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Virginia Commonwealth University  
School of Basic Health Sciences

This is to certify that the dissertation prepared by Wayne Thomas Shaia entitled "Relationships Among the Distribution of Terminal Fields of Sensory Afferents Projectioins to the Deep Layers of the Superior Colliculus within the Cat" has been approved by his comittee as satisfactory completion of the thesis requirement for a Master's degree in Anatomy.

[REDACTED]  
M. Alex Meredith Ph D., Director of Thesis

[REDACTED]  
Barry E. Stein, Ph D., School of Basic Health Sciences

[REDACTED]  
Robert F. Spencer Ph D., School of Basic Health Sciences

[REDACTED]  
William P. Jollie Ph D., Department Chairman

[REDACTED]  
S. Gaylen Bradley, Dean, School of Basic Health Science  
Chairman, MCV Graduate Committee

20 August 1993  
Date

**Relationships Among the Distribution of Terminal Fields of Sensory  
Afferent Projections to the Deep layers of the Superior Colliculus  
within the Cat**

**A thesis submitted in partial fulfillment of the requirements for a  
Master's degree in Anatomy at the Medical College of Virginia,  
Virginia Commonwealth University**

**BY**

**Wayne Thomas Shaia  
B.S., Virginia Polytechnic Institute and State University, 1992**

**Director: M. Alex Meredith, Ph D.  
Associate Professor, Department of Anatomy**

**Virginia Commonwealth University  
Richmond, Virginia**

**August, 1993**

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## List of Abbreviations

<b>AEA</b>	<b>Anterior Ectosylvian Auditory</b>
<b>AES</b>	<b>Anterior Ectosylvian Sulcus</b>
<b>AEV</b>	<b>Anterior Ectosylvian Visual</b>
<b>ALLS</b>	<b>Antero-Lateral Lateral Suprasylvian Sulcus</b>
<b>AMLS</b>	<b>Anterio-Medial Lateral Sulcus</b>
<b>DLS</b>	<b>Dorso-Lateral Sulcus</b>
<b>PLLS</b>	<b>Posterio-Lateral Lateral Suprasylvian Sulcus</b>
<b>PMLS</b>	<b>Posterio-Medial Lateral Sulcus</b>
<b>SAI</b>	<b>Stratum Album Profundum</b>
<b>SGI</b>	<b>Stratum Griseum Intermediale</b>
<b>SAP</b>	<b>Stratum Album Profundum</b>
<b>SGP</b>	<b>Stratum Griseum Profundum</b>
<b>SGS</b>	<b>Stratum Griseum Superficiale</b>
<b>SO</b>	<b>Stratum Opticum</b>
<b>SZ</b>	<b>Stratum Zonale</b>
<b>SIV</b>	<b>Somatosensory Area Four</b>
<b>SV</b>	<b>Somatosensory Area Five</b>
<b>TRSNs</b>	<b>Tecto-reticulo-spinal Neurons</b>



## **Introduction**

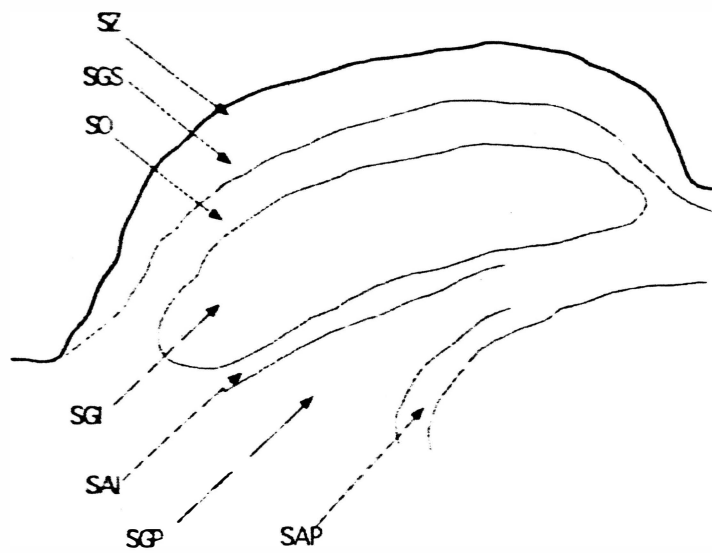
While it is well known that the different sensory modalities are primarily represented at separate locations within the central nervous system, there are numerous sites in which information from the different sensory modalities converge. Perhaps the best known structure where inputs from different sensory modalities converge is the superior colliculus. Here, not only are visual, auditory and somatosensory inputs present, but they also form organized representations of auditory and visual space as well a map of the body surface. In addition, neurons that receive inputs from more than one sensory modality (i.e. multisensory) are found here in abundance. Although a great deal is known regarding the physiological properties of these multisensory neurons and how these characteristics apply to multisensory neurons elsewhere in the brain, little is known regarding the anatomical basis for multisensory convergence and integration. Therefore, the present

study is focused on the following problem: How does the organization of the inputs from different sensory modalities to the deep layers of the superior colliculus relate to the multisensory nature of its constituent neurons?

### **Anatomical Structure:**

The superior colliculus is a laminated structure found on the dorsal surface of the mammalian midbrain. It is physiologically divided into two major regions: superficial layers (Laminae I-III) and deep layers (Laminae IV-VII). As seen in Figure 1, the superficial layers consist of the Stratum Zonale (SZ), Stratum Griseum Superficiale (SGS), and the Stratum Opticum (SO). These most dorsal layers primarily receive visual afferents and therefore contain multitudes of unimodal, visual neurons. Neurons in these layers rarely receive inputs from more than one modality and, therefore, the superficial layers will not be discussed further.

The deep layers of the superior colliculus consist of the Stratum Griseum Intermediale (SGI), Stratum Album Intermediale (SAI), Stratum Griseum Profundum (SGP), and Stratum Album Profundum



**FIGURE 1:** THIS FIGURE IS A CROSS-SECTION OF THE SUPERIOR COLLICULUS WITH THE DIFFERENT LAMINAE LABELED. THE SUPERFICIAL LAMINAE SZ, SGS, SO AND THE DEEP LAMINAE SGI, SAI, SGP, AND SAP.

(SAP). The SGI is also subdivided into 3 sublaminae that are arranged dorso-ventrally: upper, middle, and lower, as illustrated in Figure 2. The neurons that are contained within these layers range in size from 8 to 60  $\mu\text{m}$  in diameter (Norita '80) and have dendritic trees that can extend as far as 1.2 to 1.4 mm (Behan et al '88, Moschovakis and Karabelas '85). Thus, it is possible for dendrites of these neurons to cross laminar boundaries and even to extend from the deep layers into superficial layers. (Mooney et al. '84, Moschovakis and Karabelas '85, Moschovakis et al.'88).

The deep layers contain a mixture of multimodal and unimodal neurons. The multimodal neurons are neurons whose response is influenced by inputs from two or more sensory modalities. Of the total number of neurons present within the deeper layers, 55% are multisensory: 30% respond to both visual and auditory stimuli, while only 14% of these neurons activated by both visual and somatosensory. Even fewer neurons, 8%, were activated by all three of these modalities while only 3% were activated by auditory and somatosensory stimuli (Stein and Meredith '93).

