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INTRAHEMISPHERIC AND COMMISSURAL CONNECTIONS BETWEEN AND WITHIN COMMISSURALLY AND NONCOMMISSURALLY INTERCONNECTED REGIONS IN THE PRIMARY AND SECONDARY SOMATIC SENSORY CEREBRAL CORTEX: THEIR POSSIBLE ROLE IN INTERHEMISPHERIC TRANSFER OF LEARNING IN THE RACOON

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By

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ABSTRACT

INTRAHEMISPHERIC AND COMMISSURAL CONNECTIONS BETWEEN AND WITHIN COMMISSURALLY AND NONCOMMISSURALLY INTERCONNECTED REGIONS IN THE PRIMARY AND SECONDARY SOMATIC SENSORY CEREBRAL CORTEX: THEIR POSSIBLE ROLE IN INTERHEMISPHERIC TRANSFER OF LEARNING IN THE RACCOON

by

Paul Herron

The intrahemispheric and commissural circuitry of the primary (SI) and secondary (SII) somatic sensory cortical regions in the raccoon was investigated utilizing horseradish peroxidase (HRP), autoradiographic and anterograde degeneration techniques. The purpose of these experiments was to determine if intrahemispheric or commissural axons connect cortical foci in SI and SII that receive projections from unrelated parts of the peripheral body surface (nonhomotopic connections) in addition to those which connect cortical foci that receive projections from related parts of the peripheral (homotopic connections). Four sites were chosen for study: the forepaw regions of SI and SII (noncommissurally connected regions) and the hindlimb and trunk regions of SI and SII (commissurally connected regions).

The site of injection was determined by using:
(1) the electrical response after stimulating the appropriate receptors, and
(2) the gyral pattern which, in many instances, demarcates functional subdivisions of SI. The HRP was injected using pressure and iontophoresis simultaneously. The tritiated amino acids were injected using pressure. After survival periods of 12-72 hours, the HRP was visualized in 40μm sections by using the chromogens dihydrochlorobenzidine and tetramethylbenzidine on alternate sections. The distribution of tritiated amino acids were visualized indirectly in a thin layer of photographic emulsion above the 40μm sections.

The results showed that injections of HRP in the hindlimb and trunk regions (commissurally connected) regions of SII labelled the cell bodies of intrahemispheric homotopic afferents in the ipsilateral SI cortical area and commissural afferents in the contralateral SII cortical region. Injections of HRP in this region also produced labelled cell bodies of nonhomotopic afferents in the ipsilateral SII forepaw region and the junctional area between the ipsilateral face regions of SI and SII.

Injections of HRP in the hindlimb and trunk (commissurally connected) regions of SI labelled the cell bodies of intrahemispheric homotopic afferents in the ipsilateral SII cortical region as well as nonhomotopic afferents in the ipsilateral hindpaw region. These HRP injections also labelled the cell bodies of commissural afferents in the contralateral SI hindlimb and trunk regions. Injections of tritiated amino acids in the hindlimb and trunk regions of SI resulted in silver grains above fibers and terminals in the ipsilateral SII hindlimb and trunk regions.

Injections of HRP in the forepaw (noncommissurally connected) area of SII labelled the cell bodies of homotopic afferents in the ipsilateral SI forepaw area. In addition, these injections also labelled the cell bodies of nonhomotopic afferents in the ipsilateral SII hindlimb area.

Injections of HRP in the forepaw (noncommissurally connected) region of SI labelled the cell bodies of intrahemispheric homotopic afferents in the ipsilateral SII forepaw region. Small injections in the distal volar representation areas of digits 3 and 4 labelled the cell bodies of intrahemispheric nonhomotopic afferents in the more proximal volar representation areas of digits 3 and 4 in the SI forepaw region. A lesion in the SI forepaw area resulted in degenerated fibers and terminals in the SII forepaw area.

The labelled cell bodies of each fiber system investigated were organized into rostrocaudally oriented strips. The majority of the neurons labelled have pyramidal shaped cell bodies. The laminar distribution of the labelled cell bodies exhibited a variety of patterns. The most common pattern was a focus of labelled cell bodies distributed in all layers except layer I. The heaviest concentration of labelled cell bodies was in layers III and V.

In a pilot study, the functional significance of the SI forepaw, SI face, and SII cortical representation areas was investigated using an ablation technique. Seven subjects were trained to discriminate rough vs smooth tactile and temperature tasks in one forepaw and subsequently tested for performance with the second paw to determine if intermanual transfer had occurred. Two subjects had bilateral ablation of the forepaw representation area in SI, one subject had bilateral ablation of the gyral crown of the SI face representation area, and one subject had a partial unilateral ablation of the SII forepaw area and bilateral ablation of the gyral crown of SI face representation areas. There were also two normal subjects and one sham operated subject.

The subjects with bilateral ablation of the SI forepaw region were unable to perform the tasks while animals with SII and SI face ablations were able to perform, learn and transfer the discrimination tasks. These results are in sharp contrast to findings in the cat where SI lesions did not prevent the acquisition of discrimination learning and SII lesions interfered with transfer of discrimination learning.

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INTRODUCTION

In their quest to understand the functional significance of neural circuitry in complex mental activities of the brain, Sperry and Myers used subjects whose forebrain commissures (notably the corpus callosum) had been sectioned (Gazzaniga et al., 1965; Myers, 1959, 1962, 1965; Sperry, 1955, 1961, 1962, 1966, 1967). They found that subjects without these commissures intact had essentially two separate brains within one skull. Things experienced and remembered in one hemisphere are unconnected with the things experienced and remembered in the other hemisphere. Animals with surgically separated hemispheres may be trained concurrently and simultaneously to do diametrically opposite tasks, something that subjects with normal unified brains could not do (Myers, 1962; Sperry, 1967; Trevarthen, 1960).

The ablation method was subsequently used to further localize the site of learning and memory within one cerebral hemisphere. When the somatic sensory cortical region is left intact and hippocampus, anterior thalamus and most of the caudate and amygdaloid complex are removed in one hemisphere of split brain cats, that hemisphere can still learn new tactile discrimination (Sperry, 1959). It was shown that a small island of somatic sensory cortex was sufficient for tactile discrimination learning in cats. Complete destruction of the somatic sensory cortical region makes it impossible for the animal to learn new tactile discriminations. These data also showed that intracortical fibers connecting related sensory cortical regions were functionally important. In the monkey, intracortical connections between the visual cortex and the temporal cortex was found to be indispensible for learning visual tasks other than brightness discrimination (Chow, 1967).

The role of the corpus callosum in the intermanual transfer of tactile learning

Several studies showed that the corpus callosum was necessary for the transfer of sensory learning between the hemispheres. Bykov (1924, from Ebner and Myers, 1962) first reported that sectioning of the corpus callosum tended to prevent the usual contralateral transfer of cutaneous conditioning of salivary reflexes in dogs. However, later investigations of the role of the corpus callosum in intermanual transfer of tactile learning were not always consistent. Normal subjects, of all mammals investigated, required considerably less time for second hand solving after experience through the first hand (Glickstein and Sperry, 1960; Myers, 1962). Smith (1951) worked with patients whose corpus callosum had been sectioned and found that intermanual transfer of stylus-maze learning was interfered with but not blocked. A human patient with corpus callosum agenesis showed complete absence of intermanual transfer of discrimination learning (Russel and Reitan, 1955). In another study, a human patient with corpus callosum agenesis showed excellent transfer of tactile discrimination learning (Myers, 1962). In rhesus monkeys, Ebner and Myers (1962) found that sectioning of the corpus callosum blocked transfer of tactile discrimination between the extremities. Using the same species of monkeys, Glickstein and Sperry (1960) found that sectioning of the corpus callosum blocked transfer in a majority of the tests. In callosal sectioned cats, there is complete absence of intermanual transfer of tactile discrimination learning (Stamm and Sperry, 1957).

Glickstein and Sperry (1960) argued that the corpus callosum was responsible for the direct intermanual transfer of "distinctive sensory knowledge" between the extremities in all species. However, extra-callosal systems that are capable of transmitting information to the "untrained" hemisphere have developed in primates. Factors such as the type and difficulty of the tests or injury to the "trained" hemisphere determine the potency of this extra-callosal system in the transfer of learning. If the corpus callosum is sectioned and the somatic sensory projection areas in the "trained" hemisphere damaged prior to training, the extra-callosal system is used to transfer the learning to the "untrained" hemisphere (Glickstein and Sperry, 1960).

Functional localization in the corpus callosum. Localization of functions in the corpus callosum was found in the cat and monkey. Transection of the anterior part of the corpus callosum did not interfere with the transfer of visual discrimination learning in cats. However, a definite decrement in interocular transfer was observed after destruction of about 25% of the corpus callosum along the posterior end. When the transection extended beyond 50% of the posterior part of the callosum, there was complete or nearly complete interference with transfer (Myers, 1959; Sperry et al., 1956). Similar decremental effects were observed on the transfer of tactual learning between the hemispheres after transection of the posterior part of the corpus callosum in monkeys (Myers and Ebner, 1976).

These data provided strong evidence for the role of commissures in the interhemispheric integration of learning and memory. The information transferred across the corpus callosum is not, however, a faithful reproduction of information received and learned in the first hemisphere. Sperry (1967) suggested that only an abbreviated and abstracted part of the original sensory input crosses the callosum. This hypothesis received support from experiments which demonstrated that neither cats nor monkeys showed a 100% saving in the "untrained" hemisphere when compared to the final performance of the "trained" hemisphere (Myers, 1962; Glickstein and Sperry, 1953).

Myers (1962) monocularly trained animals on a discrimination task and made lesions of varying sizes in the "trained" hemisphere of different animals; when the 'untrained' hemisphere was tested for transfer, its performance was at or near chance level and remained so for a number of testing sequences. These data suggest that the commissural connections are very important for interhemispheric transfer and must be intact in order for the "untrained" hemisphere to show any savings.

The results of the studies discussed above and the fact that complex mental functions like language and mathematics are consistently found in one hemisphere (typically the left) led Sperry (1967) to hypothesize that the role of the callosum was to inhibit the bilateralization of learning and memory. Information transmitted across the callosum is complemental and supplemental to design rather than symmetrical (Sperry, 1965, 1967). He suggested that detailed anatomy of the callosum might reveal greater assymmetry of callosum connections than the strict homotopic projections suggested by Bremer (1958).

Anatomical and Electrophysiological Organization of Commissural Connections in the Somatosensory Areas

Cytoarchitectural Areas of SI and SII. The projection of somesthetic receptors to two separate and distinct areas of the cerebral neocortex - the primary somatosensory area (SI) and the second somatosensory area (SII) - has been established electrophysiologically in a variety of mammals (Adrian, 1940; Herron, 1978; Johnson et al., 1974; Lende, 1963; Pimentel-Souza et al., 1978; Pinto Hamuy et al., 1956; Pubols and Pubols, 1971; Welker and Seidenstein, 1959; Woolsey and Fairman, 1946). The receptive fields of both SI and SII are somatotopically organized; that is, the somatic receptors are represented on the cortical surface in a manner that reflect their actual relationships on the animal's body surface.

The cell bodies in SI and SII are arranged into vertical columns. Physiological investigations of columns in the sensory projection areas have shown that the excitatory receptive fields of each neuron within a vertical column are all situated in roughly the same receptor area (Creutzfeldt, 1978; Powell and Mountcastle, 1959).

Based on the morphology of their cell bodies neurons in SI and SII can be divided into two broad classes. Neurons with pyramidal shaped cell bodies make up one class and neurons with nonpyramidal shaped cell bodies constitute the other class (Jones, 1975). Most nonpyramidal shaped neurons have stellate shaped cell bodies. The two classes of neurons are organised into six distinct laminae. There is considerable variation in the concentration of each class of neurons in different areas of SI and SII (Sanides, 1972). In some areas, the concentration of pyramidal neurons in layers III and V is minimal and that of the stellate cells in layer IV is maximal. These areas of SI and SII are termed "granular" cortices.

The other areas in SI and SII have a maximum concentration of pyramidal cells in layers IIIand V and a relatively small concentration of stellate cells in layer IV. These areas are called "agranular" cortices (Akers and Killackey, 1978; Ebner, 1967, 1969; Jones, 1975; Welker, 1976).

Afferent Connections of the Cytoarchitectural Areas. The cytoarchitectural differences between these cortices in SI and SII is a reflection of different afferent and efferent connections. The granular cortices of SI receive projections from the densely innervated regions of the body such as the distal limb parts and, consequently, the bulk of the thalamocortical afferents. Ebner (1967, 1969) studied the differential distribution of thalamocortical afferents to SI in the opossum, cat, and monkey and suggested that the granular cortices are specialized for receiving specific thalamic projections. In rats, discrete aggregations of stellate cells in layer IV termed "barrels" (Woolsey and van der Loos, 1970), receive equally discrete clusters of thalamocortical afferents (Killackey, 1973; Killackey and Leshin, 1975).

Using the electron microscope to study serial sections, (White, 1978) showed that most thalamocortical afferents, in SI of rats, terminate on the dendrites and cell bodies of non-spiny stellate neurons in layer IV. The remainder of the thalamocortical afferents terminate on the dendritic spines of spiny stellate neurons, dendrites and cell bodies of bipolar neurons, and apical dendrites of layer V pyramidal neurons, and the basal dendrites of layer III pyramidal neurons (White, 1978).

Ebner and Myers (1965) first pointed out that, in the cat and raccoon, the parts of SI and SII containing the representation of the forelimb and the distal segments of the hindlimb, i.e. the granular areas, do not contain degenerating axons following section of the corpus callosum. Similarly, the granular areas were acallosal in SI and SII of monkeys (Jones and Powell, 1969; Jones and Wise, 1977; Pandya and Vignolo, 1968), rats (Wise and Jones, 1976), cats (Jones and Powell, 1968b) and mice (Caviness and York, 1972).

In contrast, the agranular cortices in SI and SII are characterized by their rich commissural connections and, in SI at least, relatively sparse thalamic connections (Ebner, 1967, 1969; Jones and Wise, 1976). The differential density in thalamic input to the granular and agranular cortices of SII has not been investigated.

Electron microscopic studies by Sloper (1973) have shown that, in the motor cortex of monkeys, commissural afferents terminate on the apical and basal dendrites of pyramidal neurons. The thalamocortical receiving zones in the agranular cortices of SI receive projections from the lightly innervated regions of the body such as the axial body parts (Ebner, 1967; Jones and Powell, 1968b).

Commissural and Intracortical Connections. Utilizing the anterograde degeneration, horseradish peroxidase, and autoradiographic techniques, several studies have shown that agranular cortices of SI and SII are reciprocally and homotopically connected with the contralateral SI and SII agranular cortices (Jacobson and Trojanowski, 1974; Jones and Powell, 1968b, 1969b; Jones and Wise, 1977; Pandya and Vignolo, 1968; Wise and Jones, 1976). The agranular cortex of SI also sends well-ordered somatotopically organized projection to the contralateral SII (Jones and Powell, 1968b, 1969b; Pandya and Vignolo, 1968). In those instances where heterotopic commissural connections have been observed, the heterotopic projections were never between agranular and granular cortices. Jones et al (1975) suggest that commissural axons may arise from and terminate upon exactly homotopic groups of pyramidal cells.

In nonprimates, horseradish peroxidase studies have shown that the cells of origin of commissural afferents are in layer III and V and arranged in distinct clusters. In the rat, cat (Jacobson and Trojanowski, 1974) and monkey (Jones and Wise, 1977), the clusters have an average diameter of 0.5-1.00 mm and are oriented in medial-lateral strips. In monkeys, the commissural projecting cells of SI and SII originated from layer IIIV. That the commissural projecting cells may also receive commissural terminals is inferred from autoradiographic data in monkeys; this data showed that commissural fibers terminated in patches, 0.5 - 0.8 in diameter, and were distributed over layers II-IV in a pattern that resembles the shape of an hour glass. It was suggested that this pattern is a result of callosal fibers terminating preferentially on the apical and basal dendrites of pyramidal neurons in layer IIIB (Jones et al., 1975).

The intracortical connections between SI and SII in the cat and rhesus monkey were observed to be well-ordered and somatotopically organized (Jones and Powell, 1968a, 1969a). There were topographical and reciprocal connections between granular areas as well as agranular areas of SI and SII but no connections between dissimilar cortices of SI and SII.

Akers and Killackey (1978) made small lesions in the granular cortex of SI in rats and observed degenerating fibers and terminals in the surrounding agranular cortex of SI. Using autoradiography, Jones et al. (1978) investigated the intracortical projections of the Brodmann's areas 3, 1 and 2 in SI. These data showed that neurons in the more granular area 3 projected to neurons in the adjacent and less granular area 1.

In the rhesus monkey)Loe et al., 1978) and raccoon (Herron, 1979), the granular and agranular cortices of SI differ from the granular and agranular cortices of SI differ from the granular and agranular cortices of SII in their thalamic connections. The SI granular and agranular cortices receive projections from the ventral posterior lateral and ventral posterior medial nuclei (ventrobasal complex in raccoons) whereas SII receives the bulk of its projections from the ventral posterior inferior nucleus.

Electrophysiological Responses of Neurons in the Granular and Agranular Cortices to Peripheral and Contralateral Cortex Stimulation

The electrophysiological activities of the granular cortices differ from that of the agranular cortices. Welker (1976) mapped the facial projections of SI of rats and found that units in the granular cortices are small, modality specific and topographically organized. On the other hand, recordings from narrow patches of agranular cortex, intercalated between the barrels in the facial projection area of SI, were found to be generally unresponsive to peripheral stimulation. The agranular units that could be driven by peripheral stimulation were responsive to the same kind of stimulation as that of units in the adjacent granular cortex.

The receptive field properties for some units in the agranular cortices of SII are unusually large and are not somatotopically organized with respect to adjacent units (Carreras and Andersson, 1963). Many of the units that are somatotopically organized in SII receive bilateral input. Over 90% of the units in the unanesthetized monkey (Whitsel et al., 1969) and 63% in the unanesthetized cat (Robinson, 1973) were responsive to bilateral stimulation of the body surface. Robinson (1973) and Innocenti et al (1972) have shown that the pathway for the major share of the input from the ipsilateral body parts to these bilateral units involves input through the corpus callosum from the contralateral SI and SII cortices.

There is a discrepancy between anatomical and electrophysiological data concerning corpus callosum afferents to the SI and SII cortices. In contrast to the acallosal zones observed in anatomical studies, evoked potentials were recorded when stimulating and recording electrodes were situated at all symmetrical points in the somatosensory areas of monkeys (Bremer, 1958; Curtis, 1940). In addition, Curtis (1940) recorded potentials at points asymmetrical to the location of the stimulating electrodes.

Innocenti et al (1974) recorded from single fibers in the anterior part of the corpus callosum in cats and found that all parts of the body were represented in the population of fibers they studied. The amplitude of the responses did not change from area to area within the corpus callosum. The average latency of responses from the distal segments were longer than that of responses from the axial body parts (Innocenti et al., 1972, 1973, 1974).

Innocenti et al., (1974) recorded from a small group of fibers in the corpus callosum while stimulating a small area of SI. Several short latency waves were elicited. The first wave had a latency of 0.4 to 0.6 msec. and was thought to be the result of direct asynaptic excitation of callosal projecting cells. The second wave had a latency of 0.8 to 1.0 msec. and was thought to be caused by excitation of pre-synaptic fibers impinging on callosal projecting cells and consequent transynaptic activation of the latter (Innocenti et al., 1974). They did not identify the source of the presynaptic fibers.

In cats, a disproportionately large percentage of the callosal fibers were responsive to stimulation of the face and distal segments (Innocenti et al., 1974). The projections of facial and distal segments through the corpus callosum is commensurate with the projections of facial and distal segments to the SI and SII areas. These fibers had localized receptive fields, were modality specific and possessed electrophysiological properties that were the same as those observed for units in the granular cortices of SI and SII. However, 90% of the fibers terminated on units in SII that had unusually large and bilateral receptive fields were not somatotopically organized with respect to adjacent unit. Thus, in cats, the units which send axons into the corpus callosum do not also receive callosal input.

Peripheral and commissural input were observed to converge on 10% of the units investigated by Robinson (1973). Commissural afferents from SI and SII were observed to converge on 36% of the SII units that were recorded (Robinson, 1973).

