgehog (*Erinaceus*) and reported a completely cl cortical representation pattern The hedgehog is a member of infraclass Eutheria, cohort Unguiculata, order Insectivora. Lende (1970) examined the tree shrew (*Tupaia*) and again found only cl projections. The tree shrew is an insectivore-like primate, cohort Unguiculata, order Primates. In their study of the spider monkey (*Ateles*) cortex Pubols and Pubols (1971) found only two loci with ips intraoral data in 420 responding punctures. The spider monkey is a member of cohort Unguiculata, order Primates. The porcupine (*Erethizon dorsatum*) was studied by Lende and Woolsey (1956) and again only cl projections were seen in SI. The porcupine is a member of cohort Glires, order Rodentia. Woolsey and Wang (1945) studied the rabbit and reported cl and ips face projections but did not report the relative proportions of each. The rabbit is a member of cohort Glires, order Lagomorpha. Adrian (1943) reported completely ips projections from the perioral surfaces in the sheep and the goat and completely cl projections in the pig and the horse. Woolsey and Fairman (1946) found both ips and cl projections in the sheep and pig. They also found ips and cl representation from the face in the dog and the cat. Pinto-Hamuy, Bromiley, and Woolsey (1956) studied the dog and reported that the palate, teeth, and lips are represented on the ips side. The sheep, goat, and pig are all members of cohort Ferungulata, order Artiodactyla. The horse is a member of cohort Ferungulata, order Perissodactyla and the cat and dog are members of cohort Ferungulata, order Carnivora.

These studies are almost completely consistent with the hypothesis put forward; i.e. more "advanced" mammalian groups show a tendency toward a higher degree of ips representation in the thalamus and cortex. Among non-eutherian mammals studied ips projections seem to be insignificant. In cohorts Unguiculata and Glires ips representation has been reported but in all cases the ips projections from the face and mouth seem to be small. Large amounts of ips representation have been reported in all ferungulates studied except the horse. In other words the variation in character of projections to the higher centers of the medial lemniscal system is consistent and systematic in light of Simpson's (1945) classification of mammals..

A second hypothesis to account for the variation seen in this and other studies is that these variations represent specializations (which are of course evolutionary changes) at levels lower than the major mammalian groups which

Simpson (1945) called cohorts. In other words if more animals from various groups were examined variations within groups may prove to be as great as variations between groups. Only further systematic studies which pay particular attention to the projections from the face and mouth will resolve this question.

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