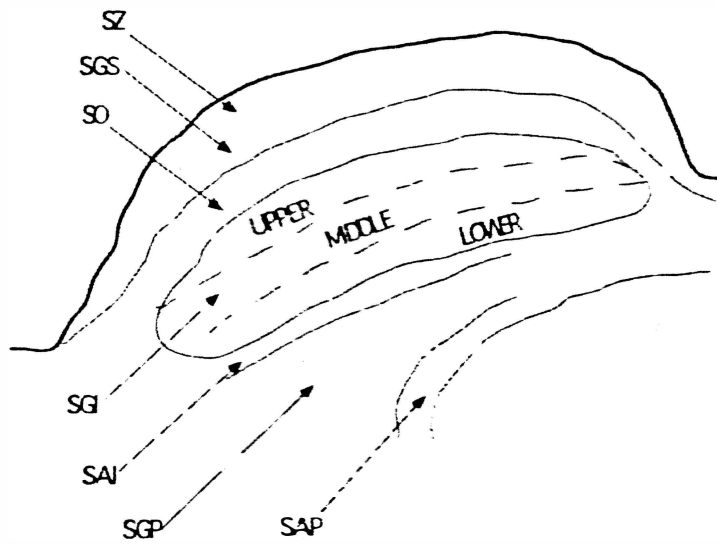


FIGURE 2: A CROSS-SECTION OF THE SUPERIOR COLLICULUS THROUGH THE ROSTRAL MOST PART OF THE CAUDAL ONE-THIRD SHOWING THE LAMINAE AND THE SUBLAMINAE OF THE SGI.

### **Afferents:**

These visual, auditory and/or somatosensory responses are a result of the afferent pathways that converge upon the deep layers. For each modality that targets the deep layers, inputs ascend primarily from brainstem or spinal cord levels as well as descend from the neocortex. These afferents are not homogeneously arranged in the deep layers, nor are they random. Instead, in cross-sectional views, each set of afferent terminations exhibits a patch-like clustering within specific laminae while also avoiding other laminae. These patch-like terminal patterns occupy specific domains within the deep layers that are consistent for a given projection. There are many known projections to the deep layers of which many are described in great detail while others are not. The terminations of some afferent pathways are robust and form dense patches, while others are much more sparse. Those pathways with the most robust projections are described below.

### **Visual Afferents:**

The **AMLS** cortex is described by Harting et al. 1992 as projecting primarily within the SGI layer in the form of irregular clusters. The **PMLS** cortex, which also has substantial inputs to the superficial layers, also has terminations found within the upper sublamina of the SGI layer (Harting et al. '92). The projections from **ALLS** cortex form two tiers of terminations within the deep layers. One tier found in the dorsal sublamina of the SGI and the other tier is found in the ventral sublamina of the SGI, as well as into the SAI and SGP layers (Harting et al. '92). The **PLLS** cortex has terminations that primarily are focused upon the lower portion of the superficial layers with major extensions into the dorsal and middle sublaminae of the SGI layer (Harting et al. '92). The **DLS** cortex also follows this two-tiered fashion, one dorsal and one ventral within the SGI layer, but avoids the middle sublamina of the SGI layer (Harting et al. '92). The dorsal and ventral sublaminae of the SGI also contain many axon terminals originating from the AEV. The AEV projects into the SAI and SGP layers (Harting et al. '92). Others visual areas that project to the deep layers, although sparsely include: Area 7, Splenial Sulcus, Anterior Cingulate Gyrus (Harting et al. '92).

### **Auditory Afferents:**

The auditory region of the AES cortex, **AEA**, projects to the SGI layer. These terminations form two tiers along the ventral and dorsal sublamina of lamina IV with some extensions into the SGP layer (Meredith and Clemo '89). The **Periauditory Belt**, which contains both visual and auditory neurons, has terminations within the ventral region of the SGI layer with extensions to the SAI and SGP layers (Harting et al. '92). The **inferior colliculus** also projects to the superior colliculus (Kudo and Niimi '80), but the laminar pattern of afferent terminations has not been described.

### **Somatosensory Afferents:**

Somatosensory structures including the **Dorsal Column Nuclei** and the **Spinal Trigeminal Nucleus** and the cortical representations **SIV** and **SV** all send projections to the superior colliculus that terminate in restricted regions of the deep layers. The **Dorsal Column Nuclei** and the **Spinal Trigeminal Nucleus** each have terminations within the middle sublamina of the SGI as well as a



wedged shaped termination zone within the SGP (Wieberg and Blomqvist '84, Harting and Van Lieshout '91). Likewise, the somatosensory cortical areas **SIV** (in the anterior ectosylvian sulcus) and **SV** (in the rostral suprasylvian sulcus) each project specifically to the middle sublamina of the SGI layer as well as to the SGP, with little or no terminal labelling found in intervening tissue (Mchaffie et al. '88, Harting et al. '92).

**Other Afferents:**

Inputs from numerous other areas, even those not directly involved in the processing of visual, auditory, and somatosensory information are known to reach the deep layers of the superior colliculus. Motor afferents arrive from the Lateral and Medial Frontal Eye Fields, Area 4 (Harting et al. '92), Substantia Nigra (Harting et al. '88), Pedunculo-pontine Tegmental Nucleus (Harting and Van Lieshout '92), Nucleus Posterior Commissure (Huerta and Harting '82), Deep Cerebellar Nuclei (Kawamura et al '82), Zona Incerta (Ficalora and Mize '89), Nucleus Prepositus Hypoglossi and Intercalatus (Steichson et al. '85), and the Superficial Layers of the Ipsilateral Superior Colliculus (Behan and Appel '92). The following

areas also project to the deep layers: The Reticular Nucleus of the Thalamus, Ventral Lateral Geniculate Nucleus, Contralateral superior colliculus, Mesencephalic Nucleus Reticular Formation, Perilemniscal Area, Pericentral Nucleus of the Inferior Colliculus, Locus Ceruleus, Dorsal Raphe, Lateral Parabrachial Nucleus, Pontine Reticular Nuclei, Ventral Nucleus of the Lateral Lemniscus, Dorsomedial Preolivary Nucleus, Medullary Reticular formation, Lateral Cervical Nuclei, Layer IV of the Spinal Cord levels C<sub>1</sub>-L<sub>5</sub>. (Edwards et al. '79).

**Modular Organization of Afferent Inputs:**

Each set of afferents to the deep superior colliculus terminates in a distinctive pattern and this patterning of different terminal fields has led to the idea that this structure exhibits a compartmental, or modular, organization. Each afferent pathway terminates within restricted areas or modules, and different afferent pathways often occupy different modules. This modular organization is most evident within the SGI and has been extensively described by Huerta and Harting (1984). This modular organization has been thought to play a role in bringing functionally related

inputs into close proximity with one another and to exclude those which are unrelated. This hypothesis has received a great deal of support, especially with the observations that motor related inputs from the frontal eye fields and substantia nigra terminate in zones close to or in register with one another as well as with the output neurons that influence orienting behavior, while the sensory related inputs from SIV were excluded from these same zones (Illing and Graybiel '85, '86). Thus, while this modular theory appears to provide the morphological basis for this sensorimotor role of the superior colliculus, it is not known whether modules are formed by afferents from different modalities and whether these modules are arranged in a manner that might contribute to the generation of the multisensory properties so characteristic of many deep layer neurons.