The role of SI and SII and their intracortical and commissural connections in the interhemispheric transfer of tactual learning

Teitelbaum et al (1968) showed that SI and SII were functionally important for the intermanual transfer of learning in cats. Unilateral ablation of SII blocked interhemispheric transfer of learning in both directions: the animals did not show transfer of learning when the damaged hemisphere was trained first and the normal hemisphere tested for saving or when the normal hemisphere was trained first and the damaged hemisphere tested for transfer. Similarly, unilateral ablation of the forepaw area in SI blocked the interhemispheric transfer of learning from the damaged to the normal hemisphere. Unilateral ablation of SI forepaw areas did not block transfer of learning from the normal to the damaged hemisphere (Teitelbaum et al., 1968). Thus, in the cat at least, SII is necessary for both receiving and transferring tactual learning while SI is only necessary for transferring learning.

The role of SI and SII intracortical and commissural connectivity in the interhemispheric transfer of tactual learning have been interpreted in several ways. One hypothesis is that only regions representing midline or axial body structures and/or bilateral input exchange interhemispheric information; the commissural connections "sew" together the midline body structures and provide to each hemisphere a continuous mapping of the midline activities in the other hemisphere (Choudhury et al., 1965; Jones and Powell, 1968b, 1969b; Pandya et al., 1971; Pandya and Vignolo, 1968). Jones and Powell (1968b) wrote: "The absence of callosal connexions between the regions representing the distal portions of the limbs make it unlikely that intermanual transfer of tactual learning occurs through direct commissural connexions."

However, in the sensory systems of rats and mice this hypothesis is inconsistent with the anatomical data. In these species, an axial body region, the face area, receives and sends very sparse commissural projections (Akers and Killackey, 1978; Caviness and York, 1975; White and De Amicis, 1977). Using autoradiography, Wise and Jones (1976) showed in rats that a few narrow patches of agranular cortex, intercalated between the barrels in the granular cortex, receive dense commissural input. Similar results were obtained with the lesion method (Akers and Killackey, 1978).

Another hypothesis is that the commissural connections between SI and SII mediate the interhemispheric transfer of learning. Innocenti et al., (1974) suggested that tactile information through the corpus callosum is more related to the densely innervated regions of the body than to midline body structures.

Boyd et al (1971) suggested two explanations for the contrasting results obtained by anatomical and electrophysiological studies of the commissural connections between the somatosensory cortical areas.

They suggested that either a synapse was interposed between the granular (acallosal) and agranular (callosally connected) areas, or that anatomical techniques failed to detect the commissural fibers and terminals in the acallosal zones (Boyd et al., 1971). The study by Akers and Killackey (1978) supports the former explanation. This data showed that neurons in the granular cortex of rats project intracortically to the surrounding agranular cortex (Akers and Killackey, 1978). Presumably, the intracortical fibers terminate on callosally projecting cells which then transmit the information through the corpus callosum to the contralateral somatosensory areas.

Summary

Investigators used the split brain approach to localize the site of learning and memory within one hemisphere. The visual and somatic sensory areas were capable of learning, respectively, brightness and tactile discriminations.

The corpus callosum mediated the interhemispheric transfer of learning. In cats and monkeys, localization of visual and somatic sensory functions were observed in the corpus callosum.

The somatic sensory projection areas contained at least two electrophysiologically defined short latency representations of the receptors on the animal's body surface. There are cytoarchitectural areas in SI and SII related to those areas which receive projections from the densely innervated regions on the animal's body surface and those that are interconnected with the contralateral SI and SII cortical regions. Granular areas in the SI and SII cortical regions are those areas which contain a relatively higher concentration of neurons with stellate shaped cell bodies whereas agranular areas in the SI and SII cortical regions are those areas which contain a relatively higher concentration of neurons with pyramidal shaped cell bodies.

Anatomically and electrophysiologically, the intrahemispheric and commissural afferent and efferent connections in SI and SII can be characterized in the following manner: (a) homotopic connections are connections between cortical areas that receive projections from the same or very similar peripheral body parts, and (b) heterotopic connections are connections between cortical areas that do not receive projections from the same or very similar peripheral body parts, in other words, connections between cortical areas which receive projections from very different peripheral body parts. Heterotopic connections can also be defined as nonhomotopic connections.

The granular areas of SI receive projections from the densely innervated regions of the body and, consequently, heavy thalamic input from its referent specific thalamic nucleus. The agranular areas of SI and SII agranular cortices were reciprocally and homotopically connected with respectively, the contralateral SI and SII agranular cortices. SI sends a somatotopically organized projection to SII as well.

In monkeys, the cell bodies of commissural projecting neurons in SI are located in layer IIIB. Intracortical afferents originated from layer IIIA in SI and layers III, IV, and V in SII. In nonprimates, intracortical afferents originated from all layers except layer I.

In rats, small lesions in the granular cortex of SI resulted in degenerated fibers and terminals in the surrounding agranular cortex.

Electrophysiological studies, in contrast to anatomical studies, show that all areas of SI and SII are homotopically connected. These studies also showed that some points on the cerebral neocortex project to heterotopic sites.

Recordings from single fibers in the corpus callosum showed that the callosal projecting units had the same electrophysiological characteristics as those observed for units in the granular areas. However, these axons terminated on very different type of cells: cells with unusually large and bilateral receptive fields.

Behaviorally in cats, ablation of SI blocked the interhemispheric transfer of learning from the damaged to the normal hemisphere. Ablation of SI did not block the transfer of learning from the normal to the damaged hemisphere. Ablation of SII blocked the transfer of learning to, as well as from, the damaged hemisphere.

The rationale for this study

Potential sources of confusion in the study of interhemispheric transfer of learning are the contrasting results of electrophysiological and anatomical studies: electrophysiological studies of commissural projections show that all symmetrical cortical areas in SI and SII are connected whereas anatomical studies indicate the granular cortices are devoid of commissural connections. This discrepancy between the electrophysiological and anatomical studies regarding commissural connections can be resolved by understanding the intrahemispheric and commissural circuitry which allows for synaptic interaction of agranular (commissurally connected) and granular cortices of SI and SII. One could postulate a shema of organization which shows that, in addition to the intrahemispheric axons which connect those cortical foci in SI and SII that receive projections from related parts of the periphery, intrahemispheric axons also connect cortical foci that receive projections from unrelated parts of the periphery. Therefore, information from the granular cortices (i.e. the noncommissurally connected regions of SI and SII) destined for the contralateral homotopic areas is first relayed via intrahemispheric connections to agranular cortex. The information is then transmitted to the contralateral hemisphere via commissural connections and then to the homotopic granular area by intrahemispheric connections (Fig. 1).

As a first step in testing this schema, the purpose of this study was to establish the cells of origin of the intrahemispheric and commissural connections in the granular and agranular reigons of SI and SII in raccoons. Horseradish peroxidase and autoradiographic techniques were used to determine; (1) the intrahemispheric afferents and efferents of neurons in two sites of the granular cortex of SI, the 4th and 5th digital area, (2) the intrahemispheric and commissural afferents and efferents of neurons in one site of the agranular cortex of SI, the trunk region, (3) the intrahemispheric afferents and efferents of neurons in the granular cortex of SII, and (4) the intracortical afferents and efferents of neurons in the agranular cortex of SII.

In a pilot study using raccoons, the functional significance of these connections of SI and SII in the interhemispheric transfer of learning were determined by bilaterally ablating either SI or SII and testing for transfer of tactual and temperature discrimination learning.

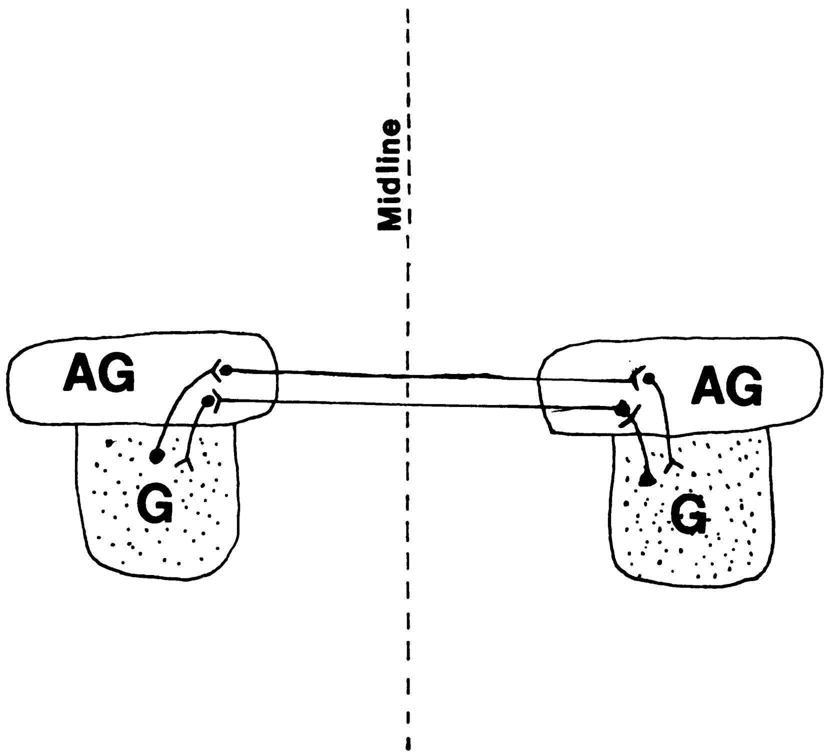


Figure 1: Schematic diagram of postulated intrahemispheric and commissural connections between Si and SII. G, granular cortex, AG, agranular cortex.

The subjects used in this study

The questions proposed above can best be investigated in animals such as the raccoon which exhibit a neural specialization of its sensory system that correspond well with its behavior specialization (Welker and Campos, 1963; Johnson 1979 for review). The adaptive life-style of an animal and its predecessors may select for the outstanding development of the somatic sensory system in an animal relative to the development of other sensory systems in the same animal. The raccoon, which makes extensive use of its forepaw in the manipulation and tactile exploration of its environment, has a somatic sensory system that exhibits both a specialized anatomical and physiological development. The SI and SII cortical regions are dominated by their extensive forepaw projections. According to Welker and Seidenstein (1959), SI can be discretely separated into individual "digit" and "foot pad" gyri. These projections are 60% of the total SI area in the raccoon compared to only 20% and 30% forepaw projection in the SI cortical region of the dog and cat, respectively, related carnivores (Welker and Seidenstein, 1959). Similar differential patterns of peripheral projections are observed in SII of the raccoon where forepaw projection are 70% of the tactile SII cortical area (Herron, 1978). By studying the anatomical, physiological, and behavioral characteristics of such a sensory system, properties are manifested which otherwise may not be noticed (Welker and Seidenstein, 1959).

METHODS

In 17 adolescent and adult raccoons, the origin and termination of intracortical and commissural connections to the SI and SII cortical areas were investigated by the horseradish peroxidase, autoradiographic and anterograde degeneration techniques.

The first part of this presentation of anatomical methods will discuss the procedures used in the horseradish peroxidase and autoradiographic experiments and the second part will discuss the procedures used in the anterograde degeneration experiments.

Anatomical Experiments: Intracellular Transport of Horseradish Peroxidase and Tritiated Amino Acids. The brains of 17 raccoons were used for this investigation. The raccoons were trapped in the wooded areas surrounding the Michigan State University campus.

The animals were anesthetized with chloralose (initial dosage, 17 mg/kg) or sodium pentobarbital (initial dosage, 37 mg/kg). The head was placed in a stereotaxic apparatus and the cranium exposed. Small holes approximately 2 mm in diameter were drilled in the skull above the area of experimental interest and a surface recording electrode placed on the dura to determine, electrophysiologically, the area's general location with regard to the somatotopic map. Small incisions were made in the dura of the drilled sites chosen for further investigation and a microelectrode was lowered into the cortex to determine the detailed receptive field properties. The electrophysiological information along with the gyral patterns were used to determine the injection site.

Horseradish peroxidase (HRP) and tritiated amino acids (TAA)

(1:1 mixture of L-leucine [4, 5 ^{3}H] and L-proline [^{3}H], Schwarz/Mann) were the tracers injected. The injection procedure is a modification of the pressure injection procedures developed by Droz (1975) and Price et al (1977) and the iontophoretic procedure developed by Graybiel and Devor (1974). Without introducing any air bubbles, beveled pipette electrodes, tip diameter of 60-120μ, were sealed onto the tip of a 1 μl Hamilton syringe with wax. The injection apparatus consisted of two interconnected B-D Yale Syringes (6 ml and 20 ml) which transmitted the driving force of a Harvard Apparatus infusion pump (Figure 2). The two syringes, the micropipette and all the tubing were filled with paraffin oil. An electrical lead for iontophoresis was attached to an outlet of the syringe needle. HRP was then injected by applying both pressure and current simultaneously.

Two types of HRP solutions were injected into the same site. Firstly, HRP solution A was injected via pressure and current. Solution A was a 30-40% HRP solution which consisted of equal amounts of Sigma type VI and type IX, Worthington and Miles HRP powder or crystals and 1% poly-l-ornithine dissolved in tris buffer with 0.2 - 1.0 M potassium chloride.

Secondly, solution B was injected by pressure alone. Solution B contained both HRP and TAA. The TAA mixture was dehydrated by passing a slow stream of nitrogen gas over it and reconstituted with an HRP solution which contained water as the solvent instead of tris buffer and potassium chloride.

The pressure injection rate was 1μl/1.2-1.6 hours and 1-3 microamps were used (Midguard High Voltage Precision current source). These methods of injection of the HRP and then the HRP and TAA combined allowed for better labeling of terminals and cell bodies without increasing the size of the injection site. The range of injection site sizes are discussed in the RESULTS section.

After survival periods of 12-72 hours, the animals were perfused and the brain removed, the location of the injection site marked on a photograph and the brain processed according to the protocol developed by Mesulam and Rosene (1977). The perfusion solution contained 1% paraformaldehyde and 1.5% glutaraldehyde in 0.1 M phosphate buffer. Frozen sections 40 μm thick were cut in the coronal plane and stored for either autoradiography or HRP histochemistry.

The HRP was visualized by incubating the tissue in a solution which contained tetramethylbenzidine (TMB) or dihydrochlorobenzidine (DCB) in the presence of hydrogen peroxide (Mesulam and Rosene, 1977). The sections were then counterstained in buffered 1% neutral red and cover-slipped.

The sections for autoradiography were dehydrated and dipped in a 1:1 mixture of water and NTB-2 Kodak emulsion. These sections were stored in a light-proof container in the refrigerator at 4^{o}C for 5-20 weeks. The sections were then developed in D-19 at 12-14^{o} for 3 minutes and 15 seconds followed by fixation of the emulsion and counterstaining of the tissue in 1% thionine.

Anterograde Degeneration Technique

The brains of 2 raccoons were used for this investigation. An opening approximately 1 cm in diameter was made in the skull above the cortical area of interest. The dura was incised in 4 directions, then peeled away, and with the aid of a dissecting microscope, the site of the lesion in the cortical area of interest was determined. The lesion was made with a small pipette attached to a suction pump with tygon tubing.

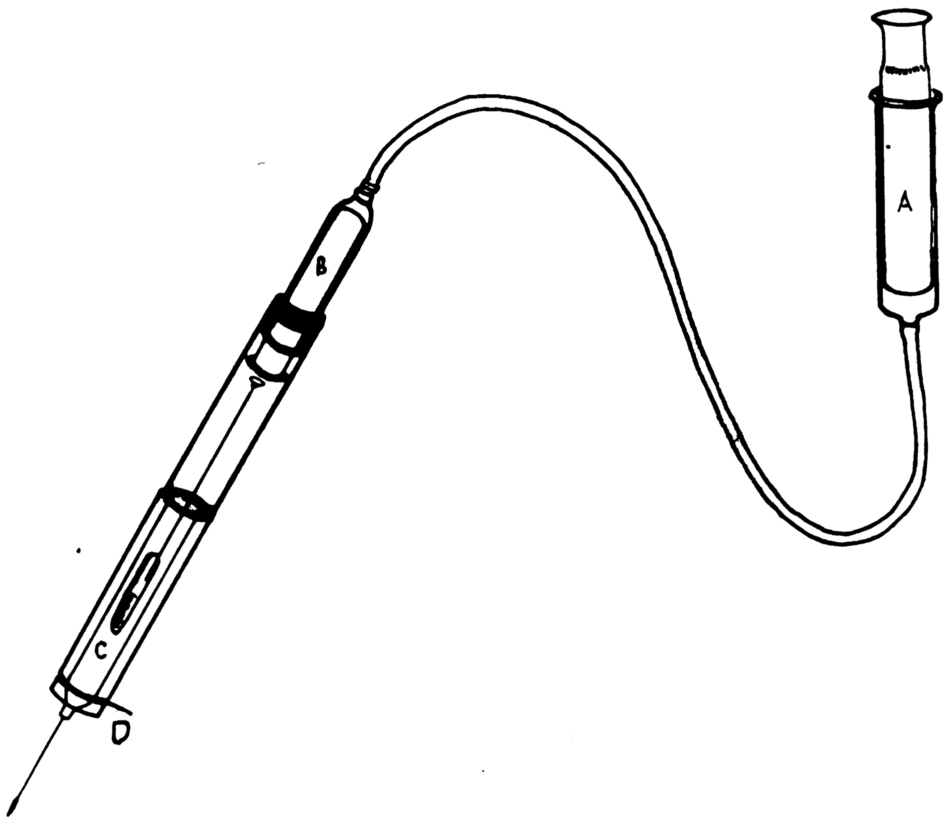


Figure 2: Schematic diagram of the injection apparatus. The apparatus consisted of two syringes (6 ml and 20 ml) connected together by tygon tubing filled with paraffin oil. The syringes transmitted the driving force of an infusion pump. The apparatus permitted both a pressure and ionotophoretic injections simultaneously. A. 1 µl syringe inside syringe holder. A. Syringe whose plunger drove the plunger of the 1 µl syringe. C, 20 ml syringe. D. Outlet for electrical lead for iontophoresis.

Following a 48 hr survival time, the animals were perfused intracardially and the brain processed according to the protocol developed by De Olmos (1960). The perfusion solution contained 4% paraformaldehyde, 4% sucrose and .067 M sodium cacodylate at a ph of 7.2-7.4. The brain was embedded in gelatin and frozen sections, 40 μm thick, were cut in the coronal plane. Some of the sections were stored for cupric silver staining and others were stored for thionine staining. The sections were incubated in a copper silver solution for 5 days and then stained with silver nitrate.

The sections were reduced in a solution which contained 12 ml of 10% commercial formalin, 7 ml 1% citric acid and 100 ml of 95% ethanol in 881 ml of distilled water.

The sections were mounted out of creosote or acetate buffer (modification by Robert Switzer, personal communication) and cover slipped.

Analysis of Data

In all HRP, autoradiographic and lesion experiments, the brains were blocked in a standard plane perpendicular to the ventral base of the brain resting on a horizontal surface and sectioned at 40 μm. In the HRP experiments, adjacent sections, taken at 200 μm intervals through the brain, were stained with TMB and DCB. The HRP, autoradiographic and cupric silver sections were examined microscopically and, respectively, the foci of labeled cell bodies, silver grains, and degenerated fibers and terminals were charted on projected tracings of the histological sections. The distribution and approximate density of labeled cell bodies in each section was indicated by placing small dots in comparable locations in the tracing. In the tracings the blackened area indicates the central core and the stippled area indicates the diffusion of the reaction product in the injection site.

The approximate density of the silver grains or degenerated fibers and terminals was indicated in each tracing by very small dots in places comparable to those observed in the histological section.

RESULTS

Features of the injection site. Horseradish peroxidase injection sites exhibited several distinctive features. A prominent feature of each TMB or DCB injection site was the differential concentration of the HRP reaction product in the injection site. Under the light microscope, the injection sites of DCB and TMB consisted of three zones. Each zone was representative of a different concentration of HRP reaction product. These zones of concentrations observed in the injection sites of DCB and TMB are very similar to those described for diaminobenzidine-tetrahydrochloride (DAB) (Vanegas et al., 1978).

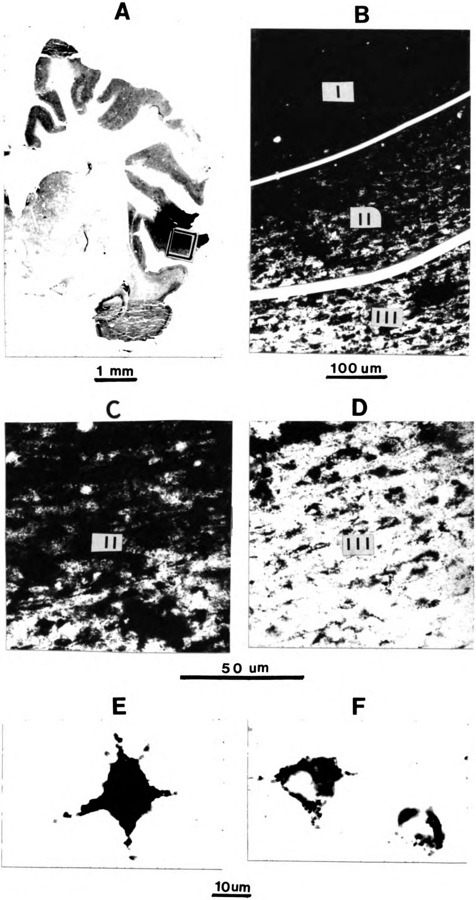
Zone 1 was the area in the center of the injection site and surrounded the needle track. When DCB was used as the chromogen, zone 1 was characterized by a very dark blue staining background (Figure 3). The dense concentration of the HRP reaction product in the background prevented the identification of individual neural elements. The relative density of the staining in zone 1 in several experiments appeared to be a function of the injection rate: a given quantity of HRP injected over a longer period of time resulted in denser concentration of the reaction product.

Zone II, the area of the injection site surrounding zone 1, was characterized by a lesser concentration of the reaction product in the background than that observed in zone 1 (Figure 3). Zone II contained the profiles of densely filled cell bodies and dendrites.

In zone III of a DCB injection site, the background was clear of the reaction product. Many of the cell bodies and dendrites were densely filled with granulated HRP (Figure 3).

Figure 3: Photomicrographs of the differential concentration of HRP reaction product in experiment 78593. A. Photomicrograph of a coronal section through the HRP injection site. B. Higher magnification of an area in the injection site indicated approximately by the small rectangle in A. Note the differential concentration of HRP reaction in zones I, II and III. C and D. Higher magnification of, respectively, zones II and III show the relative difference in the amount of reaction product in the background of the labeled neurons. E. Photomicrograph of a cell body with diffused HRP. F. Photomicrograph of cell bodies filled with granulated HRP.

Figure 3



The relative size of each zone in an injection site was a function of the postinjection survival time. Zones II and III were relatively larger for shorter survival times. Similar to the results of Vanegas et al., (1978), it was observed in these experiments that zone 1 is relatively larger with longer survival times.

The injection site in a given experiment was larger in TMB stained tissue than that observed in the adjacent section stained with DCB. In most, but not all of the experiments, the labeling of terminals and cell bodies in the thalamic nuclei were most extensive in TMB stained tissue than that observed in the adjacent section stained with DCB. The visualization of terminal labeling was enhanced by shorter survival times.

The difficulties in accurately defining the zones which are effective in labeling afferent and efferent processes are now well recognized. Some investigators consider the central core to be the only zone effective in labeling the afferent and efferent processes in the injection site (Jones et al., 1977; Vanegas et al., 1978). In these experiments, the relationship between labeling in the ventrobasal or ventroposterior inferior thalamic nuclei and zone 1 were the most consistent indicator of the effective region of the injection site.

Nature of staining - horseradish peroxidase. Under the light microscope, HRP labeling of cell bodies were seen as coloured particles when using bright field or as brilliant points of light when using dark field illumination. Occasionally the reaction product was homogeneous diffused throughout the cytoplasm of the cell body. It is widely believed that only cell bodies and dendrites with a granular HRP pattern indicate the presence of retrogradely transported HRP.

Diffusely filled neurons are known to be the result of injury to the axons in the injection site (Jones et al., 1974, Vanegas et al., 1978). The cell bodies of injured neurons may also contain granulated HRP in a manner similar to that of physiologically labeled neurons.

The criterion for distinguishing an injured population of labeled cell bodies from that of a physiologically labeled population was the presence of diffusely filled cell bodies. In zone III of the injection site, foci of labeled cell bodies containing a few cell bodies with diffused reaction product and other cell bodies with granulated reaction product. It is probably that many of the cell bodies with granulated reaction product are the result of physiological uptake and transport. However, the suspected presence of injured neurons whose cell bodies contained granulated reaction product makes it impossible to determine accurately which of the cell bodies are the result of physiologically transported HRP and which labeled cell bodies are the result of injury. For the purpose of this study, only those foci of labeled neurons which contained only cell bodies with granulated HRP were interpreted to be the result of physiological uptake and transport and therefore relevant data.

Those regions of the brain which are reciprocally connected with the site of injection produced an intricate and varied pattern of labeling. Often, terminals and cell bodies were labeled in these sites. The interpretation of terminal labeling distinguishable from soma and dendritic labeling was particularly difficult in lightly counterstained material. In densely labeled regions, under the light microscope, labeled terminals were an irregular distribution of HRP granules in the neuropil surrounding various cell types.

Nature of staining - autoradiography. Substantial labeling of the somata in the central core of the injection site is held to be effective for transported label to be identified at a distance. The surrounding zone of mainly neuropil labeling is held to be ineffective in labeling terminals of neurons of this region.

Since tritium particles travel approximately 1μm, the activation of the silver halide crystals results from radioactivity in only the superficial 1 μm of the 40 μm frozen sections.

The labeling of fibers exhibited features different from that of labeled terminals (see figure 22). Labeled fibers are characterized by straight chains of silver grains whereas terminals fields are characterized by an irregular and random distribtion of silver grains.

Topography of intrahemispheric and commissural connections. The intracortical and commissural connections of SI and SII in the raccoon formed a complicated and varied pattern. In the description of the results, the location of the injection site and the distribution of the afferent sources and the efferent target areas will be related to the cortical maps derived using electrophysiological mapping techniques. The maps of the raccoon's SI (Welker and Seidenstein, 1959) and SII (Herron, 1978) cortical areas are particularly useful for determining the topography of intrahemispheric connections.

The topography of the cell bodies of afferent neurons was related to the site of each injection in the following manner: (1) intrahemispheric non-homotopic afferent neurons (INA) - the cell bodies of afferents were in an intrahemispheric locus that receives projections from peripheral body parts which are unrelated to the body parts that project to the site of injection, (2) intrahemispheric homotopic afferent neurons (IHA) - the cell bodies of these afferents were located in a cortical area that received projections from peripheral body parts which also project to the site of the injection, and (3) commissural afferents (CA) - the cell bodies of afferents from the contralateral homotopic cortex. The topography of labeled or degenerated fibers and terminals were similarly related to the site of, respectively, injection or lesion.

Table I is a summary of the injection sites and the topographic distribution of labeled cell bodies within SI and SII cortical region (also see figure 4). The results of selected experiments are described below in greater detail. Results from SII injections are presented first, followed by those of SI injections.

Afferents of the SII forepaw area. The results of two experiments will be used to describe the topography of the cell bodies of INA and IHA that resulted from injections in the SII forepaw region. In experiment 78500, a combined injection of HRP and tritiated leucine and proline was made in an area that yielded a high amplitude evoked potential after manual stimulation of the contralateral middle digits of the forepaw. The diffusion of the reaction product from the injection site was approximately 2 mm in diameter.

The cell bodies of a large number of INA were labeled as a result of this injection. In transverse sections, caudal to the injection site on the inferior bank of the suprasylvian sulcus, labeled cell bodies were organized into distinct clusters. Figure 5 is a reconstruction of a series of transverse sections through the region of labeled cell bodies and shows that the clusters were part of three rostrocaudally oriented strips of labeled cell bodies. The strips of labeled cells were separated by gaps of fairly constant width where few or no cell bodies were labeled. The labeled cell bodies were localized in the hindpaw and trunk region of the somatotopically

Table 1. Summary of the experiments and results of this study

Animal #	HRP Injection site	Survival time	INA/E	IHA/E	CA/E
77606	3rd & 4th digit SI forepaw	24 hrs.	X	X	
77604	4th digit SI forepaw	24 hrs.	X	X	
77574	4th digit SI forepaw	36 hrs.		X	
77597	SI forepaw	30 hrs.		X	
77559	SI hindpaw	30 hrs.	X		X
78565	SI hindpaw	30 hrs.		X	X
77563	SI hindpaw	24 hrs.		X	
78584	SII forepaw	24 hrs.		X	
78593	SII hindpaw	45 hrs.	X	X	X
78516	SII hindpaw	39 hrs.		X	X
78511	SII forepaw & hindpaw				
Animal #	**TAA Injection site**	**Survival time**	**INE**	**IHE**	**CE**
77561	SI hindpaw	40 hrs		X	
78586	SI trunk & hindlimb	48 hrs		X	
Animal #	**Lesion site**	**Survival time**	**INE**	**IHE**	**CE**
77608	Gyral crown of 4th digit area SI	48 hrs.		X	
77609	SI hindpaw	48 hrs.		X	

Table 1 (contd.)

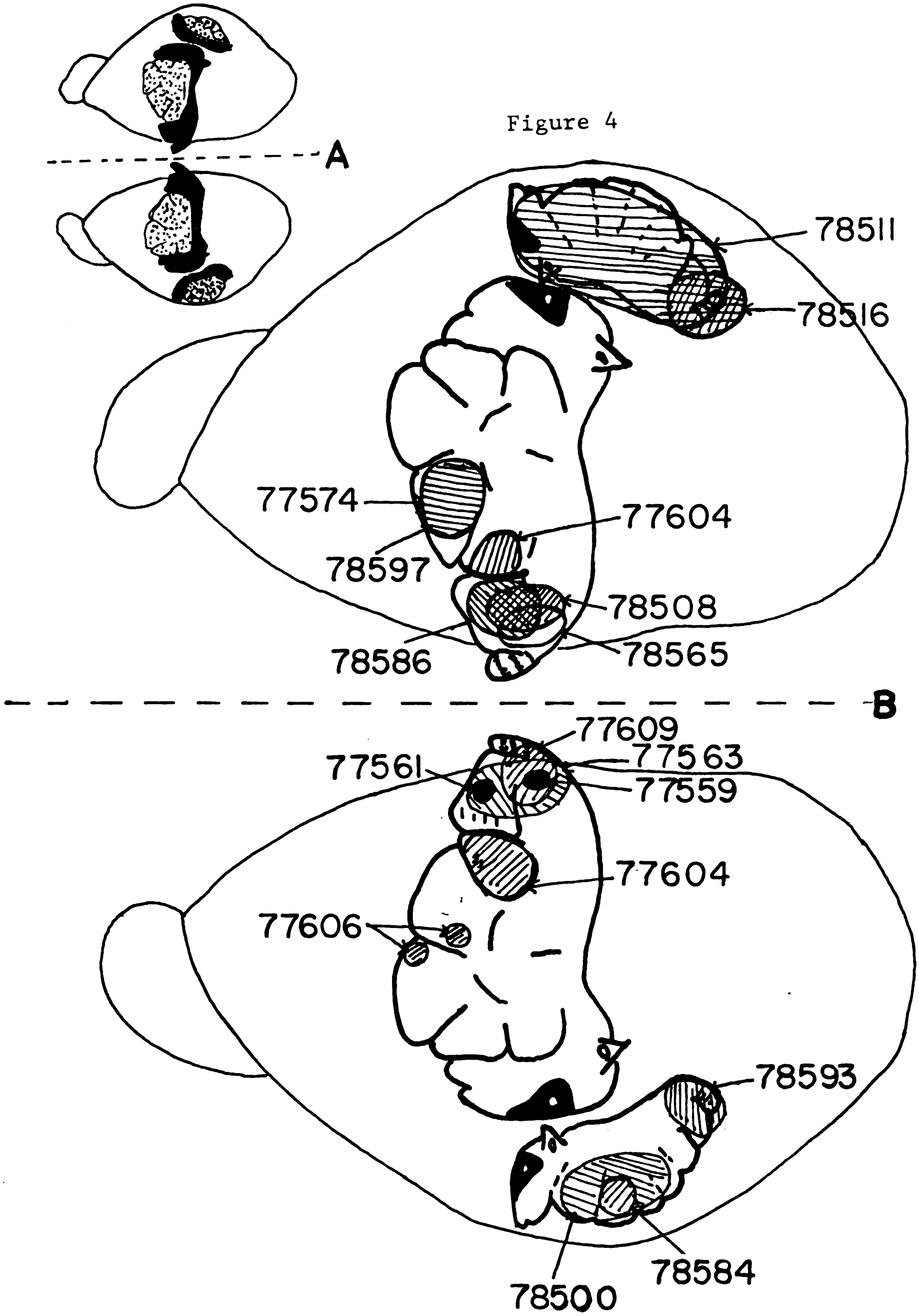
Animal #	HRP/TAA Injection site	Survival time	INA/E	IHA/E	CA/E
78500	SII forepaw	40 hrs.	INA	X	
78508	SI hindpaw	64 hrs.	INA	X	CA

Abbreviations:
- CA - Commissural afferents
- CA/E - Commissural afferents or efferents
- CE - Commissural efferents
- IHA/E - Intrahemispheric homotopic afferents or efferents
- IHA - Intrahemispheric homotopic efferents
- INA - Intrahemispheric nonhomotopic afferents
- INA/E - Intrahemispheric nonhomotopic afferents or efferents
- INE - Intrahemispheric nonhomotopic efferents

Figure 4: Schematic diagram of the injection sites listed in table 1. A. The SI and SII cortical regions are shown on the cerebral hemispheres with all the sulci removed except those in SI and SII to emphasize the relationship of SI and SII. The stippled areas in SI and SII indicate the granular cortices and the darkened areas indicate the agranular areas of SI and SII.

B. Diagram of the injection sites in the granular and agranular cortices of SI and SII. Many of the injections covered the same area in the forepaw, hindlimb and trunk representation areas of SI and SII.

Figure 4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78500

of cell bodies with granulated reaction product suggested physiological uptake and retrograde transport by this focus of neurons.

The strips of labeled cell bodies consisted of both pyramidal and non-pyramidal shaped neurons. HRP positive cell bodies were in all layers of the cortex except layer I. The bulk of the HRP positive cell bodies were in layers II, III, IV and V. Fewer labeled cell bodies were observed in layer VI.

The cell bodies of IHA in SI were also labeled as a result of experiment 78500. In transverse sections, the labeled cell bodies were organized into clusters in the sulcal cortex of the 2nd, 3rd and 4th digital representation areas (figure 6 and 7). Each focus of labeled cell bodies formed a rostrocaudally oriented strip which began in the anteriormost region of SI and extended caudally for 1 to 2 mm. Occasionally, HRP positive cell bodies were found in the cortex of the gyral crown.

In experiment 78500 the terminals of intrahemispheric homotopic efferent neurons in the SII forepaw area were demonstrated in autoradiographic processed sections that were adjacent to the HRP sections. Silver grains were observed above fibers and terminals in the 2nd, 3rd and 4th digital representation areas of the SI forepaw area. In transverse sections, the silver grains above terminals were distributed in patches. The topography of the patches was the same or very similar to the topography of clusters of labeled cell bodies observed in the HRP stained tissue.

In experiment 78584, a smaller injection of HRP was made in a zone of SII which yielded a high amplitude evoked response after manual stimulation of the second digit. Labeled cell bodies of IHA were found in the 2nd digital representation area of SI. A reconstruction of the tracing of a series of transverse sections shows that the labeled cell bodies form rostrocaudal oriented strips in the medial and

Figure 5: The distribution of HRP labeled cell bodies in the hindpaw representation area of SII following an injection in the forepaw area of SII in experiment 78500. A. Schematic diagram of the cerebral hemispheres with all the sulci and gyri removed except those in SI to emphasize the relationship of SI and SII. The darkened area in the forepaw region of SII indicates the injection site and the dots indicate the approximate distribution of the labeled cell bodies in SII. B. A tracing of the left cerebral hemisphere of a "standard" brain with the approximate locations of the transverse sections reconstructed in C. C. A series of transverse sections through the region of labeled cell bodies in SII hindpaw region. The dots represent the approximate density of labeled cell bodies in the sections. Section 1 is a transverse section through the injection site. The darkened area indicates the central core of the injection site. The shaded area indicates the diffusion of the reaction product around the central core of the injection site. Section 2 is a transverse section through the beginning of a focus of labeled cell bodies in the hindpaw region of SII and through the area of maximum labeling of cell bodies in the ventral posterior inferior nucleus of the thalamus (VPI), indicates that the injection was in SII and not in SI since no label was observed in pars externa and pars arcuata of the thalamic ventrobasal complex (Vb) (Herron, 1979). A: axial body representation area of SI: 2, 3 and 4: 2nd, 3rd and 4th digit representation areas of SI; F: face representation area of SI.

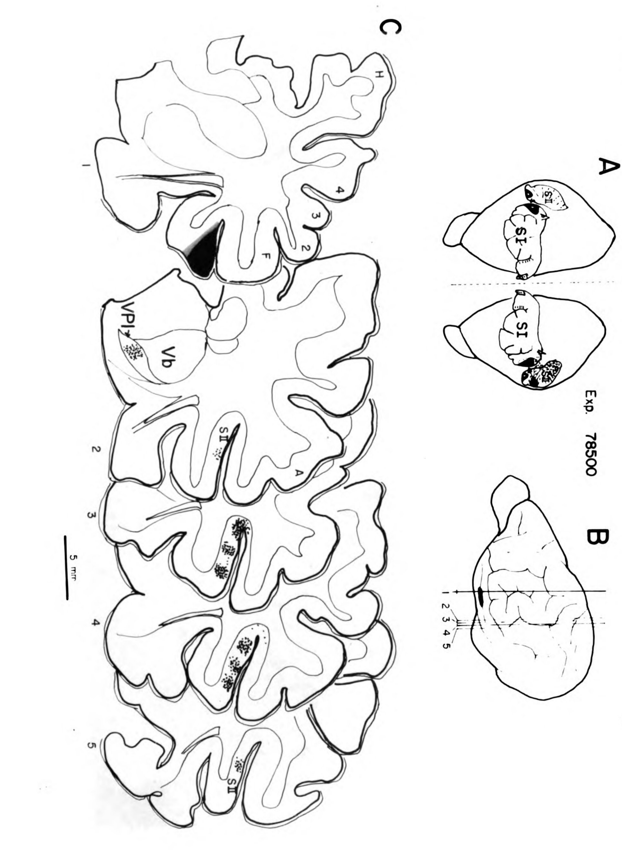

Figure 5

Figure 6: The distribution of HRP labeled cell bodies in the forepaw region of SI following an injection in the forepaw region of SII A. Schematic diagram of the cerebral hemispheres with all the sulci and gyri removed except those in SI to emphasize the relative situation of SI and SII. The darkened arrow indicates the injection site and the location of labeled cell bodies in SI. B. A tracing of the left cerebral hemisphere of a "standard" brain with the approximate locations of the transverse sections through the region of labeled cell bodies in SI forepaw region. The dots represent the approximate density of labeled cell bodies in the sections. The darkened area indicates the central core of the injection site. The shaded region surrounding the darkened area indicates the diffusion of the reaction product around the central core in the injection site. Section 11 is through the largest extent of the injection site and section 12 is through the area of maximum labeling of cell bodies in VPI (Herron, 1979). Note that the locations of foci of labeled cell bodies are more related to cortex in sulci than that of gyral crowns. 1, 2, 3, and 4: representation areas of digits 1, 2, 3, and 4: representation areas of digits 1, 2, 3 and 4; H: hindlimb; MI: primary motor cortex; Vb: pars externa of the thalamic ventrobasal complex.