### **The Methods:**

To examine whether the projections of different sensory modalities to the superior colliculus overlap one another, data was collected from numerous published accounts that described inputs from individual cortical and subcortical regions. The data was usually in the form of micrographs, although some drawings of tissue sections were also utilized. Each piece of data employed was an illustration of the cat superior colliculus representing the rostral most part of the caudal one-third of this midbrain structure. This particular level of section in the superior colliculus was chosen because terminations from a majority of afferent sites appeared to be densest here as well as to control for variations due to topographical representations of sensory space within this structure. The data was first entered into a Macintosh 153 computer using the DeskScan program. Under the dynamics of this program, the images were manipulated to represent a section through the left superior colliculus. Each image was then transferred to another program called Canvas 3.0.6 in which the

edges and laminae were traced to form a computer drawing of the cross-section. The patch-like terminations were encircled and traced in relation to the sublaminae they covered and this area was denoted with shading (line or dot pattern). Next, to help make comparisons between different tissue sections from different cases easier and more consistent each cross-section was transferred to a standard template. Figure 2 shows the template that was used and it represents a cross-section through the rostral most part of the caudal one-third of the superior colliculus (redrawn from Harting et al. 1992). In order to correlate the computer drawings with the template, the cross-sections were enlarged and/or rotated (never more than 5° degrees in any direction and only if necessary) so that their dorsal edges and midlines were aligned with those of the template. Often this was enough to bring the various laminae into alignment. When alignment did not occur, a new section of tissue was chosen from the same case and re-scanned, or the laminae that contained the terminations were given priority for alignment with the template over the edges of the sections as well as those laminae that contained no terminations. Throughout this process, the relationships of afferent terminations to the different lamina and sublamina were steadfastly maintained. This transformed data was

now in a standardized format that represented individual cases that identified inputs from the somatosensory, visual and auditory modalities as shown in figures 3, 4, and 5 respectively.

The last step was to overlap the different combinations of these standardized sections. This procedure allowed for the direct visual comparison of the distribution of inputs from different sources. The first comparisons were those of inputs that originated from areas containing the same modality. Next, inputs from regions representing different modalities were compared.

It is acknowledged that these procedures assume that a number of uncontrollable variables remain constant. For example, no attempt was made to compensate for differences among the tracers that were used, the amounts of tracer injected, the time for the transportation of the tracer, or even for minor variations in the plane of sectioning. However, variations in the size of the different sections were dealt with by aligning the medial and lateral borders of the tissue as well as by approximating the registry of the intermediate laminae of overlapped sections.

## Visual Terminations

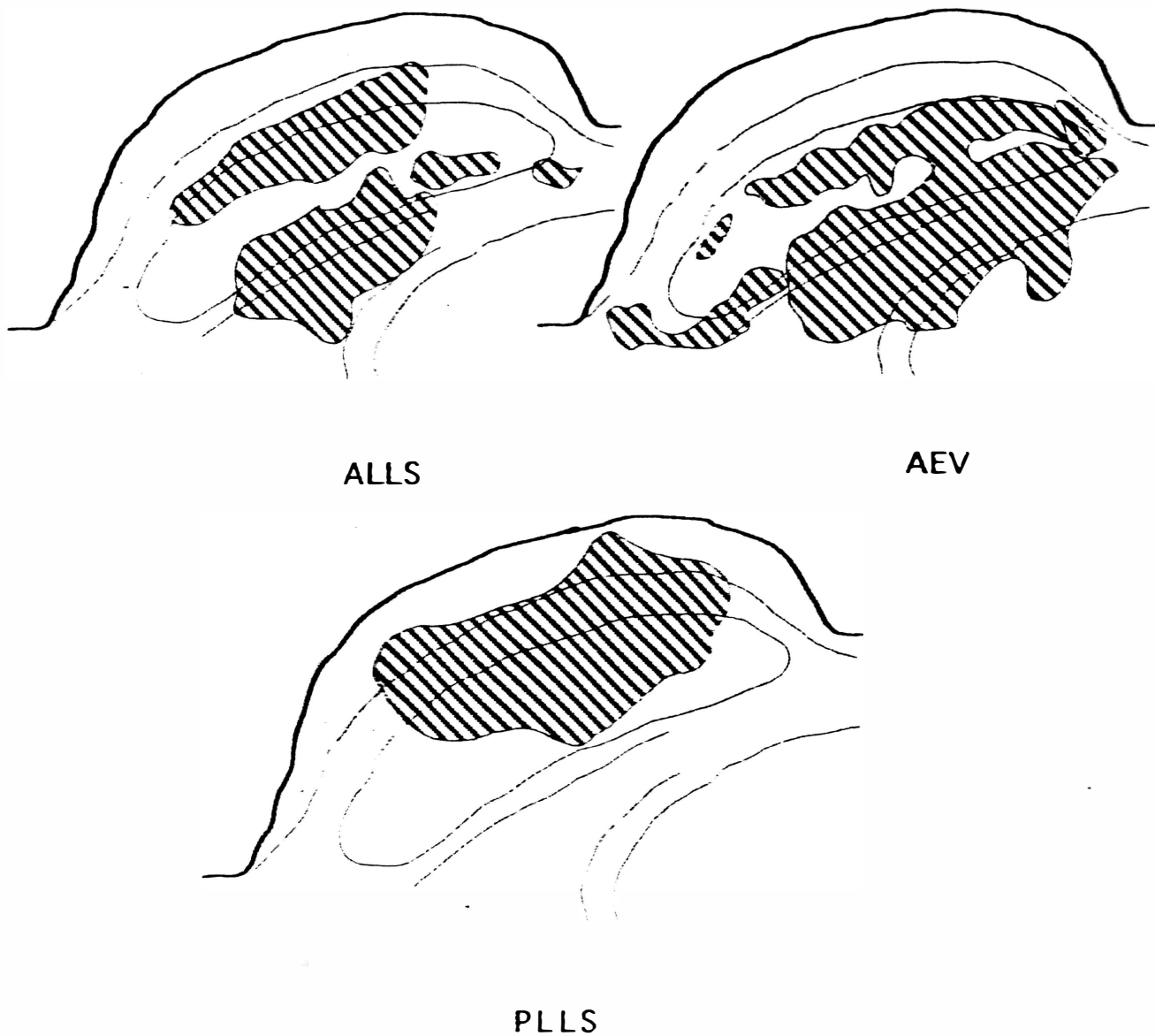


FIGURE 4: CROSS-SECTION OF THE SUPERIOR COLLICULUS WITH THE VISUAL TERMINATIONS ORIGINATING FROM THE ALLS, AEV, AND PLLS CORTICAL AREAS, FROM HARTING ET AL. '92.

## SOMATOSENSORY TERMINATIONS

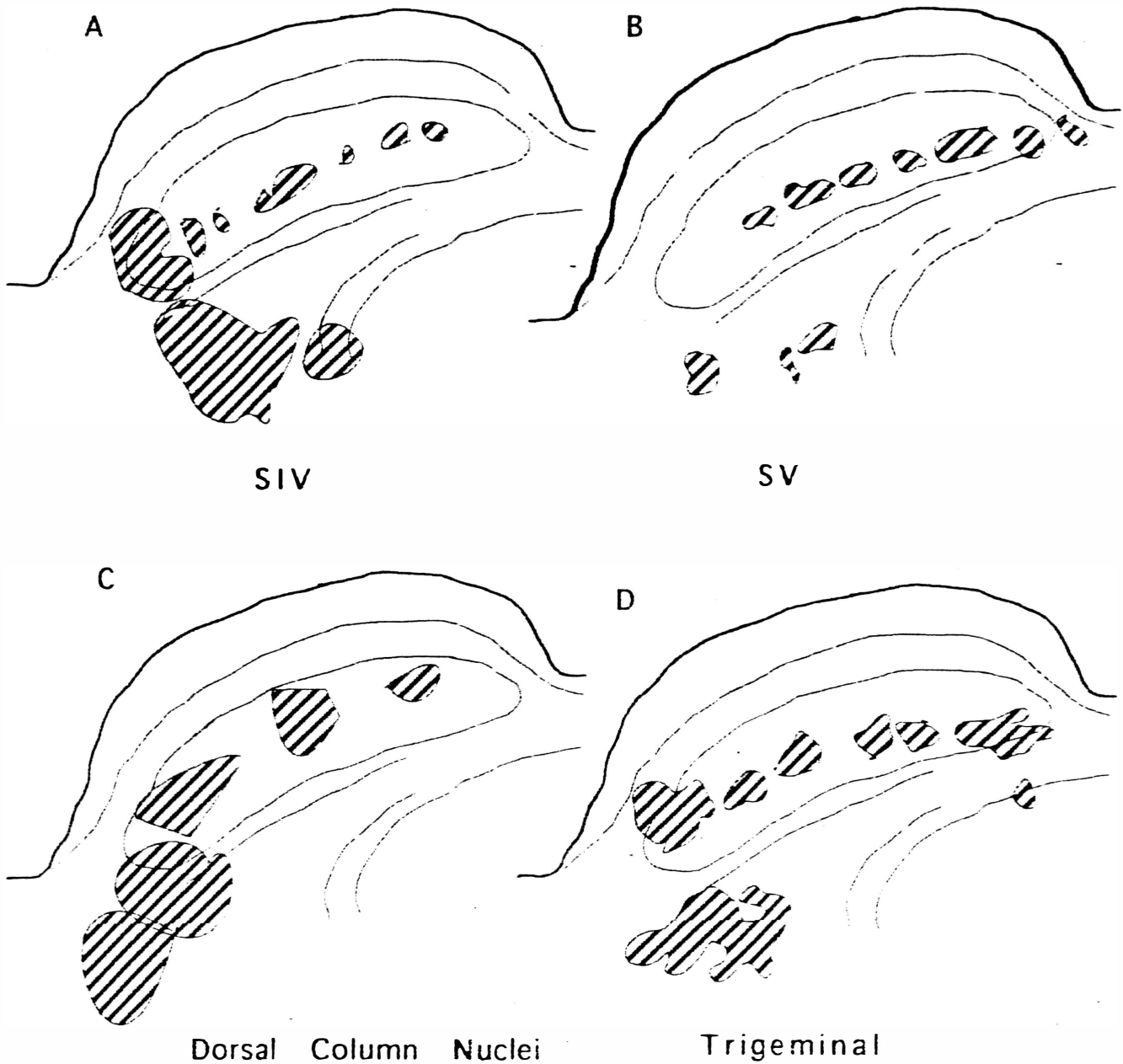


FIGURE 3: TERMINAL PATCHES OR ZONES FROM INPUTS ARISING FROM SIV (A: FROM MCHAFFIE ET AL '92) SV (B: FROM HARTING ET AL. '92) DORSAL COLUMN NUCLEI (C: FROM WEBER ET AL. '88) TRIGEMINAL NUCLEUS (D: FROM MCHAFFIE ET AL '86).



## Auditory Termination

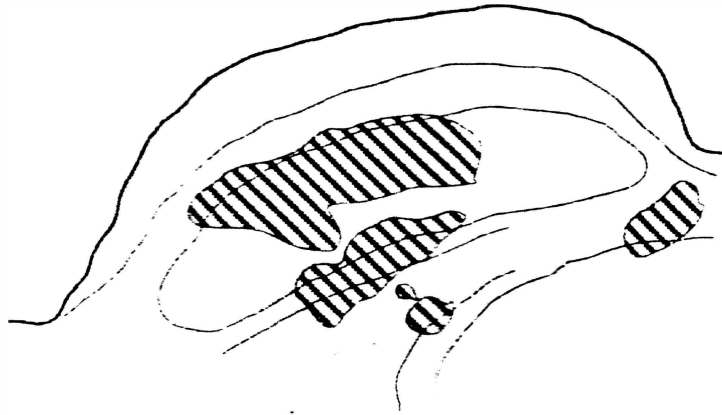


FIGURE 5: CROSS-SECTION OF THE SUPERIOR COLICULUS WITH THE DISTRIBUTION OF TERMINAL FIELDS ORIGINATING FROM THE AEA CORTEX, FROM MEREDITH AND CLEMO '89.

## *The Results*

### *Somatosensory:*

The terminal distributions of inputs within the superior colliculus from Dorsal Column Nuclei, Trigeminal, and SIV and SV are remarkably similar. Patches of terminals from each of these areas are arranged in two tiers within the deep layers of the superior colliculus. The most dorsal tier is located within the middle sublamina of the SGI, while the more ventral tier is found within the SGP, as shown in Figure 6. This pattern is consistent among the different afferent somatosensory areas examined and therefore the terminal fields from each of these regions not only appear to overlap extensively, but also are in register with one another. Furthermore, substantial portions of the deep lamina that are devoid of inputs from one somatosensory region also lack afferent terminals from other tectopetal somatosensory regions.

## SOMATOSENSORY INPUTS

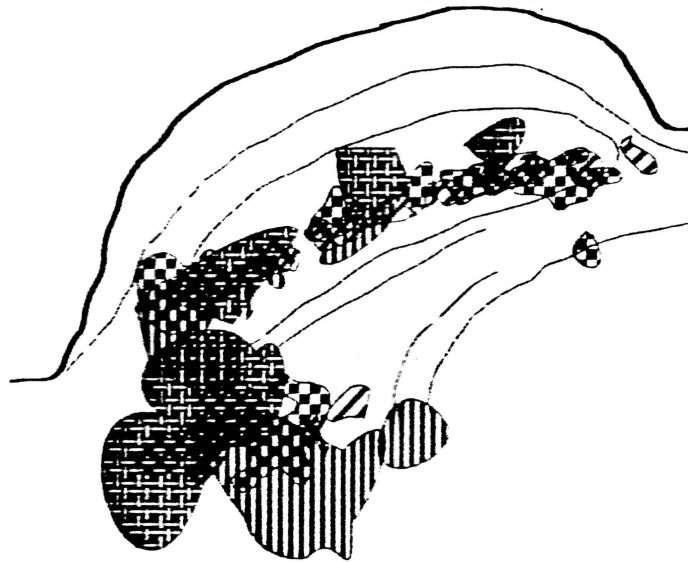


FIGURE 6: A CROSS-SECTION OF A SUPERIOR COLLICULUS WITH THE TERMINATIONS OF SIV, SV, TRIGEMINAL AND DORSAL COLUMN NUCLEI OVERLAPPED. REGISTRY OF THESE INPUTS IS SEEN PREDOMINATELY WITHIN THE MIDDLE SUBLAMINA OF THE SGI AND SGP.