Figure 6

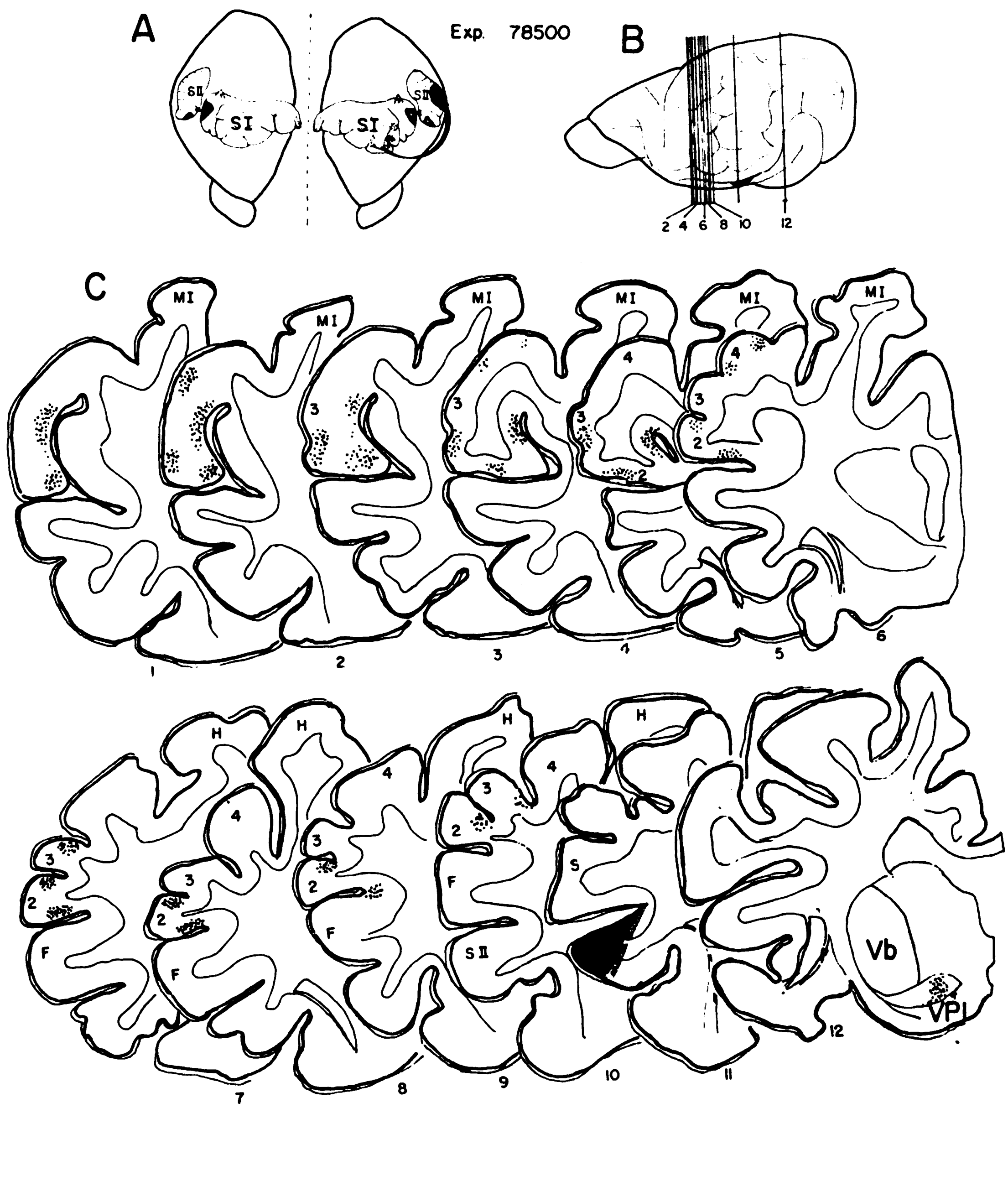
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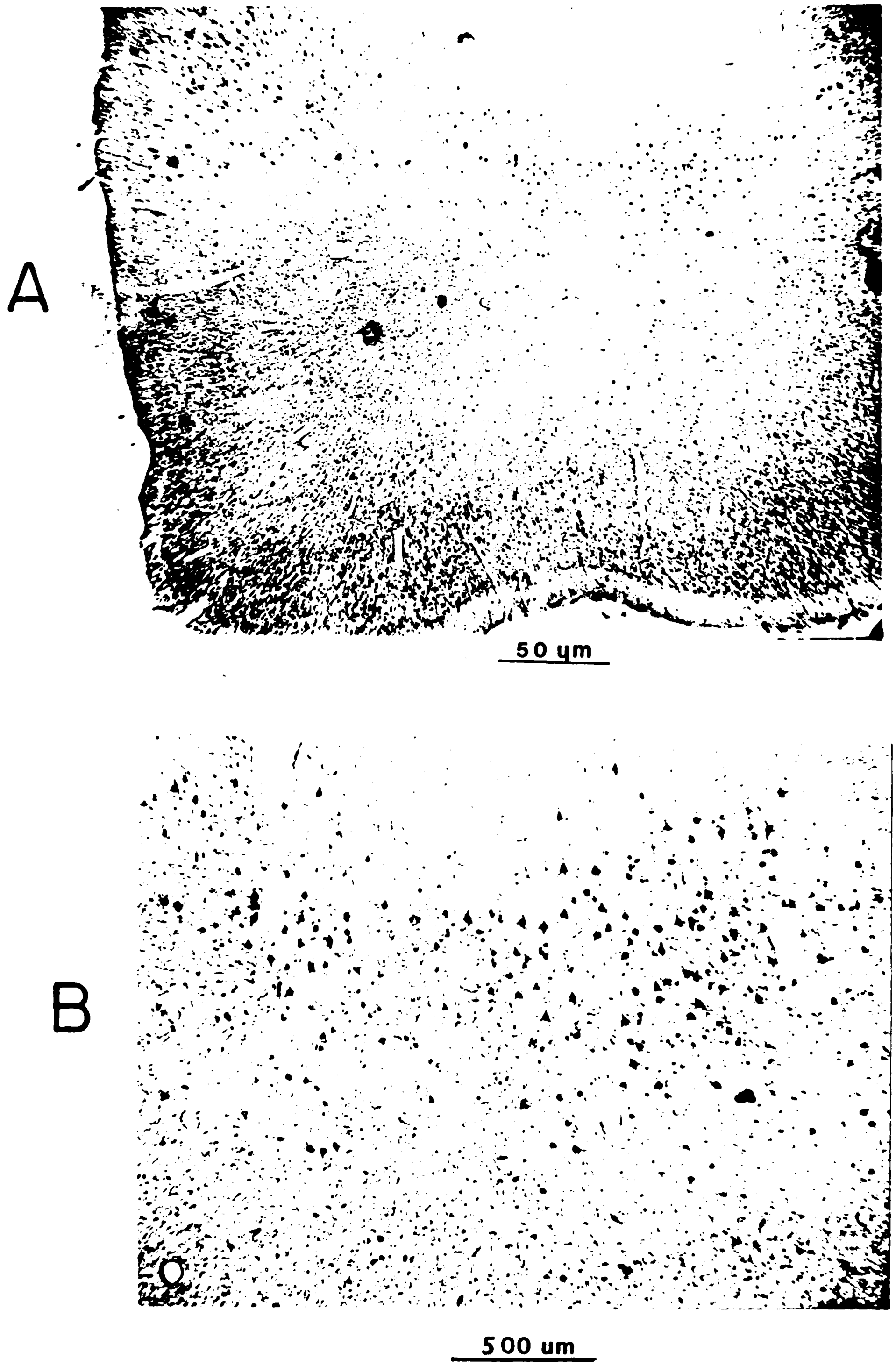
Figure 7: Photomicrograph of the cell bodies of origin of the SI to SII projection. A. Low magnification photomicrograph of the clusters of HRP labeled cell bodies observed in experiment 78500 (5X). B. Higher magnification of the cluster of labeled cell bodies in the dorsal part of A (50X) taken from a transverse section at the level of section 1 in figure 4.

Figure 7



lateral walls of the second digital representation area (figure 8). The topography of the two rostrocaudal strips of labeled cell bodies on the medial and lateral wall of the gryal crown was similar to those resulting from a larger injection in the SII forepaw area. The contralateral homotypic cortex was searched thoroughly for HRP positive cell bodies but none were found.

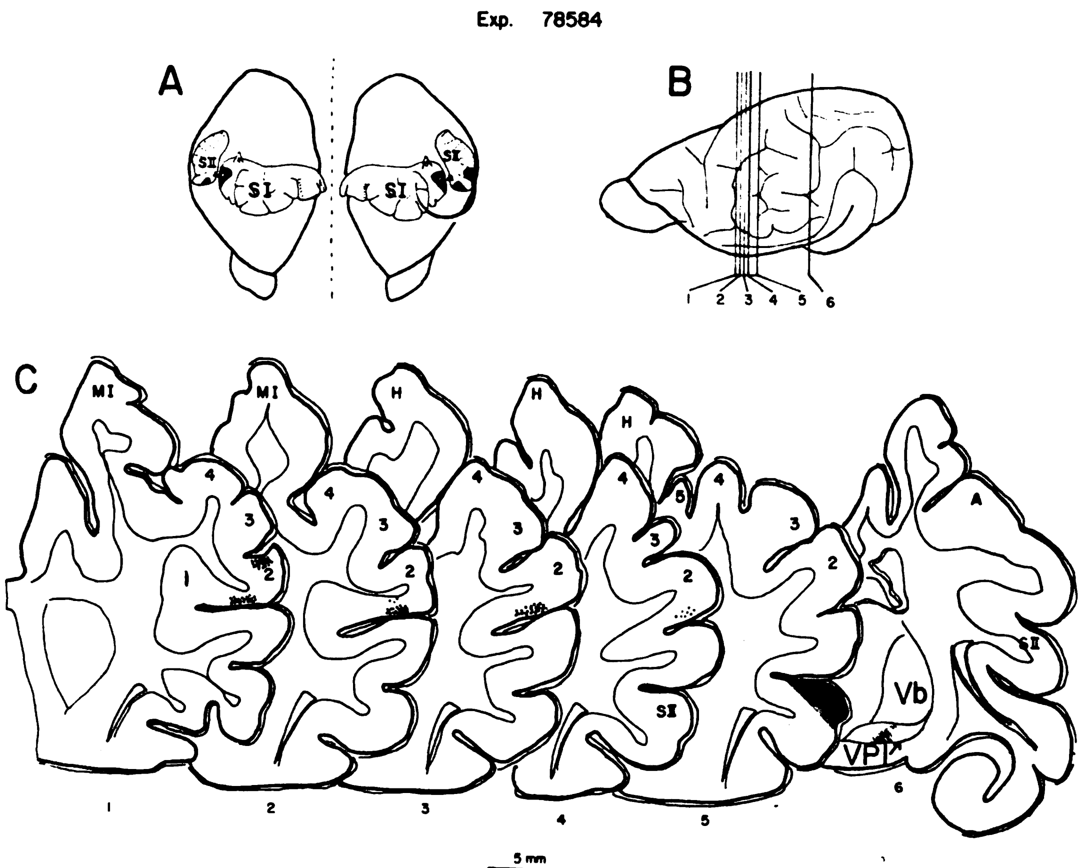
Typically, the HRP positive cell bodies were pyramidal shaped neurons in which the somata and the proximal and basal dendrites were labeled. The cell bodies of INA were primarily confined to layers II and III. The labeled cell bodies were among the largest observed in layers II and III of the forepaw area of SI. A light concentration of labeled cell bodies was sprinkled throughout the layers IV, V, and VI.

The intrahemispheric and commissural afferents of the SII hindpaw and trunk region. In experiment 78593, an injection of HRP was made in the electrophysiologically identified hindpaw and trunk region of SII. The cell bodies of INA, IHA and CA neurons were labeled as a result of this injection.

Figure 9 is a reconstruction of a series of transverse sections through the regions which contain the labeled cell bodies of INA neurons. In a series of transverse sections anterior to the injection site (sections 1-5 in figure 9), two loosely organized strips of labeled cell bodies were observed in the cortical region surrounding the depth of the suprasylvian sulcus. This cortical area corresponds to boundary region between the face regions of SI and SII. In the same series of transverse sections, a third and shorter rostrocaudally oriented strip of labeled cell bodies of INA were observed in the SII forepaw region (Section 4 in figure 9).

Figure 8: The distribution of HRP labeled cell bodies of IHA following an injection in the 2nd digit representation area of SII in experiment 78584. A. Schematic diagram of the cerebral hemispheres with all the sulci and gyri removed except those in SI to emphasize the relationship of SI and SII. The darkened arrow indicates the locations of the injection site and the region of labeled cell bodies. B. A tracing of the left cerebral hemisphere of a "standard" brain with the approximate locations of the transverse sections reconstructed in C. C. A series of transverse sections through the region of labeled cell bodies in the 2nd digit representation of SI. The dots represent the approximate density of labeled cell bodies in the sections. The darkened area indicates the central core of the injection site. The shaded region surrounding the darkened area indicates the diffusion of the reaction product around the central core of the injection site. Section 5 is through the largest extent of the injection site and section 6 is through the area of maximum labeling of cell bodies and terminals in VPI. Note that the location of foci of labeled cell bodies in SI are more related to sulcal cortex than that of the gyral crown. 1, 2, 3 and 4: representation areas of digits 1, 2, 3, and 4; H: Hindlimb; MI: primary motor cortex; Vb: pars externa of the thalamic ventrobasal complex.

Figure 8


Exp. 78584
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2
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SII
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VPI
SII
1
2
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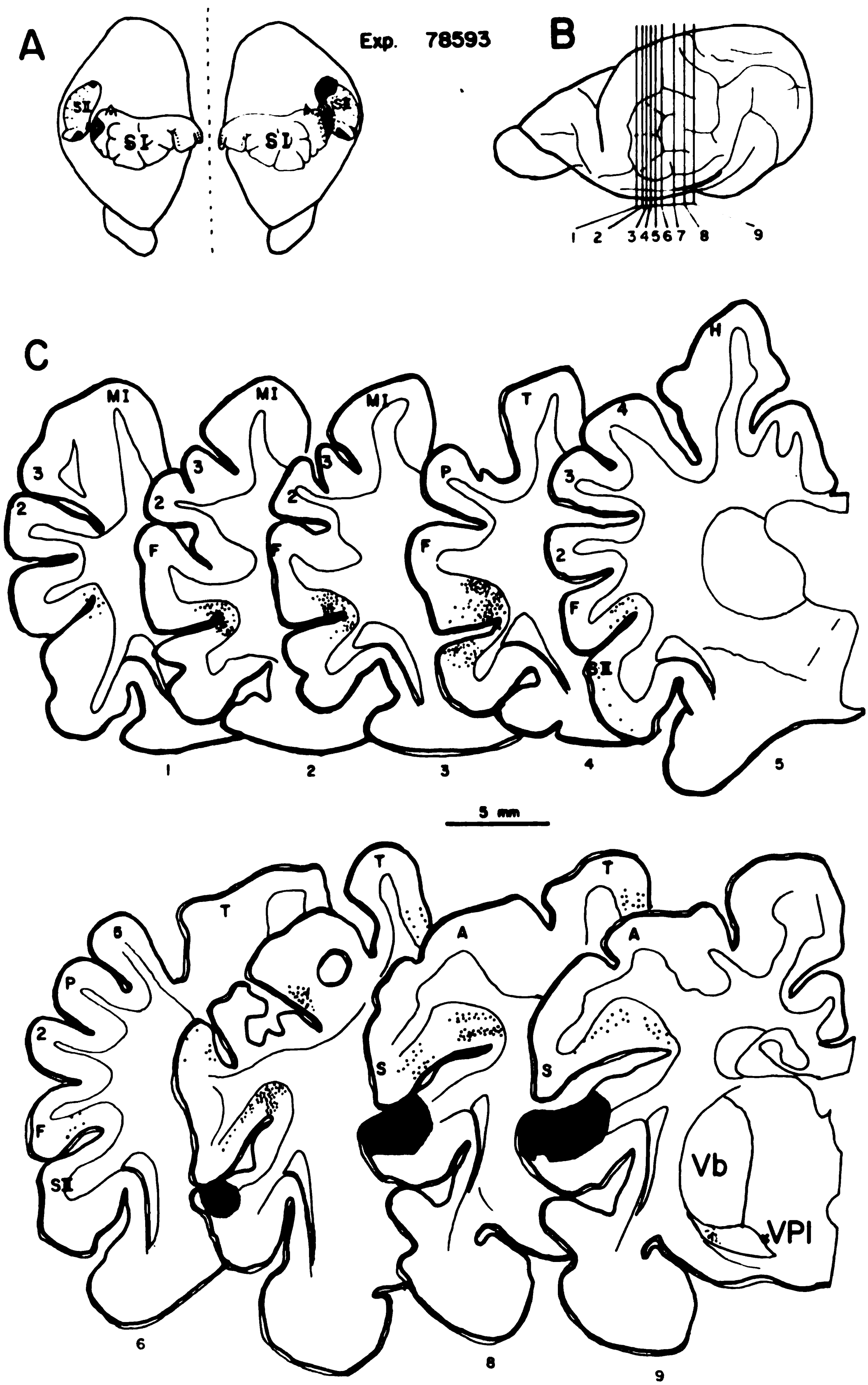
6
5 mm

Figure 9: The distribution of HRP labeled cell bodies of INA in SI and SII following an injection in the hindlimb and trunk regions of SII in experiment 78593. A. Schematic diagram of the cerebral hemispheres with all the sulci and gyri removed except those in SI to emphasize the relationship of SI and SII. The darkened area in the hindlimb and trunk region of SII indicates the injection site and the dots indicate the approximate distribution of labeled cell bodies in SI and SII. B. A tracing of the left cerebral hemisphere of a "standard" brain with the approximate locations of the transverse sections reconstructed in C. C. A series of transverse sections through the region of labeled cell bodies in SI and SII. The dots represent the approximate density of labeled cell bodies in the sections. The darkened area indicates the central core of the injection site. The shaded region surrounding the darkened area indicates the diffusion of the reaction product around the central core. Section 9 is a transverse section through both the injection site and the area of maximum labeling of cell bodies and terminals in VPI. Note that the locations of the labeled cell bodies are nonhomotopic to that of the injection site. Two foci of labeled cell bodies are observed. One focus is localized in the junctional region between SI and SII. Section 4 contains labeled cell bodies in SII. A second focus of labeled cell bodies occupies the occiput representation area of SI.

Figure 9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9

The bulk of the labeled cell bodies in this focus of labeled neurons were in layers II, III and V. Many labeled cell bodies were also observed in layers IV and VI.

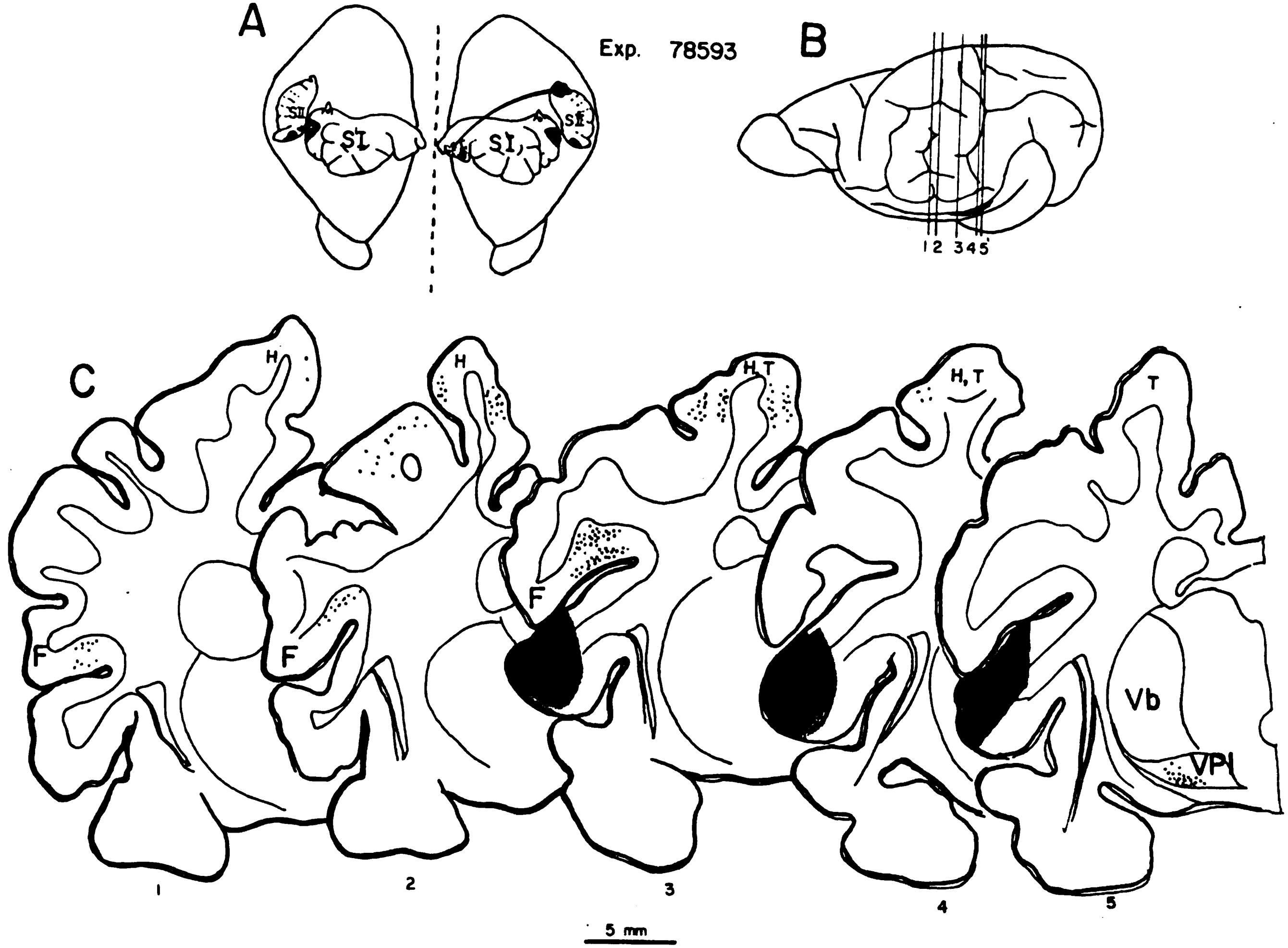
A second focus of labeled cell bodies of INA were observed in a region posterior to the first focus and medial to the injection site. The labeled cell bodies were distributed on the superior bank of the suprasylvian sulcus (sections 6-9 of figure 9). This cortex corresponds to the shoulder and occiput representation areas in SI. The foci of labeled cell bodies were well outside the zone of diffusion and all the labeled cell bodies were labeled in a granulated pattern; therefore, the labeled cell bodies are interpreted to be the result of physiological uptake by the terminals and retrograde transport by the axons of the labeled neurons.