**Visual:**

The terminal distributions of inputs from visual cortex upon the deep layers of the superior colliculus were similar to one another in arrangement and were found, for the most part, to be in a two tier fashion. In the upper sublaminae of the SGI layer, projections from all three visual cortices ALLS, PLLS, and AEV overlap, as illustrated in Figure 7. Within the more ventral tier, found within the SAI and SGP, only terminal fields originating from ALLS and AEV cortices overlap. The PLLS has its major terminations in the SGS, SO and the upper and middle sublaminae of the SGI and is excluded, for the most part, from layers deeper than the SGI. The middle sublaminae of the SGI is void of overlap between inputs from these visual cortices.

**Auditory:**

The distribution of axon terminals within the superior colliculus that originated from the auditory field in the Anterior Ectosylvian Sulcus (AEA) was also examined. Inputs from this cortical region displayed a two-tiered design within the deep layers of the superior

## VISUAL INPUTS

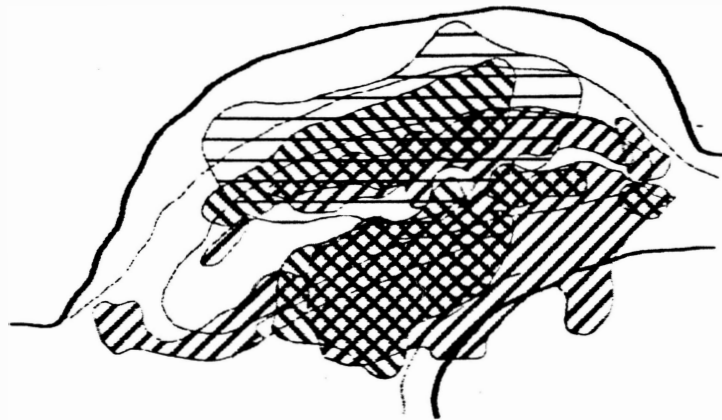


FIGURE 7: A CROSS-SECTION OF A SUPERIOR COLLICULUS SHOWING THE VISUAL TERMINATIONS FROM THE AEV, PLLS, ALLS CORTICES. PROJECTIONS FROM THE AEV AND ALLS OVERLAP IN THE UPPER AND LOWER SUBLAMINAE OF THE SGI. THOSE FROM THE PLLS OVERLAP THE OTHER VISUAL AREAS ONLY WITHIN THE UPPER SUBLAMINA OF THE SGI.

colliculus. As seen in Figure 5, one tier of terminal patches is confined to the upper portion of the SGI and the other is restricted to the lower portion of the SGI/SAI layers. Since there is lack of reliable anatomical information regarding inputs from other auditory regions upon the superior colliculus, comparisons of terminal field distributions from different auditory regions could not be made.

#### **Auditory/Visual Comparison:**

The distribution of terminal fields originating from auditory and visual structures generally displayed a high degree of correlation within the deep layers of the superior colliculus. Since modalities have terminations that are focused upon the same lamina or sublaminae.

#### **AEA/ALLS**

Both the auditory AEA and visual ALLS project primarily to the lower SO and upper SGI as well as to the lower sublaminae of the SGI with extensions into the SAI and SGP. Thus, the extensive degree

of overlap among the terminals within the superior colliculus from these different cortical regions, illustrated in Figure 8, is not surprising. Terminal patches of axons arising from AEA straddle or completely overlap patches of terminations arising from ALLS cortex in the upper sublamina of the SGI as well as in the lower sublamina of the SGI-SAI/SGP border. In a similar manner, projections from the AEA and ALLS spare the middle sublamina of the SGI as well as the SAP and permit little overlap of afferent terminals in these regions. Therefore, given that afferents from these different cortices share as well as spare similar regions of the superior colliculus, these terminations appear to be in register with one another.

AEA/PLLS:

Inputs from the auditory AEA and the visual PLLS have terminations that overlap, but this is confined to the upper sublamina of the SGI. In contrast, as depicted in Figure 9, the AEA terminations found within the lower sublamina of the SGI and within the SAI and SGP

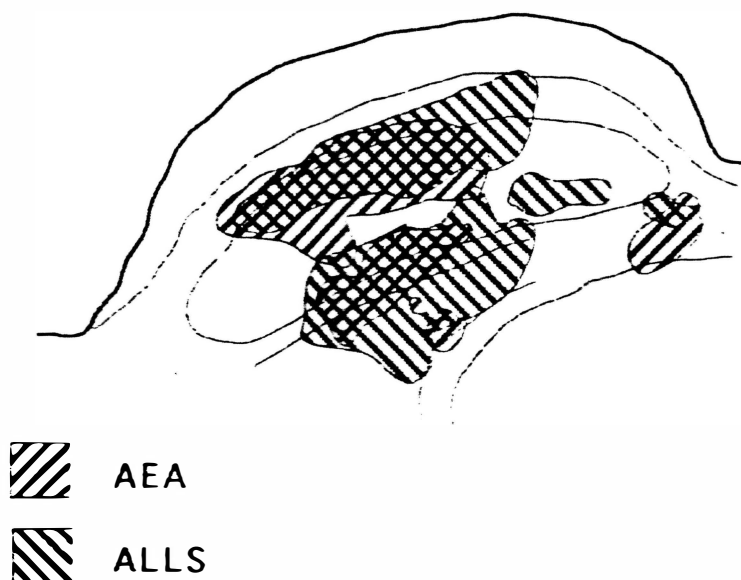


FIGURE 8: A CROSS-SECTION OF THE SUPERIOR COLLICULUS WITH THE DISTRIBUTION OF TERMINAL FIELDS FROM AUDITORY REGION AEA AND THE VISUAL REGION ALLS. OVERLAP IS SEEN WITHIN THE UPPER AND LOWER SUBLAMINAE OF THE SGI, WITH SOME EXTENSIONS INTO THE SGP.

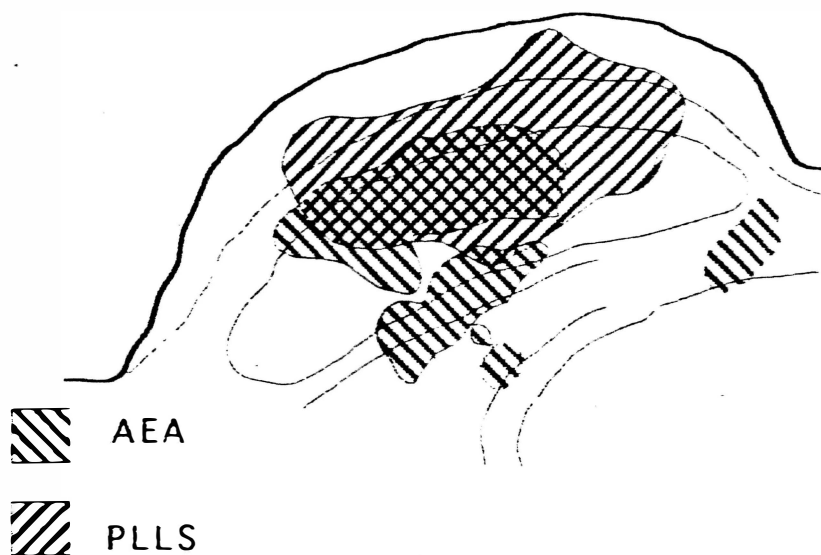


FIGURE 9: A CROSS-SECTION OF A SUPERIOR COLLICULUS WITH THE DISTRIBUTION OF TERMINAL FIELDS OF INPUTS ORIGINATING FROM THE AUDITORY CORTEX, AEA, AND THE VISUAL CORTEX PLLS. OVERLAP IS SEEN PRIMARILY WITHIN THE UPPER SUBLAMINA OF THE SGI.



remain, for the most part, void of any overlap from terminations arising from PLLS cortex.

**AEV/AEA:**

Visual afferents originating from AEV cortex and auditory afferents originating from AEA have zones of termination in common, as seen in Figure 10, in the upper SGI sublamina and in the lower sublamina of the SGI with extensions reaching into the SAI and upper SGP. In contrast, their few terminations within the middle sublamina of the SGI did not overlap one another.

**Somatosensory/Visual Comparison:**

Since the terminations within the SGI from all somatosensory structures examined are primarily confined to the middle sublaminae of that layer, and the inputs from the visual cortices examined are predominately found within the upper and lower sublaminae of that layer, the overlap within the superior colliculus between the terminations of these two modalities is minimal. Given

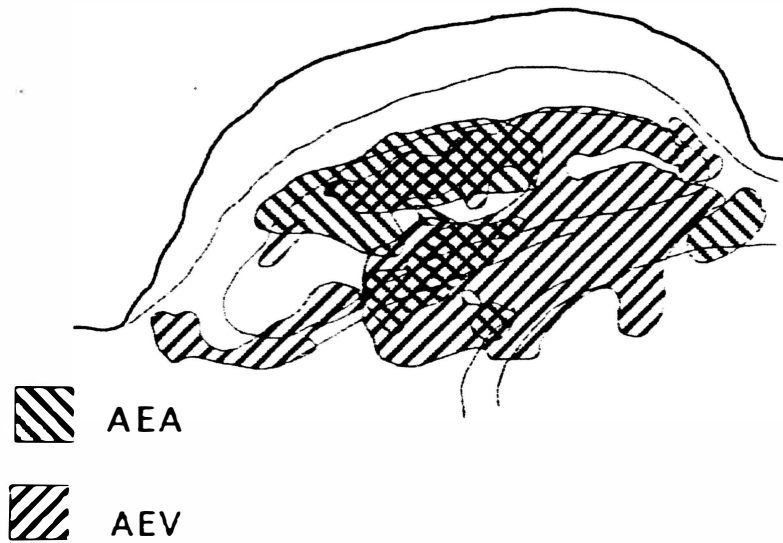


FIGURE 10: A CROSS-SECTION OF A SUPERIOR COLLICULUS WITH THE DISTRIBUTION OF TERMINAL FIELDS OF INPUTS ORIGINATING FROM THE AUDITORY CORTEX, AEA, AND THE VISUAL CORTEX, AEV. OVERLAP IS SEEN WITHIN THE UPPER AND LOWER SUBLAMINAE OF THE SGI, WITH SOME EXTENSIONS INTO THE SAI AND SGP.

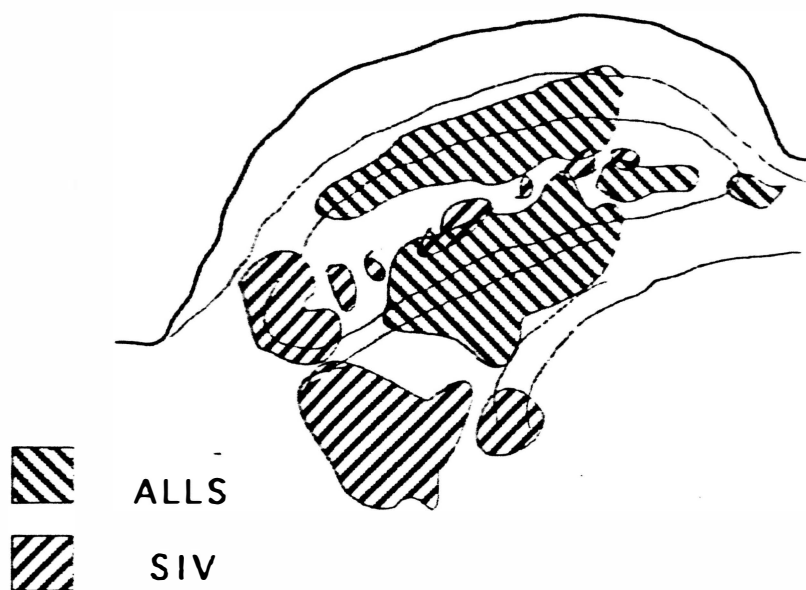
the similarity of the different somatosensory projections to the superior colliculus, inputs from SIV cortex are used here as representative of the entire group.

SIV/ALLS:

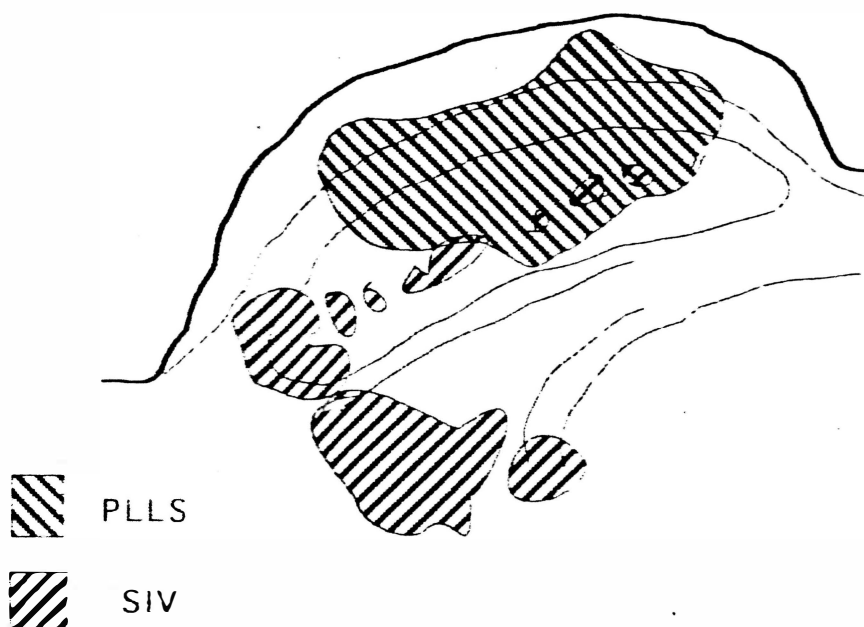
As depicted in Figure 11, inputs from visual ALLS cortex remained segregated from inputs originating from somatosensory SIV cortex. ALLS lacks projections within the middle sublamina of the SGI where most of the SIV cortical terminations are found. The ALLS does have projections within the SAI and SGP that somatosensory regions as SIV does, but these terminations do not overlap one another. Thus, the distribution of terminal fields from these two regions are not only out of register with one another, but they also occupy mutually exclusive domains within the superior colliculus.