The posterior strip of labeled cell bodies of INA was highly laminated. Labeled cell bodies were confined almost exclusively to layers II, III and V. Occasionally, small bridges of labeled cell bodies were observed in layer IV between those in layers III and V (section 7 of figure 9).

In experiment 78593, the cell bodies of IHA were found in a region of SI which corresponds to the trunk and hindlimb regions. Figure 10 is a reconstruction of transverse sections through the region of labeled cell bodies of IHA in SI and shows that the HRP positive cell bodies are organized into rostrocaudally oriented strips. Similar to the topography of the strips of labeled cell bodies observed in SI forepaw region following an injection in the forepaw region of SII, the strips of labeled cell bodies were located in the sulcal cortex (figure 10).

Figure 10: The distribution of HRP labeled cell bodies of IHA in the ipsilateral hindlimb and trunk regions of SI following an injection in the hindlimb and trunk regions of SII in experiment 78593. A. Schematic diagram of the cerebral hemispheres with all the sulci and gyri removed except those in SI to emphasize the relationship of SI and SII. The arrow indicates the injection site and the location of labeled cell bodies. B. A tracing of the left cerebral hemisphere of a "standard" brain with the approximate locations of the transverse sections reconstructed in C. C. A series of transverse sections through the region of labeled cell bodies in SI. The dots represent the approximate density of labeled cell bodies in the sections. The darkened area indicates the central core of the injection site. The shaded region surrounding the darkened area indicates the diffusion of the reaction product around the central core. Section 5 is a section through both the injection site and the area of maximum labeling of cell bodies in VPI. Note that the gyral crowns are free of labeled cell bodies. H: hindlimb representation area; T: trunk representation area; Vb: pars externa of the ventrobasal complex: and VPI: ventral posterior inferior nucleus of the thalamus.

Figure 10


A
SII
SI
SI
SII
Exp. 78593
B
1 2 3 4 5
C
H
F
F
H
O
F
H,T
F
H,T
T
Vb
VPl
1
2
3
4
5
5 mm

The cell bodies of IHA were concentrated primarily in the middle layers. In some instances, labeled cell bodies of IHA were found only in layers III and V.

In experiment 78593, the cell bodies of CA were observed in the contralateral homotopic cortices of SI and SII. In the contralateral SII region, the strips of labeled cell bodies surrounded a small cortical region which was free of labeled cell bodies. The island of cortex free of labeled cell bodies contained a marked increase in stellate shaped cell bodies and a lesser concentration of pyramidal shaped cell bodies than that of the cortex which contained labeled cell bodies. The island that was free of labeled cell bodies corresponds to the hindpaw region of SII.

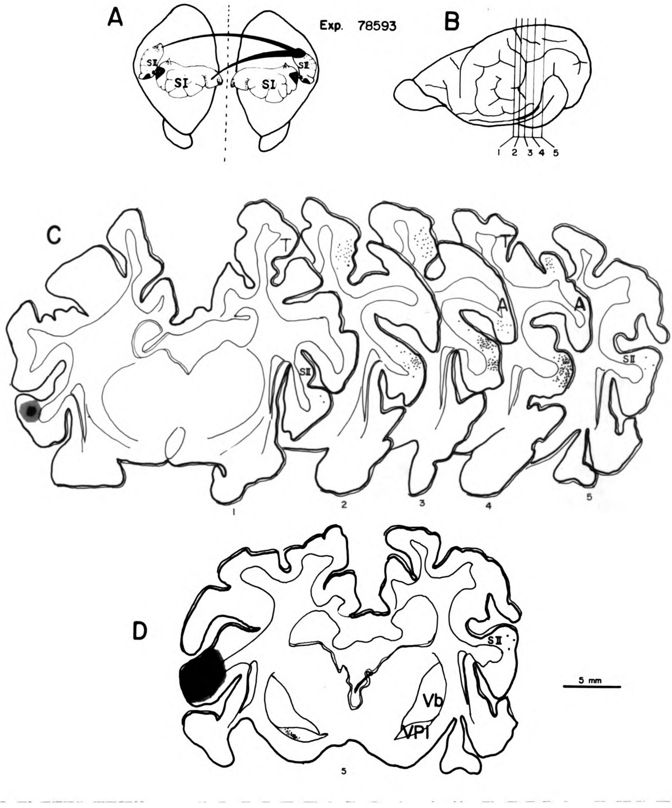
The density of labeled cell bodies of CA in SI were light compared to the density of labeled cell bodies of CA in SII. Figure 11 is a reconstruction of a series of transverse sections through the region of labeled cell bodies in SI and SII. It shows that the HRP positive cell bodies in SI and SII are loosely organized into rostrocaudally oriented strips.

The labeled cell bodies of commissurally projecting neurons were found in all layers except layer 1. Most of the HRP positive cell bodies were found in layers II, III and V. Fewer labeled cell bodies were found in layer IV.

Measurements were made of various parameters of the clusters of labeled cell bodies in experiment 78593 to better understand the organization of the diverse afferent sources. Measurements were made of the diameter of clusters and intercluster distances in order to determine if the spatial relationships of clusters in one functional region were consistent with those in another functional region. These results showed no consistent relationships between clusters in one

Figure 11: The distribution of HRP labeled cell bodies in the contralateral SI and SII region following an injection in the hindlimb and trunk regions of SII in experiment 78593. A. Schematic diagram of the cerebral hemisphere with all the sulci and gyri removed except those in SI to emphasize the relationship of SI and SII. The darkened area in the hindlimb and trunk regions of SII indicates the injection site and the arrows indicate the region of labeled cell bodies in the contralateral hindlimb and trunk regions of a "standard" brain with the approximate locations of the transverse sections reconstructed in C. C. A series of transverse sections through the region of labeled cell bodies in SI and SII. The dots represent the approximate density of the labeled cell bodies in the sections. In section 5, the darkened area indicates the central core of the injection site and the shaded area indicates the diffusion of the reaction product around the central core. Section 5 is also through the area of maximum labeling of cell bodies in VPI. Note the distribution of labeling of cell bodies in section 3 in the contralateral SII and the axial and trunk representation areas in SI. A: axial body representation area; T: trunk representation area; VPI: ventral posterior inferior nucleus; and Vb: pars externa of the ventrobasal complex.

Figure 11


A
Exp. 78593
SII
SI
SI
SII
B
1
2
3
4
5
C
T
A
A
T
SII
SII
SII
1
2
3
4
5
D
SII
Vb
VPl
5 mm
5

functional region or between clusters in different functional regions.

The diameter of the clusters of labeled cell bodies of INA in the boundary region between SI and SII ranged between 200 to 700 μm. The cell bodies of INA afferents in the hindlimb and trunk regions of SI were slightly larger (300-800 μm).

The intercluster distances varied widely within each functional region. Clusters were closer together in SII than they were in SI. In SI, as seen in transverse sections, the intercluster distances ranged between 70 to 1000 μm. Generally in SI, the clusters were in the sulcal cortex of adjacent sulci and, therefore, the intercluster distances were determined by the width of the gyral crown. The intercluster distances of labeled cell bodies in SI were typically around 1000 μm. In the loosely organized clusters of labeled cell bodies of CA in the SII hindlimb and trunk regions, the diameter of clusters were generally larger (500 μm - 1000 μm) than the clusters in the ipsilateral cortex but the intercluster distances were shorter (60 - 200 μm).

In experiment 78511, a large injection of HRP was made in the SII region. The reaction product in the injection sites covered much of the somatotopically organized region of SII. In contrast to the results of other injections in SII, labeled cell bodies in IHA were found in the cortex of the gyral crown of hindlimb representation area of SI. A thin layer of HRP positive pyramidal shaped cell bodies in layer V were distributed between two clusters of labeled cell bodies in the sulcal cortices (figure 12). The labeled cell bodies were among the largest in the SI hindlimb and trunk region.

Figure 12: Labeled cell bodies of the SII hindlimb to SI hindlimb projection. A. Low magnification of labeled cell bodies in SI hindlimb regions following an injection in the SII hindlimb region (50X). Higher magnification of pyramidal neurons in layer V of photomicrograph A (250X).

Figure 12

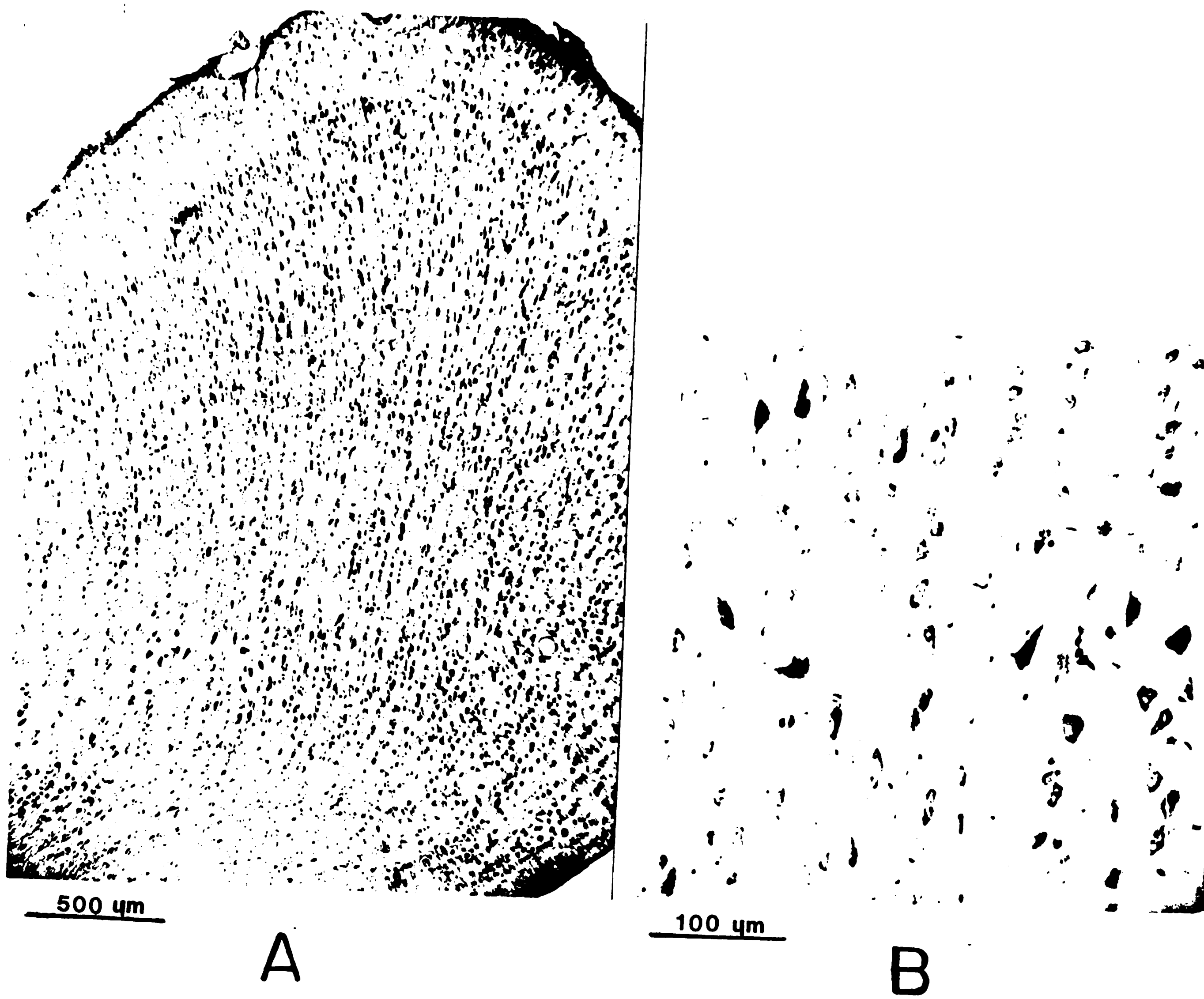
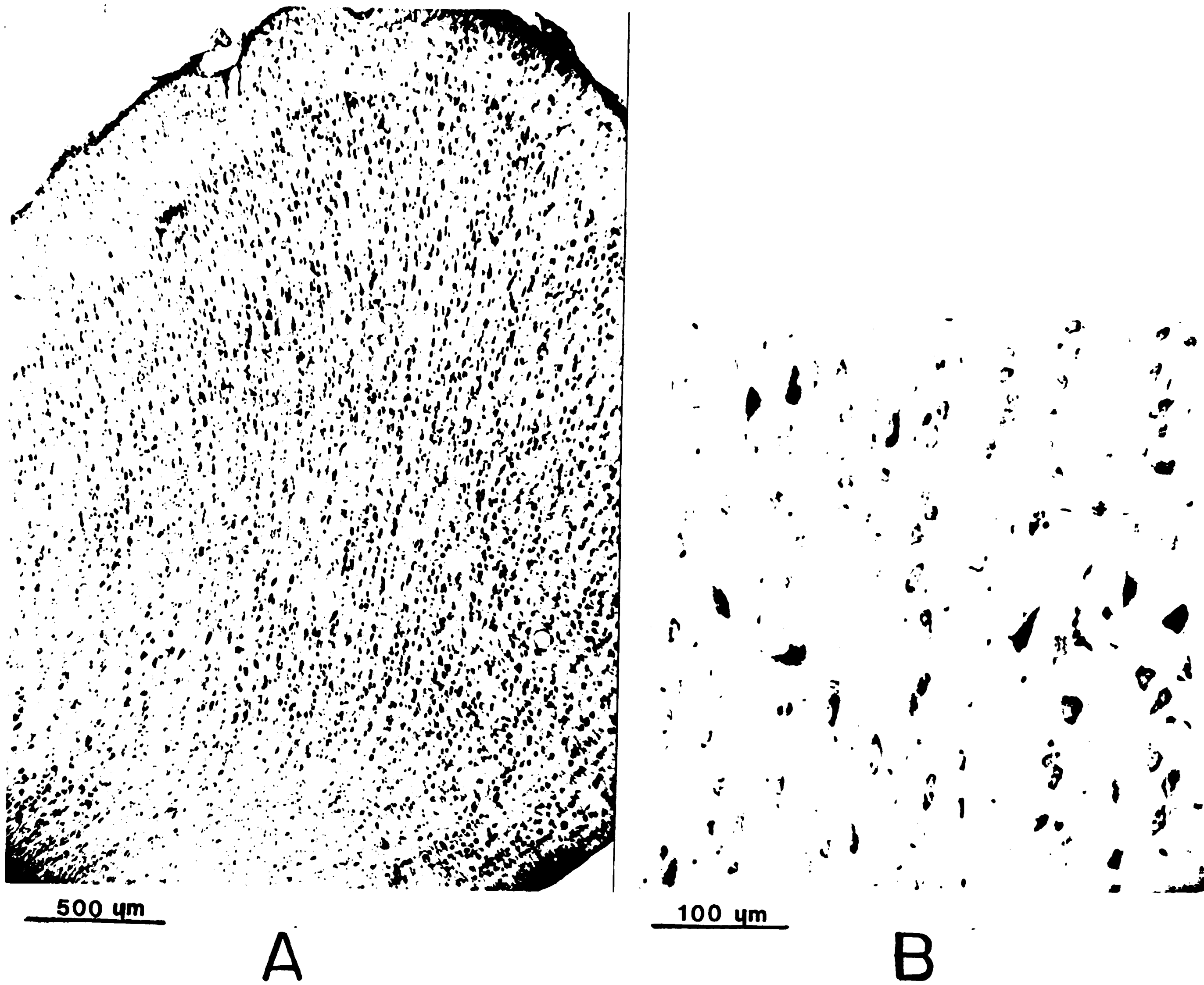


Figure 12: Labeled cell bodies of the SII hindlimb to SI hindlimb projection. A. Low magnification of labeled cell bodies in SI hindlimb regions following an injection in the SII hindlimb region (50X). Higher magnification of pyramidal neurons in layer V of photomicrograph A (250X).

Figure 12



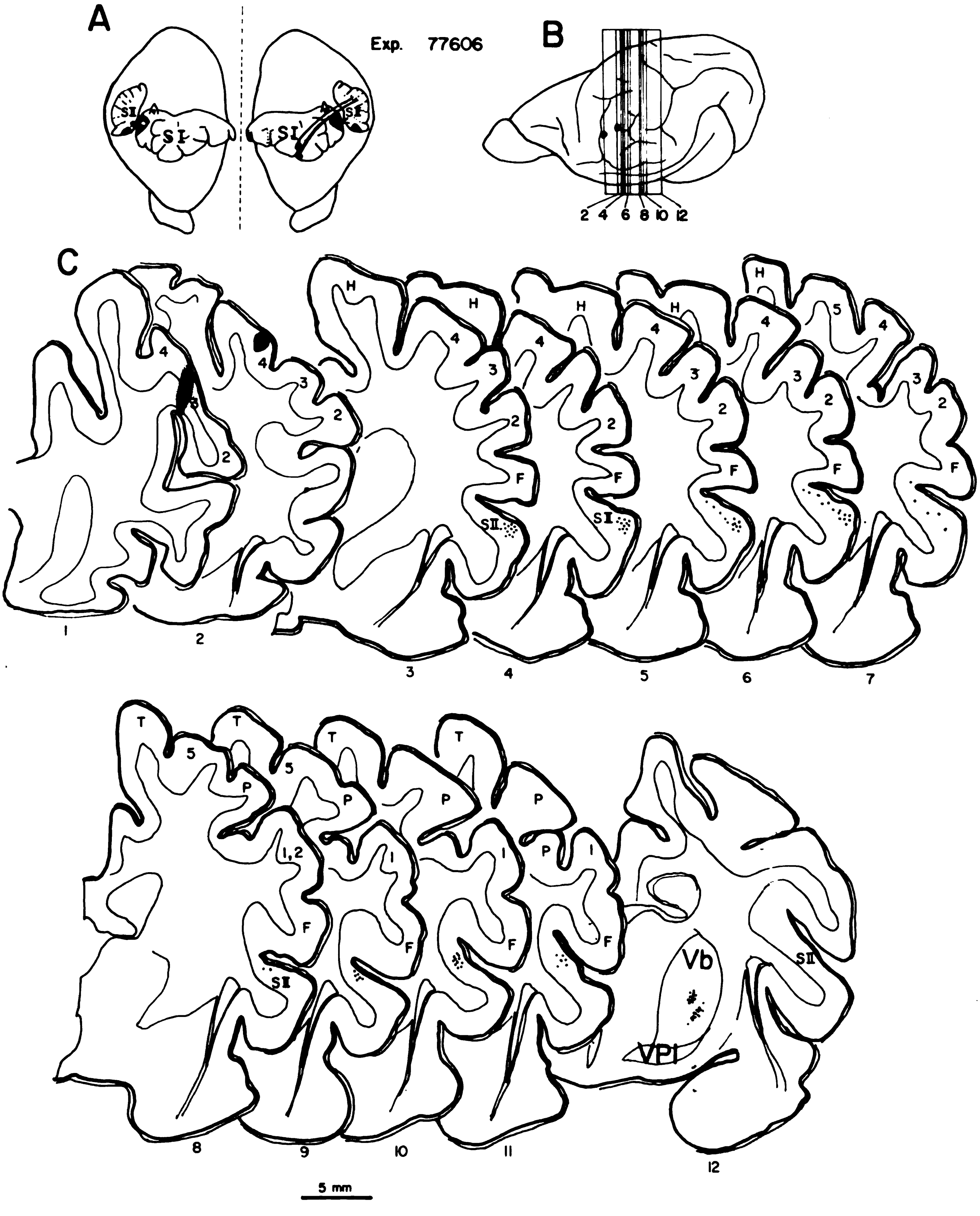
The intrahemispheric afferents of the SI forepaw region. Experiment 77606 exemplified the intrahemispheric afferents of the 3rd and 4th digit projection areas in SI. Two small injections were made in these digit representation areas to determine if corresponding pairs of foci of labeled cell bodies of intrahemispheric afferents would be produced. One injection was in the anterior gyral crown of digit 3 representation and a slightly smaller injection was posterior to the first injection in the gyral crown of digit 4 representation area. Small foci of labeled cell bodies were observed in the 3rd and 4th digital representation areas of Vb.