SIV/PLLS:

Similarly, the terminations of inputs originating from SIV and PLLS cortices are found, for the most part, in separate sublaminae of the superior colliculus. As seen in Figure 12, the visual inputs from the



**FIGURE 11:** A CROSS-SECTION OF A SUPERIOR COLICULUS WITH THE PROJECTIONS ORIGINATING FROM ALLS AND SIV REGIONS. THE TERMINAL FIELDS FROM THESE TWO REGIONS STAY, FOR THE MOST PART, SECLUDED FROM ONE ANOTHER.



**FIGURE 12:** A CROSS-SECTION OF A SUPERIOR COLICULUS WITH THE PROJECTIONS FROM VISUAL AREA PLLS, AND SOMATOSENSORY AREA SIV. OVERLAP BETWEEN THE TERMINAL FIELDS BETWEEN THESE TWO REGIONS IS SPARSE AND RESTRICTED TO THE MIDDLE SUBLAMINA OF THE SGI.

PLLS cortex result in terminal fields that are confined to the SGS and SGI layers while SIV has terminations that are confined primarily to the middle sublaminae of the SGI with some extensions into the SAI and SAP layers. The terminations from either region, for the most part, display no overlap and therefore are not in register with one another.

SIV/AEV:

Again, the cortical terminations found within the deep layers from these two regions are located mostly in different sublaminae. As seen in Figure 13, the projections from the visual cortex AEV within the SGI are remote from those originating from the SIV cortex. All other tectopetal terminations arising from either of these cortical PLLS cortex result in terminal fields that are confined to the SGS and SGI layers while SIV has SGI terminations that are confined to the middle sublaminae of the SGI. Although the SIV region projects to other collicular layers such as SAI and SGP; no prominent overlap is demonstrated between afferent terminations from either cortical region other than those found within the middle sublaminae of the

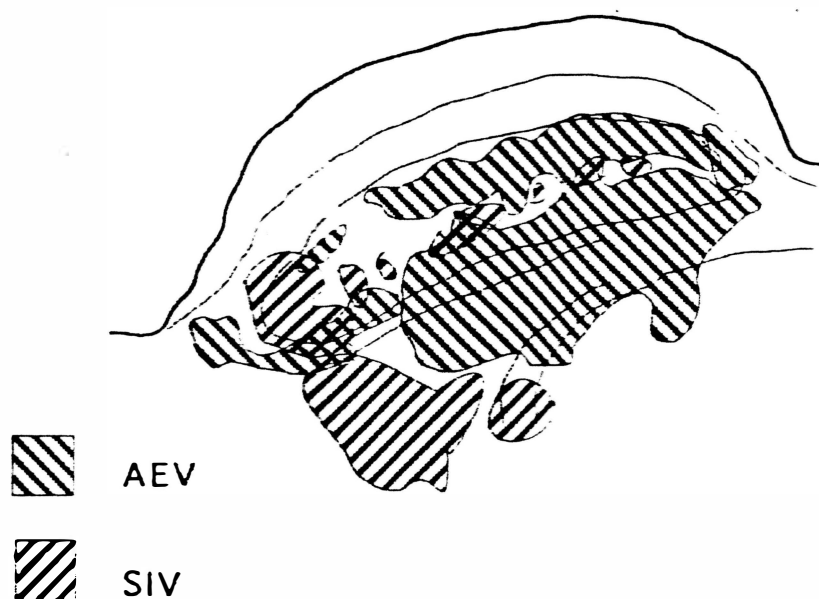


FIGURE 13: A CROSS-SECTION OF A SUPERIOR COLLICULUS WITH THE PROJECTIONS FROM THE VISUAL AREA, AEV, AND THE SOMATOSENSORY AREA SIV. OVERLAP BETWEEN THESE TWO REGIONS IS MINIMAL.

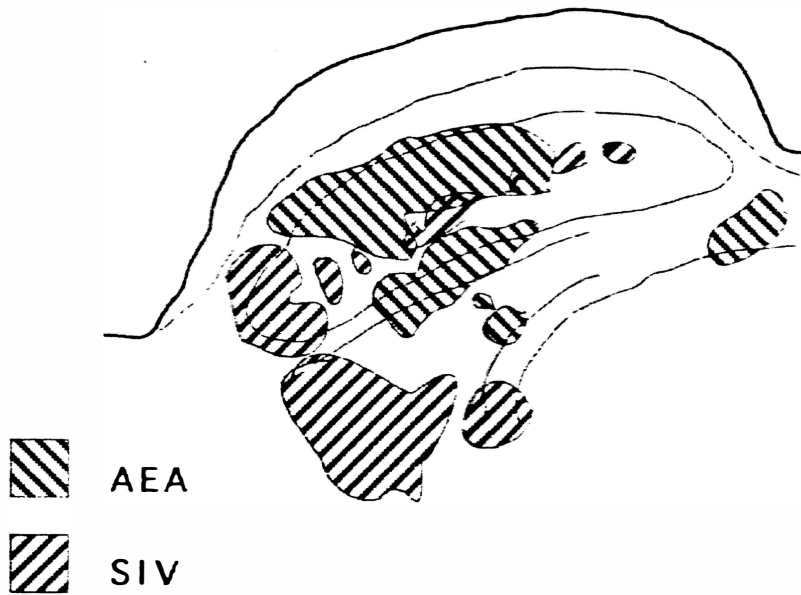
SGL. These regions have terminal fields that do not overlap substantially and are not in register with one another. All other terminations arising from either of these cortical areas that project to deeper layers of the superior colliculus, also exhibit no overlap.

### **Somatosensory/Auditory Comparison:**

Given that visual-auditory projections reveal a great deal of overlap and visual-somatosensory projections do not, little registry between the auditory-somatosensory projection was expected or observed.

### SIV/AEA:

Somatosensory inputs from the SIV cortex and auditory inputs from the AEA cortex have terminal fields that are, almost exclusively, sequestered from each other. As depicted in Figure 14, SIV primarily projects to the middle sublamina of the SGL layer and the SGP. In contrast, the terminal fields of inputs originating from AEA, are located primarily in the upper and lower sublaminae of the SGL. The AEA also has terminal fields within other layers of the superior



**FIGURE 14:** A CROSS-SECTION OF A SUPERIOR COLLICULUS WITH THE PROJECTIONS ORIGINATING FROM THE AUDITORY REGION, AEA, AND THE SOMATOSENSORY REGION SIV. OVERLAP BETWEEN THE INPUTS FROM THESE TWO REGIONS IS SPARSE.



colliculus, but none of which overlap with terminal fields of inputs arising from the SIV cortex. Given the similarity of afferent projections from all somatosensory structures, there was also little overlap among AEA projections and those from SV, Trigeminal and the Dorsal Column Nuclei (not pictured).