Two foci of labeled cell bodies of IHA were found in the SII region. One focus of labeled cell bodies were located medial and posterior to the other focus on the inferior bank of the suprasylvian sulcus. The focus of labeled cell bodies were in a region which corresponds to the 3rd digit representation area (figure 13). The second focus of labeled cell bodies was anterolateral to those of the first focus and corresponds to a more proximal representation of the 4th digit. The area between the two foci of labeled cell bodies was largely free of HRP positive cell bodies. The distance between the foci of labeled cell bodies was approximately the same as that of the injection sites. The cell bodies of IHA in SII were located in all layers except layer I. The largest percentage of labeled cell bodies was found in layer III and the majority of the remainder were found in layer V.

The cell bodies of INA were located in the adjacent digital and proximal volar surface representation areas in SI. Figure 14 is a reconstruction of a series of transverse sections through the region of the labeled cell bodies of INA observed in the experiment 77606.

Figure 13: The distribution of HRP labeled cell bodies in the forepaw region of SII following an injection in the 3rd and 4th digital representation areas of SI. A. Schematic diagram of the cerebral hemispheres with all the sulci and gyri removed except those in SI to emphasize the relationship of SI and SII. The two arrows indicate the injection sites and the locations of the labeled cell bodies in SII. B. A tracing of the left cerebral hemisphere of a "standard" brain with the approximate locations of the transverse sections reconstructed in C. C. A series of transverse sections through the region of labeled cell bodies in the SII forepaw region. The dots represent the approximate density of labeled cell bodies in the sections. The darkened area indicates the central core of the injection site. The shaded region surrounding the darkened area indicates the diffusion of the reaction product around the central core of the injection site. Section 12 is through the area of maximum labeling of cell bodies in Vb. Note the two foci of labeled cell bodies in SII that correspond to the two sites of HRP injections. 1, 2, 3, 4 and 5: the digital representation areas of SI; H: hindlimb representation area, P: palm representation area; F: face representation area; Vb: pars externa of thalamic ventrobasal complex; VPI: ventral posterior inferior nucleus of the thalamus.

Figure 13


A
SI
SII
SI
SII
Exp. 77606
B
2 4 6 8 10 12
C
H
4
3
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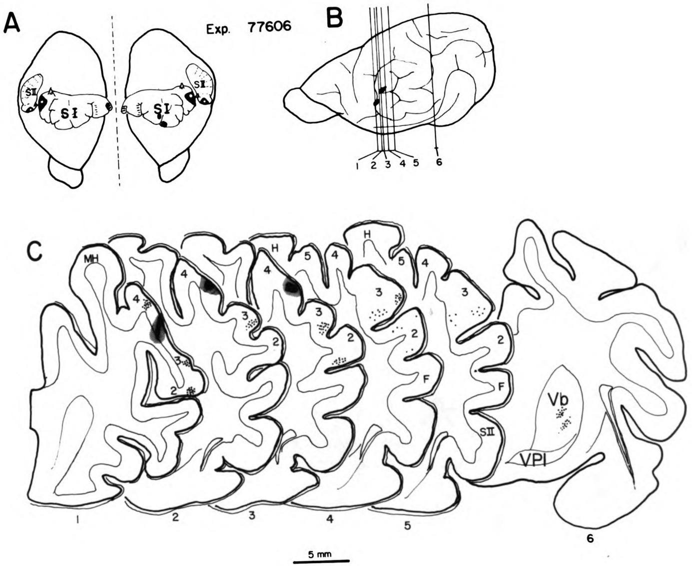
SII
5
1
2
3
4
5
6
7
T
P
1,2
I
Vb
VPl
8
9
10
11
12
5 mm

Figure 14: The distribution of HRP labeled cell bodies in SI following injections in the 3rd and 4th digit representation areas of SI in experiment 77606. A. Schematic diagram of the cerebral hemispheres with all the sulci and gyri removed except those in SI to emphasize the relationship of SI and SII. B. A tracing of the left cerebral hemisphere of a "standard" brain with the approximate locations of the transverse sections reconstructed in C. C. A series of transverse sections through the injection sites and the area of labeled cell bodies in SI. The dots represent the approximate density of labeled cell bodies in the sections. The darkened area indicates the central core of the injection site. The shaded region surrounding the darkened areas indicate the diffusion of the reaction product around the central core. Section 6 shows the two foci of labeled cell bodies in Vb. Note the labeled cell bodies posterior to the injection site in the proximal volar representation area of digit 3 in SI.

Figure 14



The topography of the labeled cell bodies are more related to sulcal cortex than with the cortex of the gyral crown.

The labeled cell bodies of INA were limited almost entirely to the supragranular layers. Most of the HRP positive cell bodies were pyramidal shaped.

No HRP positive cell bodies were found in the homotopic or heterotopic areas of the contralateral SI cortex despite thorough searches.

Intrahemispheric distribution of terminals from the SI forepaw region. The terminals of intrahemispheric homotopic efferents (IHE) were indicated by the results of experiment 77604. A short post-injection survival time (20 hrs.) enhanced the visualization of terminals. The injection covered the representation areas of palm and proximal region of the 5th digit in the SI forepaw region. The terminals were located in the SII region on the inferior bank of the suprasylvian sulcus. The terminals were distributed over layers II, III, IV and V (figure 15).

In experiment 77608, the distribution of terminals of neurons in the 4th digit representation of SI area was determined by using anterograde degeneration technique. Following a small ablation (3mm in diameter) of the gyral cortex in the 4th digit representation area of SI, degenerated fibers and terminals were homogenously distributed in layers II, III, IV and V of SII (figure 16). In contrast to the organization of cell bodies of IHA, no patches of degenerated fibers or terminals were observed. The medial-lateral width of the SII area which contained degenerated fibers and terminals was larger than that typically occupied by labeled cell bodies following injection of HRP in the SI digital representation area.

Figure 15: The distribution of HRP labeled terminals in the ipsilateral SII region following an injection of HRP in digit 5 representation area of SI in experiment 77604. A. Schematic diagram of the cerebral hemispheres with all the sulci and gyri removed except those in SI to emphasize the relationship of SI and SII. The darkened area and arrow indicate the injection site and the distribution of terminals in SII. B. A tracing of the left cerebral hemisphere of a "standard" brain with the approximate locations of the transverse sections through the region of labeled terminals in the ipsilateral SII region. C. Transverse sections through the injection site (section 1) and the region of labeled terminals in the ipsilateral SII. Section 2 contains the area of maximum labeling of terminals in Vb. Note that the terminals are distributed in the middle layers of SII.

Figure 16: The distribution of degenerated fibers and terminals in the ipsilateral SII region following an ablation of the gyral crown of the 5th digital representation area in SI in experiment 77608. A. Schematic diagram of the cerebral hemispheres with all the sulci removed except those in SI to emphasize the relationship of SI and SII. B. A tracing of the left cerebral hemisphere of a "standard" brain with the approximate locations of the transverse sections through the region of degenerated fibers and terminals reconstructed in C. C. A series of transverse sections through the region of degenerated fibers and terminals in the ipsilateral SII cortical region. The dots represent the approximate density of the degenerated fibers and terminals observed in the histological sections. Note that the medial-lateral width of the focus of degenerated fibers and terminals are much greater than the medial-lateral width of strips of labeled cell bodies following an injection of HRP in the forepaw area of SI.

Intrahemispheric and commissural afferents of SI agranular area. In experiment 78565, a 1 µl injection of HRP was made in an area that yielded a high amplitude evoked potential after manual stimulation of the contralateral upper hindlimb. The effective zone of the injection site, as determined by labeled cell bodies and terminals in Vb, covered the distal limb and trunk representation areas.

The cell bodies of IHA were found in the hindlimb and trunk region of SII. Figure 17 is a reconstruction of a series of transverse sections through the region of labeled cell bodies in the SII region. These sections showed a loosely organized rostrocaudal oriented strip of labeled cell bodies. Occasionally, the labeled cell bodies were subdivided into 2 or 3 discrete clusters.

In experiment 78508, an injection of HRP was made in the trunk and leg region of SI. The distribution of labeled terminals and cell bodies in Vb indicated that the central core of the injection site covered the leg and trunk region (Figure 18). Similar to the organization of cell bodies in SII following the injection in the upper leg in experiment 77565, the labeled cell bodies in SII of IHA formed one fairly large strip of cell bodies. The strip of labeled cell bodies on the inferior bank of the suprasylvan sulcus in this experiment was slightly anteromedial to the strip of labeled cell bodies resulting from an injection in the hindlimb area of SI in experiment 77565.

The cell bodies of IHA were distributed in layers II, III, IV and V. Typically, the cell bodies were evenly distributed in these layers. Occasionally, the labeled neurons were only in the supragranular layers.

Figure 17: The distribution of HRP labeled cell bodies of IHA in the ipsilateral SII following an injection in the hindlimb and trunk region of SI in experiment 78565. A. Schematic diagram of the cerebral hemispheres with all the sulci and gyri removed except those in SI to emphasize the relationship of SI and SII. B. A tracing of the left cerebral hemisphere of a "standard" brain with the approximate locations of the transverse sections reconstructed in C. C. A series of transverse sections through the region of labeled cell bodies in the hindlimb and trunk region of the ipsilateral SII region. The dots represent the approximate density of labeled cell bodies in the sections. The darkened area indicates the central core of the injection site. The shaded region surrounding the darkened area indicates the diffusion of the reaction product around the central core in the injection site. Section 1 is through the area of maximum labeling of cell bodies and terminals in Vb. Note that most of the labeled cell bodies in SII are in layers III and V. In section 3, the labeled cell bodies in SII form 3 distinct clusters.

Figure 17

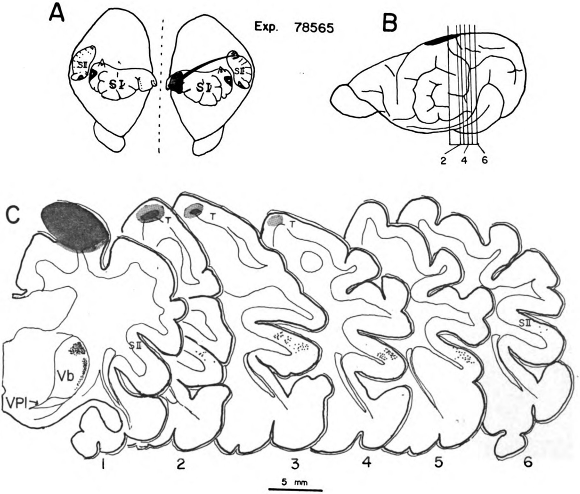
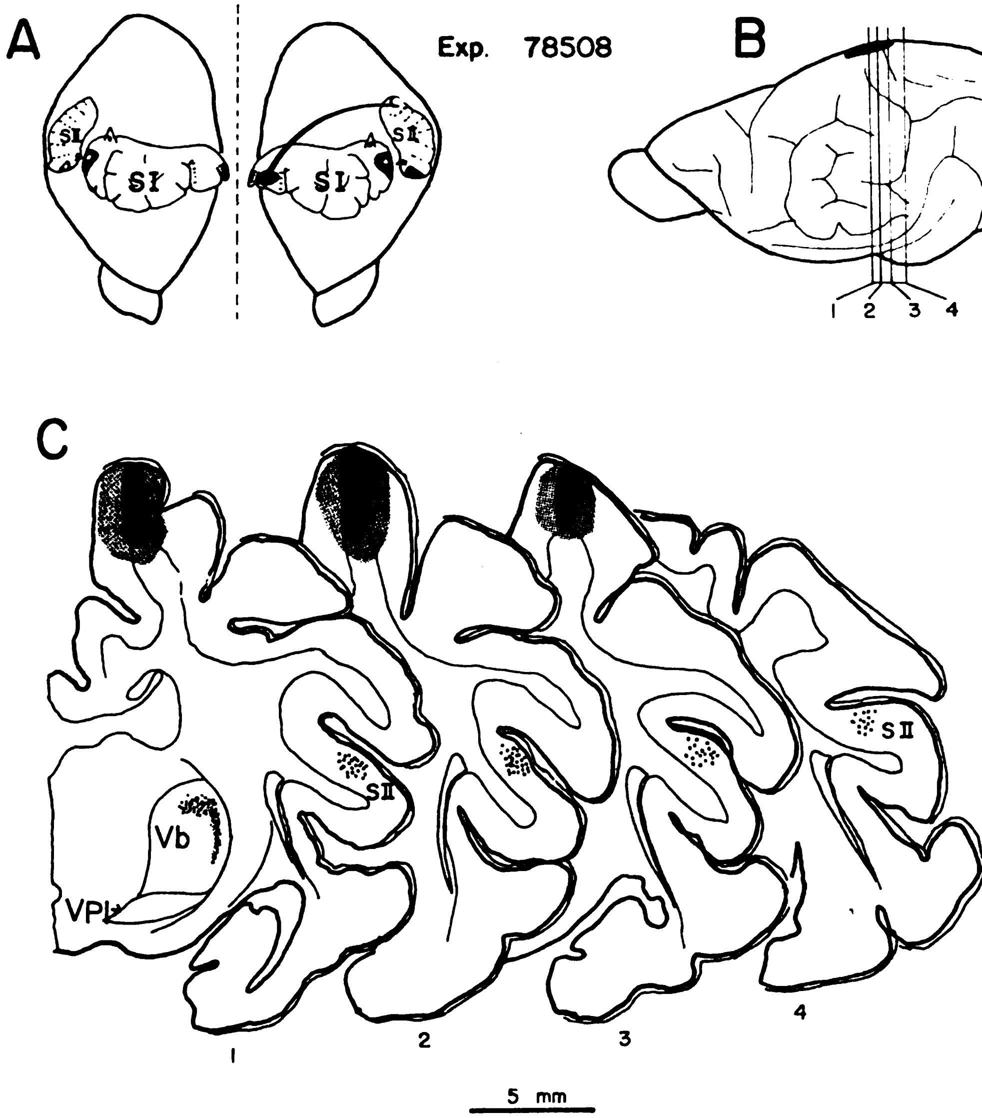


Figure 18: The distribution of labeled cell bodies in the hindlimb and trunk region of SII following an injection in the hindlimb and trunk region of SI in experiment 78508. A. Schematic diagram of the cerebral hemispheres with all the sulci removed except those in SI to emphasize the relationship of SI and SII. B. A tracing of the left cerebral hemisphere of a "standard" brain with the approximate locations of the transverse sections reconstructed in C. C. A series of transverse sections through the region of labeled cell bodies in the ipsilateral SII region. The dots represent the approximate density of labeled cell bodies in the sections. The darkened area indicates the central core of the injection site. The shaded region surrounding the darkened area indicate the diffusion of the reaction product around the central core. Section 1 is a transverse section through both the injection site and the area of maximum labeling of cell bodies and terminals in Vb. Note the formation of the labeled cell bodies in the ipsilateral SII hindlimb and trunk region into a rostrocaudal oriented strip. Vb: pars externa of ventrobasal complex; and VPI: ventral posterior inferior nucleus of the thalamus.

Figure 18



In experiment 77559, multiple small injections (.025 total amount injected) were made in a stepped vertical penetration through a region of cortex responsive to manual stimulation of the trunk. The central core of the injection site was less than 1 mm in diameter in all the cortical layers.

The injection labeled a discrete group of cell bodies in the trunk representation area of Vb. Labeled fibers exited below the injection site where some entered the internal capsule, some were observed in the corpus callosum, and others were directed laterally (Figure 19). Despite a thorough search, no labeled cell bodies were observed in the ipsilateral SII region.

In transverse sections, the labeled cell bodies of CA were distributed in the contralateral homotopic cortex over a 3 mm area (Figure 20). The diameter of the focus of labeled cell bodies was relatively larger than that of the injection site. These data suggest that the cortex in the trunk region receives commissural connections but does not receive intrahemispheric connections. In addition, the terminals of commissural neurons are convergent in the contralateral homotopic cortex.

Larger injections of HRP in the upper limb and trunk representation areas of experiment 77565 resulted in the labeling of two distinct foci of cell bodies in the contralateral homotopic cortex. Figure 21 is a reconstruction of a series of transverse sections through the region of labeled cell bodies. It shows strips of labeled cell bodies distributed primarily in the sulcal cortex. The diamter of each focus of labeled cell bodies was 500 to 1000 μm wide. The two strips of labeled cell bodies were occasionally joined by a thin

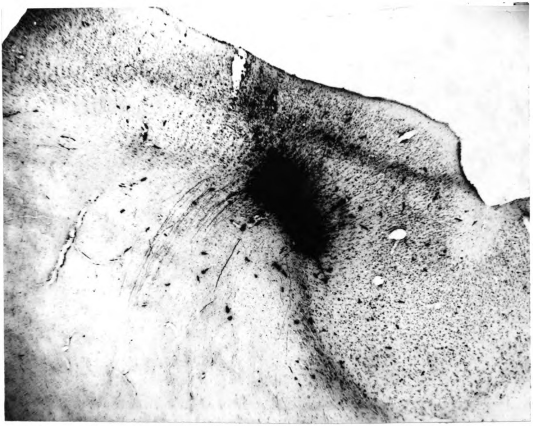


Figure 19: Photomicrograph of the HRP injection site in experiment 77559. Note the labeled fibers below the injection site.

Figure 20: The distribution of HRP labeled cell bodies in the contralateral homotopic cortex following an injection in the trunk region of SI in experiment 77559. A. Schematic diagram of the cerebral hemispheres with all the sulci and gyri removed except those in SI to emphasize the relationship of SI and SII. The arrow in A indicates the injection site and the location of labeled cell bodies. B. A tracing of the left cerebral hemisphere of a "standard" brain with the approximate locations of the transverse sections reconstructed in C. C. A series of transverse sections through the region of labeled cell bodies in the contralateral homotopic SI cortex. The dots represent the approximate density of labeled cell bodies in the sections. The darkened area indicates the central core of the injection site. The shaded region surrounding the darkened area indicates the diffusion of the reaction product around the central core. Section 5 is through the area of maximum labeling of cell bodies in Vb. Note that the distribution of labeled cell bodies in the contralateral cortex is spread over an area much greater than that of the injection site. T, trunk representation area, S, shoulder representation area. Vb: pars externa of the ventrobasal complex; and VPI: ventral posterior inferior nucleus of the thalamus.