### **The Conclusions**

An enormous amount of attention has been directed toward understanding the organization of the deep layers of the superior colliculus and how its modular arrangement may contribute to the functional role of this structure (Huerta and Harting '84). However, to date, only a small number of modules have been assigned functional roles (Huerta and Harting '84, Illing and Graybiel '85, '86). For example, the SIV cortical region terminates only within acetylcholinesterase poor zones within the middle sublamina of the SGI layer (Illing and Graybiel '86) while frontotectal and nigraltectal projections terminate in acetylcholinesterase rich zones within upper and lower sublaminae of the SGI (Illing and Graybiel '85). Since somatosensory inputs (SIV) project to different domains than the motor inputs (frontotectals and nigraltectal), the idea of a modular organization of the deep layers was supported. Furthermore, this and other data suggests that the SGI layer is constructed of multiple and distinct unimodal compartments, each

containing the terminal fields from different tectopetal projections. However this expectation is not supported by the present observations, since the terminal fields of visual and auditory inputs are rather broad and extensively overlap one another. Given that these inputs cover broad areas of the deep layers as sheets rather than patches, it is difficult to consider them as compartmentalized in the narrowest sense. Furthermore, these different inputs do not occupy mutually exclusive domains but, instead, show a remarkable degree of register with one another. Thus, it appears that, for the upper and lower sublaminae of the SGI as well as for regions of the SAI and SGP, there is a mixing of the inputs from these different sensory modalities.

Physiological studies have indicated that the sensory activity of the deep layer neurons is influenced, if not dependent, on the inputs from unimodal regions of cortex. Reversible deactivation (by cooling) of the PLLS (visual), SIV (somatosensory), or AEA (auditory) had dramatic effects on the responsiveness of the deep layer neurons to visual, somatosensory and auditory stimuli respectively (Ogasawara et al. '84, Clemo and Stein '86, Meredith and Ciemo '89). Not only are many multisensory neurons dependent on these unimodal sensory cortices for their activity, but it is convergence of

monosynaptic inputs from these different regions that appears to give these deep layers neurons their multisensory properties (Wallace et al. '93). Ultimately, deactivation of some of these areas had profound effects on the integrated responses to multisensory stimuli (Wallace et al '92) for many deep layer neurons. Given this dependence of multisensory neurons on inputs from the different corticotectal sources, the registry of terminal fields of inputs from different sensory modalities that produced this synergistic effect should have been predicted.

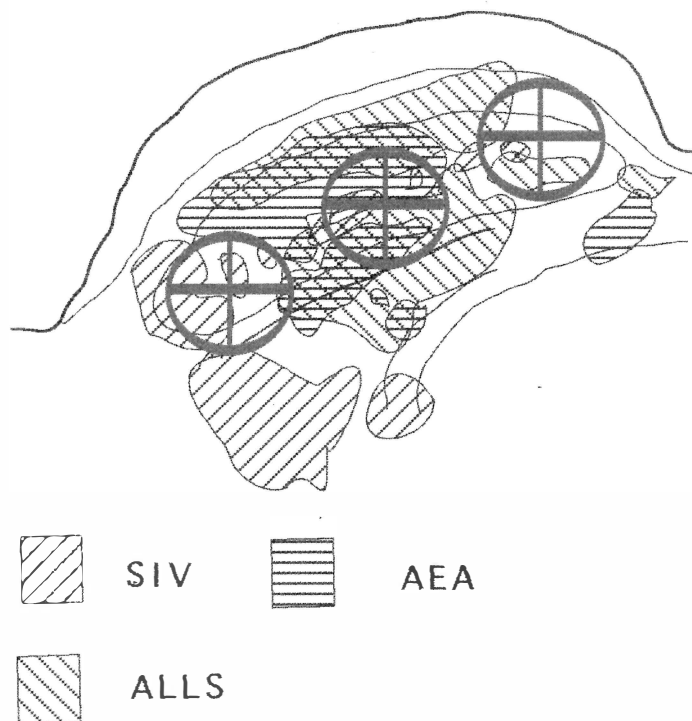
The present data shows that there is substantial overlap within the deep layers between projections from the visual and auditory modalities. Since the most abundant (69%) type of multisensory neurons is one which receives visual and auditory inputs (Stein and Meredith 93), this configuration of visual and auditory inputs into common zones no doubt plays a significant role in the production and maintenance of this particular pattern of convergence. Conversely, the least abundant type of multisensory neuron is the auditory-somatosensory type (5.4%) (Stein and Meredith 93), and the present data shows that the inputs from these modalities overlap the least of all possible combinations. These observations suggest that the overall compartmental organization of

afferents to the deep layers contributes to the genesis of neurons with multisensory properties there. However, despite the registry of inputs from different modalities, the mere proximity of these different inputs is insufficient to produce a multisensory neuron.

When inputs from different sensory modalities converge onto the dendrites or dendrosomatic regions of a neuron, the neuron is rendered multisensory. While physiological evidence for such convergence exists (Wallace et al. 93), a direct anatomical demonstration has not been documented in the superior colliculus. However, in the reptilian optic tectum (non-mammalian homologue) of the superior colliculus, visual and infrared inputs have been observed using the electron microscope to contact the same dendrite (Kobayashi et al. '92).

It has been reported that the large, efferent neurons of the deep layers can have dendritic arbors that extend 1.2-1.4 mm (Behan et al. '88, Moschovakis and Karabelas '85). Such an expansive dendritic field no doubt enhances the ability of a given neuron to gather inputs from a variety of sources. This notion is supported by the fact that up to 84% of these neurons (tecto-reticulo-spinal neurons, TRSNs) are multisensory, as opposed to only 55% of the entire population of deep layer neurons (Meredith et al. 1992).

Furthermore, a greater proportion of TRSNs are trimodal (15%) than observed in the overall population (8%). The possible mechanism for this is illustrated in Figure 15, where domains or compartments for representative visual, auditory, and somatosensory inputs are represented as shading and the dendritic arbors for 3 different neurons are indicated by the red circular icons. Even though each icon represents only 1.0 mm in diameter, each extensively overlaps inputs from all three modalities. In fact, it is difficult to position an icon within the SGI, where the somas of most TRSNs reside, in such a fashion that it does not overlap the terminal domains of at least two modalities. In order to account for the large number of unimodal neurons observed one might conclude that dendrites may have some features by which inputs from a particular modality are prevented, even though the dendrite clearly resides within its domain. Attentively it seems more plausible that the numbers of multisensory neurons within the deep layers have been substantially underestimated. Nevertheless, given the size of dendritic trees of many deep layer neurons, it is reasonable to suggest that the compartmentalization of inputs does little to restrict or reduce the incidence of multisensory convergence here. Furthermore, while the overlap and registry of



**FIGURE 15:** THIS FIGURE IS A CROSS-SECTION OF A SUPERIOR COLLICULUS WITH TERMINATIONS THAT REPRESENT AUDITORY (AEA), SOMATOSENSORY (SIV), AND VISUAL (ALLS) INPUTS. THE RED ICONS, WHICH ARE 1MM IN DIAMETER, REPRESENT THE EXTENT OF THE DENDRITIC ARBORS THAT ARE CHARACTERISTIC OF THE EFFERENT NEURONS LOCATED IN THE DEEP LAYERS.

**terminal zones from different modalities actually may enhance the incidence of the phenomenon of multisensory convergence.**



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## Vita