Figure 20

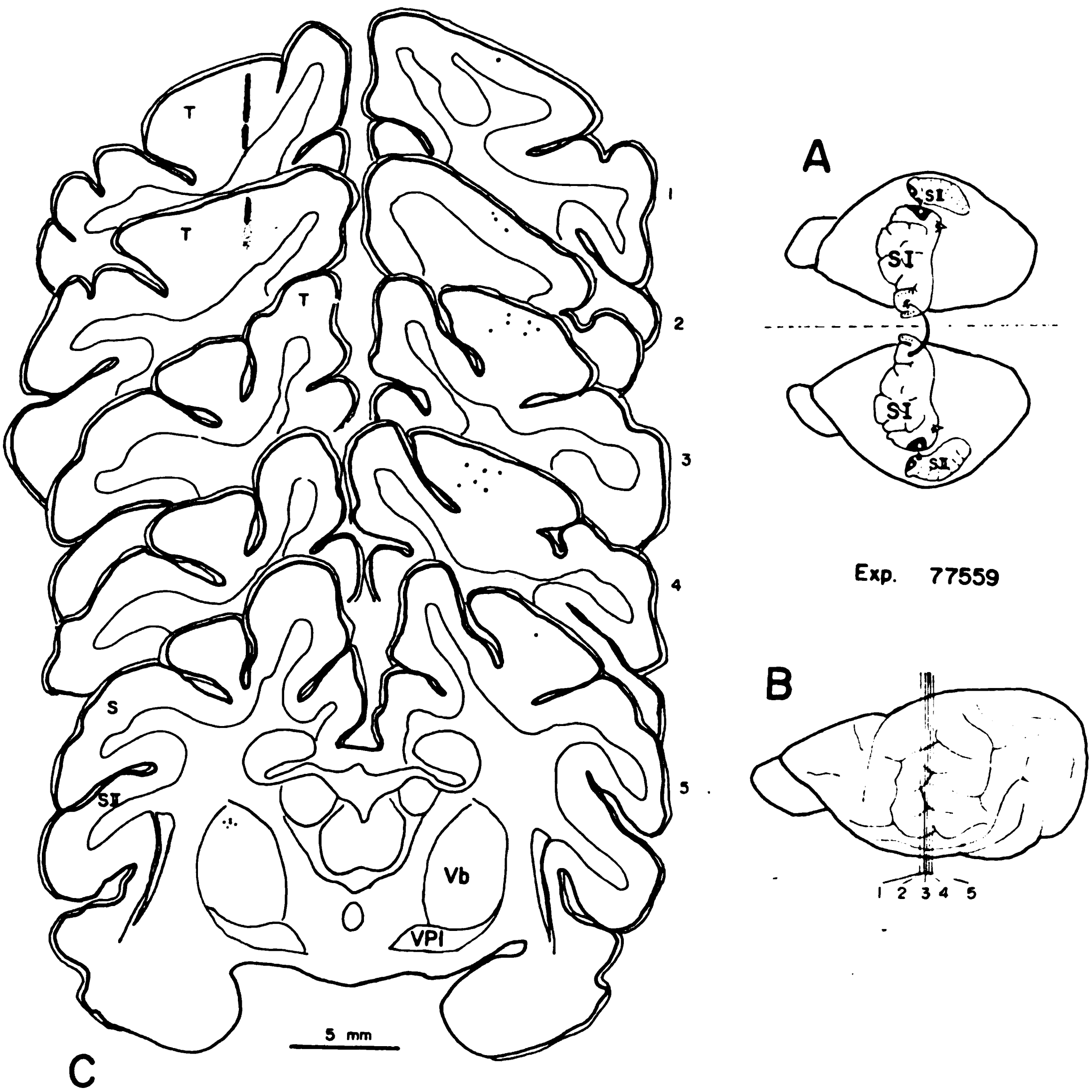
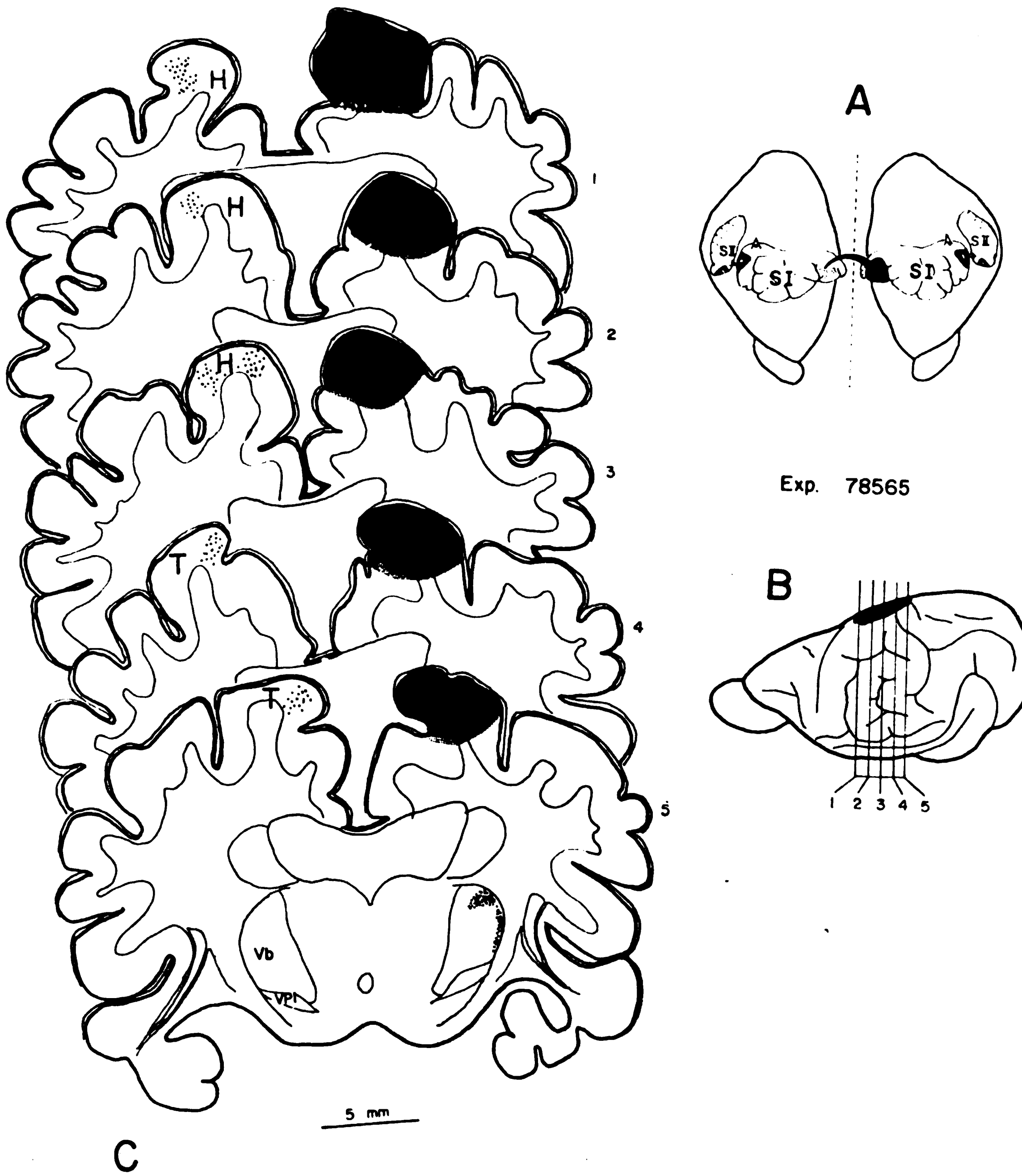


Figure 21: The distribution of HRP labeled cell bodies of CA in the hindpaw and trunk region of SI following an injection in the contralateral SI hindpaw and trunk regions. A. Schematic diagram of the cerebral hemispheres with all the sulci and gyri removed except those in SI to emphasize the relationship of SI and SII. The darkened arrow indicates the injection site and the location of the labeled cell bodies of CA. B. A tracing of the left cerebral hemisphere of a "standard" brain with the approximate locations of the transverse sections reconstructed in C. C. A series of transverse sections through the region of labeled cell bodies of CA in the hindpaw and trunk regions. The dots represent the approximate density of labeled cell bodies in the sections. The darkened area indicates the central core of the injection site. The shaded region surrounding the darkened area indicates the diffusion of the reaction product around the central core in the injection site. Section 11 is also through the region of maximum labeling of cell bodies in Vb. Note the rostrocaudal oriented strips of labeled cell bodies. In section 3, a thin lamina of labeled cell bodies connects the two clusters of labeled cell bodies. H: hindlimb representation area; T: trunk representation area; Vb: pars externa of the ventrobasal complex; and VPI: ventral posterior inferior nucleus of the thalamus.

Figure 21



layer of labeled cell bodies in layer V.

In experiments 77565 and 78508, the density of labeled cell bodies of CA was comparable to that INA and IHA. The majority of the labeled neurons had pyramidal shaped cell bodies. The laminar organization of cell bodies of CA were distributed primarily in layers II, III and V.

Intracortical and commissural efferents of SI agranular cortex. In experiment 77586, tritiated leucine and proline was injected in the middle of a zone responsive to manual stimulation of the trunk. A very dense concentration of grains was observed above fibers and terminals in the trunk and upper leg representation areas of the Vb nucleus in the thalamus.

Silver grains characteristic of fibers and terminals were observed in the ipsilateral SII cortex on the inferior bank of the suprasylvan sulcus. The grains were distributed in patterns characteristic of fibers above the white matter and sixth layer of the cortex. A random distribution of silver grains indicative of terminals was observed in layers V, IV, III and II. The heaviest concentration of grains was above terminals in layers V, III, and II (figure 22 and 23).

A dense concentration of grains was observed above fibers in the corpus callosum. No grain patterns characteristic of terminals were observed in the contralateral SI homotopic cortex.

Summary of Results. The results of this series of experiments can be summarized by the observation that the intrahemispheric and commissural connections fall into three categories. These categories are: (a) intrahemispheric homotopic connections (IHA), (b) intrahemispheric

Figure 22: Distribution of fibers and terminals originating from SI trunk region. A. Darkfield photomicrograph of silver grains above fibers which exited below the injection site. Note that the fibers exited below the injection site in two main bundles in which some of the fibers are directed laterally (left in the photomicrograph) and some of the fibers are directed medially toward the corpus callosum. B. Darkfield photomicrograph of straight chains of silver grains that are indicative of fibers in the corpus callosum. C. Darkfield photomicrograph of a patch of irregular arrangement of silver grains that are indicative of terminals in the ipsilateral SII cortical region.

Figure 22

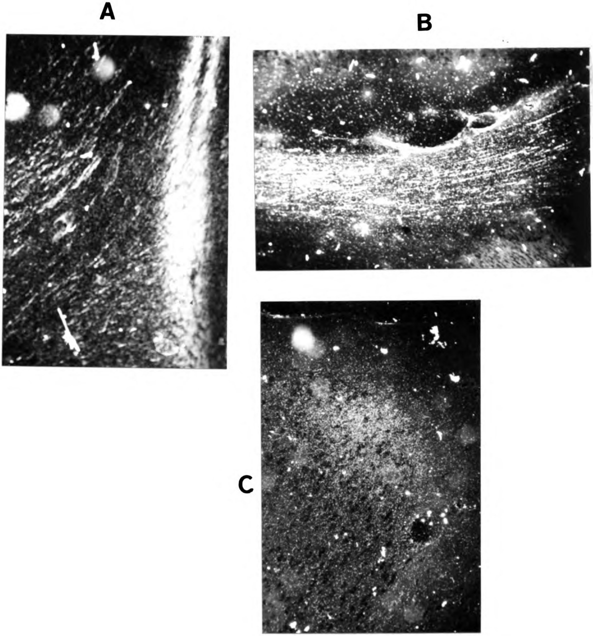
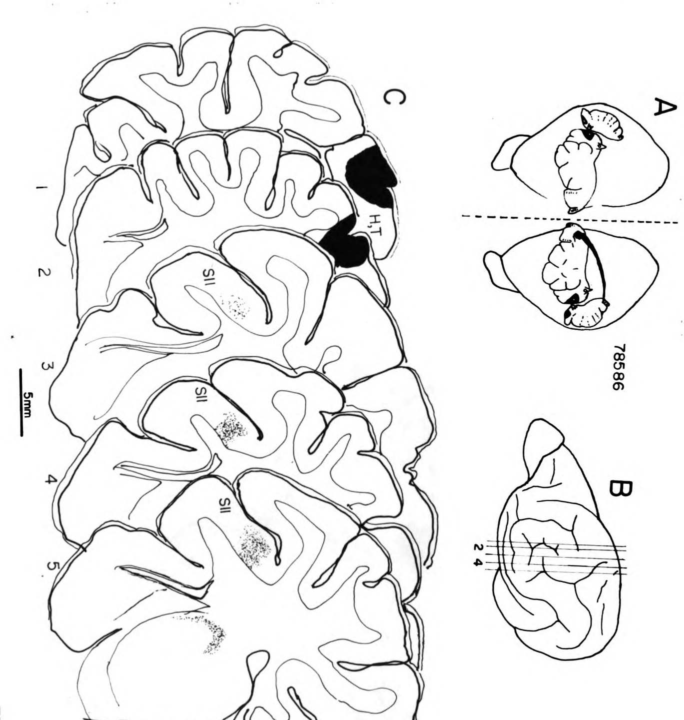


Figure 23: The distribution of grains above fibers and terminals in the ipsilateral SII cortical region following an injection of tritiated leucine and proline in the trunk region SI. A. Schematic diagram of the cerebral hemispheres with all the sulci removed except those in SI to emphasize the relationship of SI and SII. B. A tracing of the left cereberal hemisphere of a "standard" brain with the approximate locations of the transverse sections reconstructed in C. C. A series of transverse sections through the region of labeled terminals in the ipsilateral cortex. The small dots represent the distribution of grains above fibers and terminals in the ipsilateral SII region. The darkened area indicates the central core of the injection site. Section 5 is through the area of maximum labeling in Vb. H, hindlimb, T, trunk.

Figure 23



nonhomotopic connections (INA), (c) commissural connections (CA) (see table 1).

These results show that a given representation area of the periphery in SI is connected with a similar representation area of the periphery in SII.

The topography and density of cell bodies of intrahemispheric nonhomotopic afferents was varied and complex. The labeled cell bodies of intrahemispheric nonhomotopic afferents resulting from an injection of HRP in the hindlimb and trunk regions of SII are the most complex. Injections in this region labeled the cell bodies of INA in the forepaw region of SII, the anterolateral face region and the junctional area between the face regions of SI and SII.

Labeled cell bodies were found in the contralateral homotopic cortex following injections of HRP in the hindlimb and trunk regions of SI and SII, but not after injections in the forepaw regions of SI or SII.

Three dimensional reconstructions of a series of transverse sections revealed that labeled neurons are organized into rostrocaudally oriented strips. Most of the strips of labeled cell bodies of INA, IHA, and CA were located in the sulcal cortex, and relatively few labeled cell bodies were observed in the cortex of the gyral crowns.

Most of the labeled neurons had pyramidal shaped cell bodies. The laminar distribution of the labeled cell bodies of INA, IHA, and CA were uniquely related to the functional region of the injection site. The cell bodies of the intrahemispheric projecting neurons in the forepaw areas of SI were restricted to the supragranular layers whereas the cell bodies of intrahemispheric projecting neurons in the forepaw area of SII were in all layers except layer I. The bulk of labeled cell bodies were in layers II, III, and V. The arrangements of cell bodies of afferent neurons in the trunk and hindlimb regions of SI and SII were variations of that decribed for the forepaw regions of SI and SII.

DISCUSSION

Utilizing the tracers HRP and tritiated amino acids, the intrahemispheric and commissural circuitry of SI and SII areas was investigated. Figure 24 is a summary of the connections observed in this series of experiments. Similar to the investigations in the rat (White and DeAmicis, 1977), and monkey (Jones and Wise, 1977), it shows that neurons in the trunk, hindlimb and forepaw representation areas in SI and SII are reciprocally connected. The figure also shows that the results of these experiments support the hypothesis that there is synaptic interaction between the granular and agranular regions of SI and SII. Neurons in the granular region of SII or SI (the forepaw region) receive afferents from neurons whose cell bodies are located in the agranular region of SII or SI (the trunk and hindlimb region). Neurons in the agranular regions of SI or SII receive afferents from neurons whose cell bodies are located in the granular regions of SI or SII. In addition, neurons in the boundary area between the face regions of SI and SII project to SII to the hindlimb and trunk regions of SII.

Similar to the observations made in the rat, cat, and monkey, neurons in the trunk region of SI receive afferents from the homotopic area in the contralateral hemisphere. Neurons in the SII hindlimb and trunk regions receive afferents from the contralateral homotopic area in SI and homotopic areas in SI.

These results together with those in the rat (Akers and Killackey, 1978; White and DeAmicis, 1977) and monkey (Jones and Wise, 1977) suggest two principles of organization of intrahemispheric and commissural connections.

Figure 24: Summary of the connections observed in this series of experiments. The reciprocal connections between the forepaw regions of SI and SII and the trunk and hindlimb regions of SI and SII indicate one principle of organization: this circuitry is related to the electrophysiologically observed projection of peripheral receptors. The reciprocal connections between the trunk and hindlimb regions within SI and the forepaw and hindlimb regions within SII illustrate a second principle of organization: this circuitry is related to something other than the electrophysiological projection of peripheral receptors to the cortical surface. The reciprocal callosal connections are related to the second principle of organization. In this proposed schema, callosal connections transmit information accrued by the intrahemispheric nonhomotopic connections.

One principle is illustrated by the intrahemispheric homotopic reciprocal connections. The topography of these connections is intimately related to the electrophysiological projections of peripheral receptors to the SI and SII cortical regions. This study and other anatomical studies in the rat (Akers and Killackey, 1978) and monkey (Jones and Wise, 1977) have shown that neurons of each cortical sector of SI receive projections from a cortical sector in SII which receives projection from peripheral receptors in the same or very similar body parts. These connections are invariant between SI and SII and appear in all mammals investigated.

The presence of nonhomotopic connections illustrated a second principle of organization. In this study and in the rat (Akers and Killackey, 1978), connections have been demonstrated between neurons in the granular cortex and those in the agranular cortex. The topography of the cell bodies of these connections is unrelated to the topography of specific thalamocortical afferents. However, the topography of the cell bodies of INA appears to be related to the distribution of the cell bodies of callosal projecting neurons.

The topography of callosal connections is also unrelated to the topography of specific thalamocortical afferents. Jones et al (1975) suggested that, in the monkey, callosal neurons terminated on homologous neurons in the contralateral hemisphere. Akers and Killackey (1978) demonstrated in the rat that callosal and specific thalamocortical afferents terminated in adjacent but nonoverlapping areas in the face region of SI.

These anatomical results are corroborated by the electrophysiological studies. In the rat, Welker (1976) showed that zones of callosal termination were unresponsive to peripheral stimulation of specific regions of the body. In the cat, Innocenti et al (1974) have shown that 90% of the callosal projecting neurons terminate on neurons with wide and bilateral receptive fields and are not somatotopically organized.

Innocenti et al (1972) found that single fibers in the corpus callosum had small localized receptive fields from all parts of the body. Those regions of SI and SII which are devoid of anatomical connections transmit electrophysiological information in a manner similar to those regions in which anatomical callosal connections exist. These data indicate that, electrophysiologically, callosal neurons are able to transmit precise topographical information, although the neurons themselves are not driven by stimulation of receptive fields that are precise and restricted. It is probable, therefore, that tactile information from the densely innervated regions destined for the contralateral hemisphere is first relayed to the callosal neurons via the nonhomotopic connections, then to the homotopic region in the contralateral hemisphere, and then to the homotopic area via symmetrical connections.

Future studies will be needed to determine if and how these connections combine to mediate the physiological pathway for sensory information between the noncommissurally connected regions in SI and SII.

Laminar Organization and the Formation of Strips. The laminar distribution of the cell bodies of efferent neurons in SI and SII displays a variety of patterns. The laminar organization of the cell bodies of efferent neurons in some subdivisions exhibits a pattern of laminar organization that is characteristic of monkeys whereas that of other subdivisions are characteristic of nonprimates. In monkeys, the cell bodies of origin in the SI to SII projection are located in layer IIIB (Jones and Wise, 1977). In this study, the cell bodies of efferent neurons in the SI to SII projection are confined primarily to layers II and III (figure 25).

The laminar distribution of cell bodies of intrahemispheric efferent neurons in the SI trunk, SII forepaw and SII hindpaw regions was typical of that observed in other nonprimates. In mice (White and De Amicis, 1977) and cats (Jacobson and Trojanowski, 1974), and in this study, the cell bodies of origin in the SII to SI projection were in all layers except layer I. The largest concentration of cell bodies were localized in layers III and V with the majority of the remainder in layer VI.

The bulk of the cell bodies of commissural efferents were located in layers III and V. The cell bodies of commissural efferents in SII, however, were more loosely organized than those in SI.

The cell bodies of fiber systems studied in SI and SII were further organized into strips oriented in the rostrocaudal direction. The organization of the cell bodies in SI and SII into distinct strips has not been described in other nonprimates. An apparent clustering of the cell bodies of commissural efferent neurons ("waxing and waning") was reported by Jacobson and Trojanowski (1974).

The orientation of the strips of labeled cell bodies in the raccoon is different from that observed in the monkey. In the monkey, the strips of cell bodies of origin of the intrahemispheric and commissural fiber

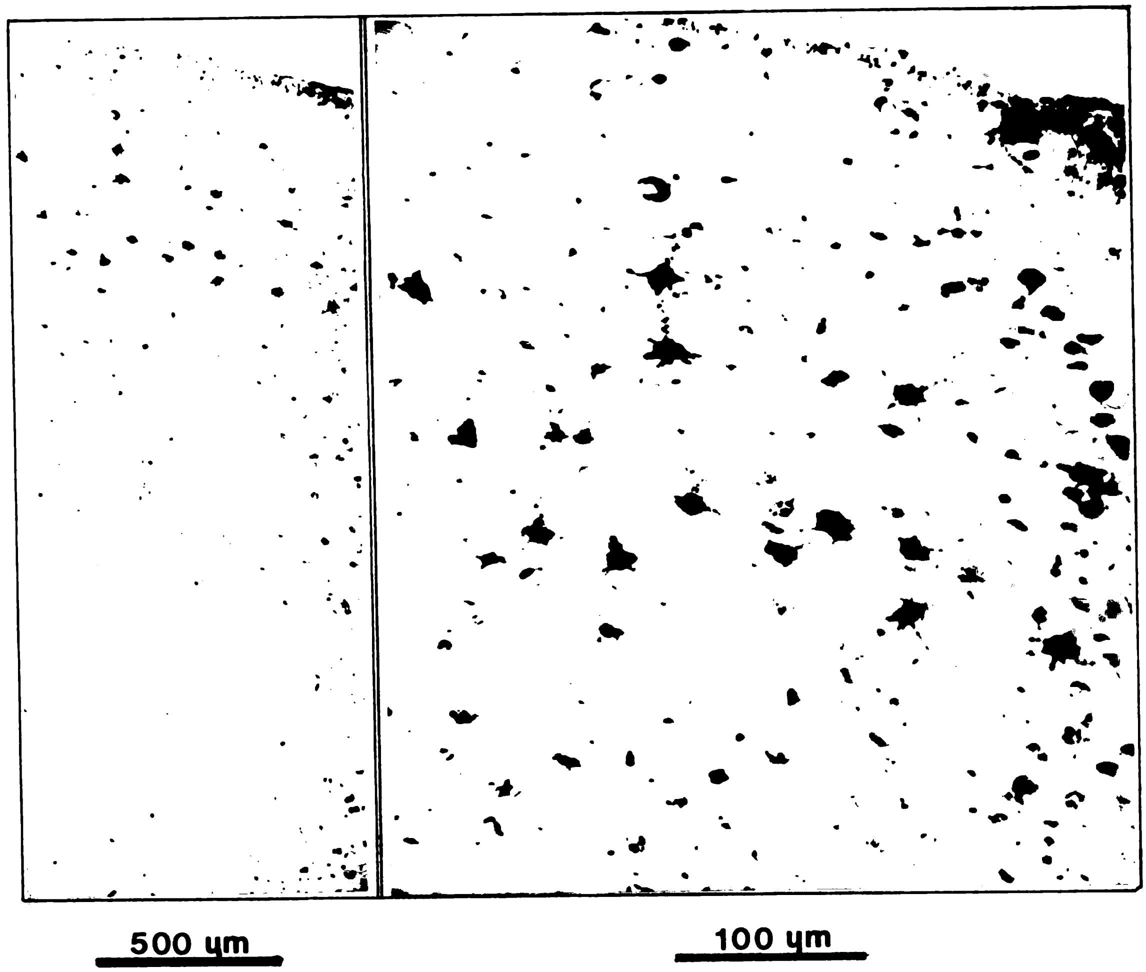


Figure 25: Pyramidal cell bodies of origin of the SI forepaw to SII forepaw projection. A. Only pyramidal cell bodies in layer II were labeled in this cluster of cell bodies. B. Higher magnification of the cluster of labeled cell bodies shown in A.

systems are oriented in a medial-lateral direction.

In the raccoon, similar to the observations made in the monkey, the diameter of the clusters of labeled cell bodies on intrahemispheric and commissural efferents ranged between 200 and 1000 μm. Typically, many neurons in a column were labeled and neurons in adjacent columns of neurons were labeled. The density of labeled cell bodies in a focus of labeled neurons indicates that most, if not all, the neurons were labeled. This suggests that the neurons of each fiber system are not intermixed. In support of this hypothesis are results of experiment 77559. In this experiment, a small injection in the SI trunk region labeled the cell bodies only of commissural afferents. The cell bodies of intrahemispheric afferents from the ipsilateral SII region were not found. Since a regular series of sections was processed for the histochemical reaction in this experiment, the explanation for the absence of labeled cell bodies may be explained as either: (1) the region in the SI trunk region which receives afferents from the contralateral homotopic cortex does not also receive afferents from the ipsilateral SII, or (2) the focus of labeled cell bodies in the ipsilateral SII is much smaller than the focus in the contralateral cortex and, consequently, was contained in the 200 μm interval of tissue not histochemically processed. The latter explanation is unlikely since, in other experiments, the lengths of the rostrocaudal oriented strips in the ipsilateral cortex are comparable to those in the contralateral cortex.

These data suggest that, in SI and SII, the cell bodies of efferents are organized into interdigitating strips. The degree to which the cell bodies of one efferent strip interact with the cell bodies of an adjacent, but different, efferent strip was undetermined.

In raccoons, the density of the cell bodies of efferents to the motor cortex is comparable to that of intrahemispheric and commissural efferents (Sakai and Herron, 1979). This suggests that the cell bodies of these fiber systems are mutually exclusive.

Behavior Procedure

Seven raccoons, 4 to 6 months old, were used in this study. Suckling infants were obtained from the Michigan Department of Natural Resources and raised in the laboratory. Young raccoons trapped in the wild were uncooperative in these behavioral experiments.

At the outset, each animal was placed in the testing cage for 15-30 minutes each day to familiarize them with the behavioral environment. The weight and food deprivation of each animal was maintained at a level in which the animal would closely pursue food placed within reaching distance. The raccoons were taught to extend their forepaw through a portal in the front end of the testing cage to obtain peanuts in a food well occluded from their sight. The portals in the testing cage were arranged such that the animal could only use his left forepaw on the left side of the testing cage and right forepaw on the right side of the cage. After the animals had acquired the "peanut reaching" behavior, they were tested to determine the amount of time required to obtain one peanut from the food well. Each animal was tested ten times a day until the amount of time it took to retrieve the peanut was stabilized at 2.2 to 2.4 seconds. Following surgery, the animals were then trained on a tactual roughness discrimination task.

Surgical Procedure Surgical operations were performed on six animals. Of these six animals, sham lesions were performed on two, ablation of the SI forepaw area was performed in two animals and partial or complete ablation of the SI or SII region in two others. Intraperitoneal injection of chloralose (initial dosage, 17 mg/kg) was used to produce general anesthesia. The hair on the dorsal surface of the head was clipped and the dorsal surface washed with Betadine surgical scrub. In an aseptic environment, the skin was incised along the midline and the muscle and fascia were retracted. A large free bone flap was removed over the area of interest and the dura widely retracted. The ablation was carried out using a glass pipette and low vacuum suction. The ablations in their entirely were carried out under visual control aided by an operating microscope. The animals were ready for training after a two week recovery period.

Testing Apparatus. The testing apparatus was a small box 4 inches wide, 5 inches high and 6.5 inches long (see figure 26). The apparatus had a circular opening (diameter, 1.75 inches) at each end. For each trial the circular opening was aligned with one of the testing cage portals. A small door attached inside of the box covered the circular opening at each end. The doors were held in place by a mild spring tension.

The animals were taught to reach through the portal of the testing cage, push the small door backward and into the apparatus to obtain a peanut butter mixture. After the animals had acquired this behavior with both forepaws, they were ready for training on a tactual roughness discrimination task. "Coarse" sandpaper was glued to one door and "fine" sandpaper glued to the other door (Production Sand-Pak, 3M Company). The "coarse" door was designated the positive rewarding stimulus of the pair and the order of the doors presentation was according to a chance sequence. After the animals had reached a criterion of 32 correct

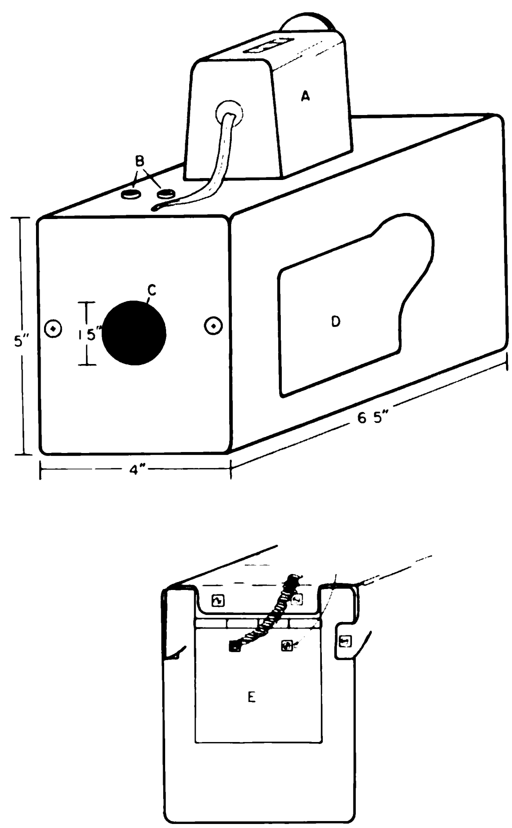


Figure 26: Schematic of the outside and the inside of one end of the testing apparatus. A. Response counter. B. Electrical outlets for response counter. C. The opening in which the animal could reach through to obtain food. The discriminants were attached to a door which covered the opening. The raccoon had to learn which was the - and + reward doors. D. Access to the food well. E. Inside view of the door covering the opening to one end of the apparatus.

responses in 40 stimulus presentations, the other forepaw was tested to determine if transfer of learning had occurred. The temperature discrimination learning task was conducted in a manner similar to the tactile discrimination task; a hot plate (37^{o}C) was attached to one apparatus door and designated the negative rewarding stimulus and another plate (24^{o}C) was attached to the other door and designated the positive rewarding stimulus.

Controls The odor of the peanut butter mixture was masked by having ten times the amount used on each reward trial sandwiched between two pieces of 1/4 inch plywood in the bottom of the apparatus. Stimulus presentation was occluded from the raccoon's view by covering the front on the testing cage and not presenting the stimulus until the raccoon extended his forepaw to the portal in the testing cage.

Figure 27 is a diagram of the extent of the bilateral lesions in the SI and SII cortical areas. In one animal, the gyral cortices of the face representation areas were bilaterally removed (part A of figure 27).

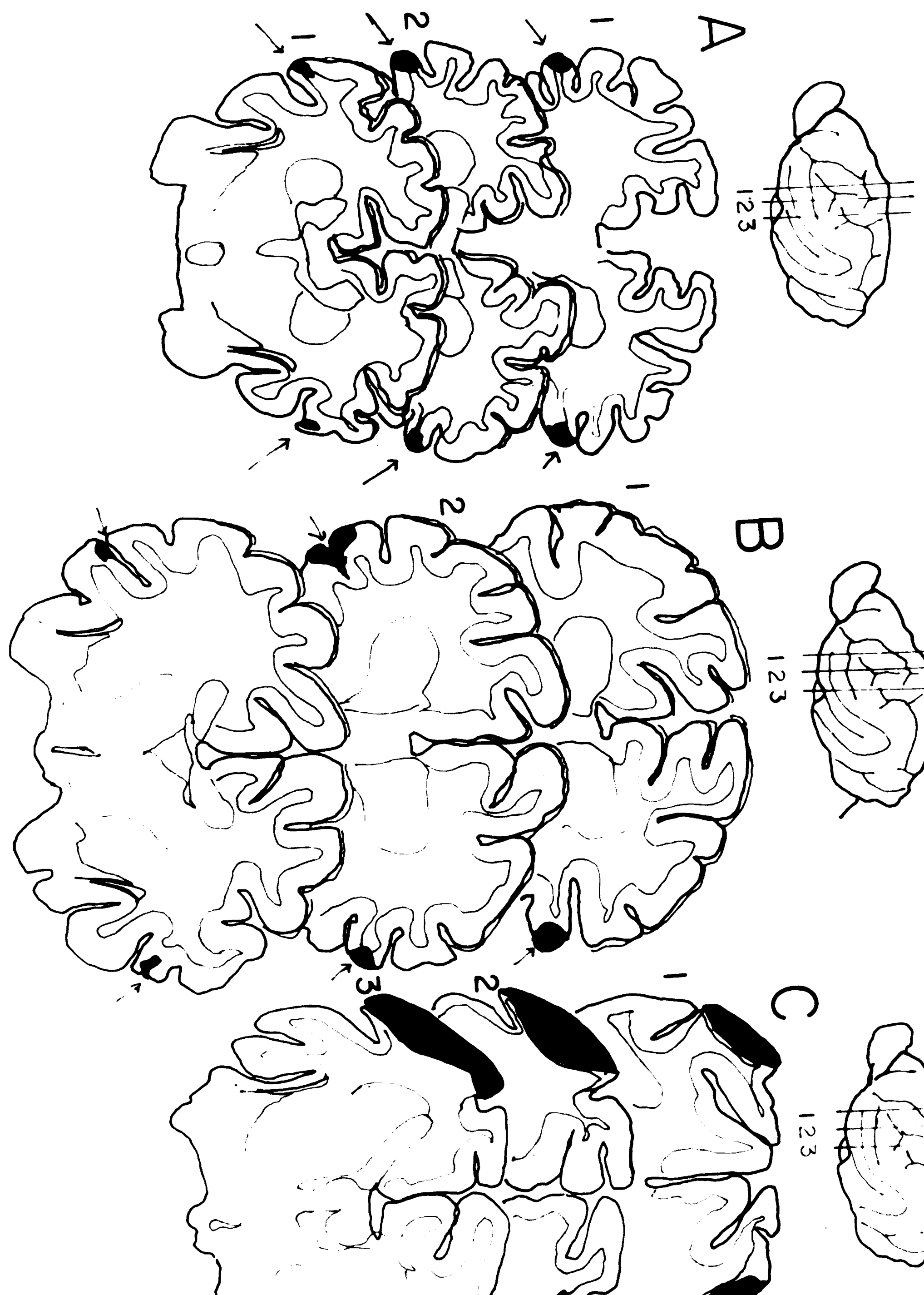
In another animal, the ablation removed part of the forepaw representation area of SII and lateral-most face representation area of SI in the left hemisphere and the gyral cortex of the face representation area of SI in the right hemisphere (SII forepaw + SI face animal) (part B of figure 27).

In two additional animals, the forepaw representation areas of SI were bilaterally removed. The bilateral ablations were very similar in the two animals. The ablations removed most of the forepaw representation areas bilaterally and occasionally extended into the underlying white matter (part C of figure 27).

The control group for the rough vs. smooth task were two normal animals and one sham operated animal. The control group for the temperature task was one normal and one sham operated animal.

Figure 27: Schematic diagram of the extent and location of bilateral lesions in the SI and SII cortical areas. A. Top: dorsolateral view of the left hemisphere of a raccoon brain with lines to indicate the approximate locations of the transverse sections through the site of lesion that is shown below. Bottom: three transverse sections to indicate the extent of the bilateral lesions in the SI cortical face representations. B. Top: dorsolateral view of the left hemisphere of a raccoon brain with vertical lines to indicate the approximate locations of the transverse sections below. Bottom: three transverse sections to indicate the lesion in the face representation area of SI and the forepaw area of SII in the left hemisphere and the gyral cortex of the face representation area of SI in right hemisphere (SII forepaw + SI face). C. Top: dorsolateral view of the left hemisphere of a raccoon brain with lines to indicate the approximate locations of the transverse sections shown below. Bottom: three transverse sections through the site of the bilateral lesions of the SI forepaw areas.

Figure 27



The animals were required to learn the tactile and temperature discrimination tasks with one forepaw and subsequently tested for saving in the intermanual transfer of the discrimination learning to the second forepaw. The saving score was calculated as:

$$\frac{\text{Learning score with 1st hand - learning score with 2nd hand}}{\text{Learning score with 1st hand + learning score with 2nd hand}} \times 100 \quad .$$

RESULTS

The animals which had bilateral ablations of the forepaw representation areas in SI showed severe impairment of reflex hopping and placing reactions. They retained the "reaching" behavior and were therefore able to perform the gross motor activities required for performing the tasks. However, they were unable to pick up the food in the rewarded trials, and therefore became uninterested after a few trials. They were unable to learn the tactile and temperature discriminations using the above procedures (see Table 2).

Reflex hopping and placing reactions were found to be unchanged for the animals with bilateral ablations of the SII forepaw + SI face animal and the bilateral SI face animal during the two week recovery period. The speed and accuracy with which they could retrieve peanuts from a food well occluded from view were comparable to that observed before the ablations (see Table 2).

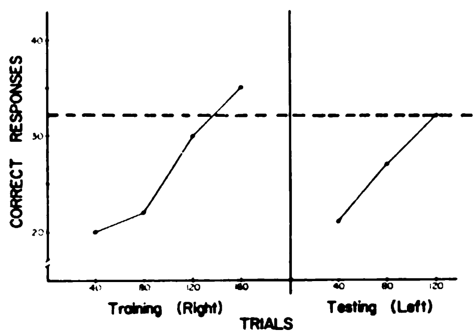
<u>Discrimination Performance and Transfer of the Rough vs Smooth Task</u>

Shown in figure 28 are the individual performance curves for each forepaw of a normal animal, the bilateral SI face animal, the bilateral SII forepaw + SI face animal and the sham animal. The animals were trained on a rough vs. smooth discrimination using one forepaw to a criterion of 80% correct (32 correct responses in 40 consecutive trials). The normal and sham controls required at least as many trials to reach criterion with the second forepaw as they did with the first forepaw.

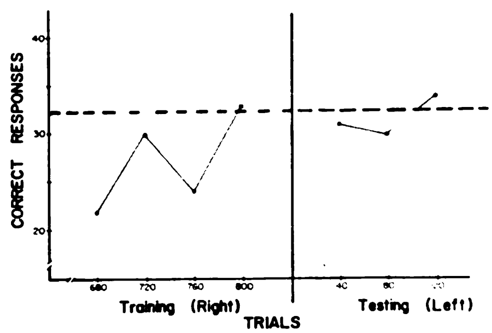
Table 2: Postlesion placing and hopping behavior and the saving scores in percentages between acquisition trials and transfer test.

Animal #	Lesion site	Post-lesion placing and hopping behavior	Tactile Discrimination	Temperature Discrimination
79579	Normal	Normal	25.0	87.3
78582	Sham	Normal	63.0	88.3
78583	Bilateral SI face	Normal	85.0	72.5
78584	SII forepaw + SI face	Normal	25.0	83.5
78586	Bilateral SI forepaw	Impaired	None	None
78587	Bilateral SI forepaw	Impaired	None	None

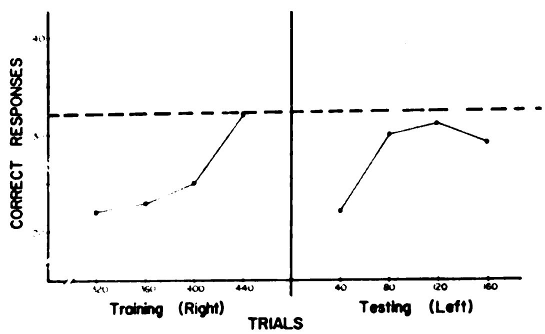
Figure 20



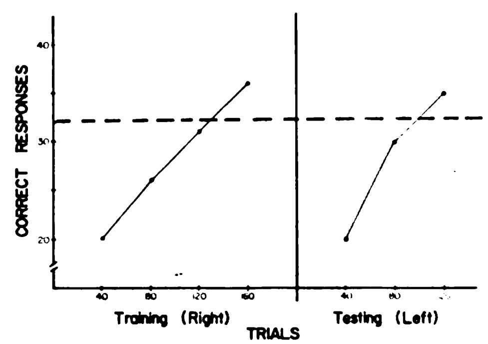
Correct responses in 40 trial blocks for normal raccoon on the rough / smooth discrimination task The left panel shows the acqusition rate for the right forepaw and the right panel shows the testing for transfer with the left forepaw



Correct responses in 40 trial blocks for a raccoon with a bilateral SI face ablation on the rough/smooth discrimination task The left panel shows the acqusition rate for the right forepaw and the right panel shows the testing for transfer with the left forepaw



Correct responses in 40 trial blocks for a raccoon with a bilateral SI, SI-SII ablation on the rough / smooth discrimination task The left panel shows the acquisition rate for the right forepaw and the right panel shows the testing for transfer with the left forepaw



Correct responses in 40 trial blocks for sham operated raccoon on the rough / smooth discrimination task The left panel shows the acqusition rate for the right forepaw and the right panel shows the testing for transfer with the left forepaw.

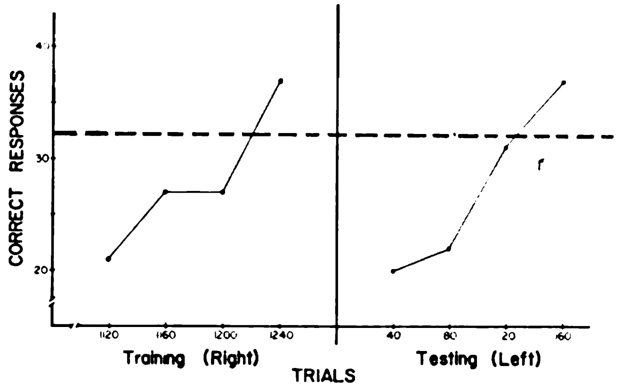
The subjects with bilateral ablation of the SI face region and the SII forepaw + SI face showed intermanual transfer of the rough vs smooth discrimination learning. The bilateral SI face animal and the SII forepaw + SI face animal required as many trials to acquire the discrimination learning with the first hand as the controls. The sham operated animal had a moderate saving (63%) while the SI face animal showed the greatest saving (85%).

Discrimination Performance and Transfer of the Temperature Task

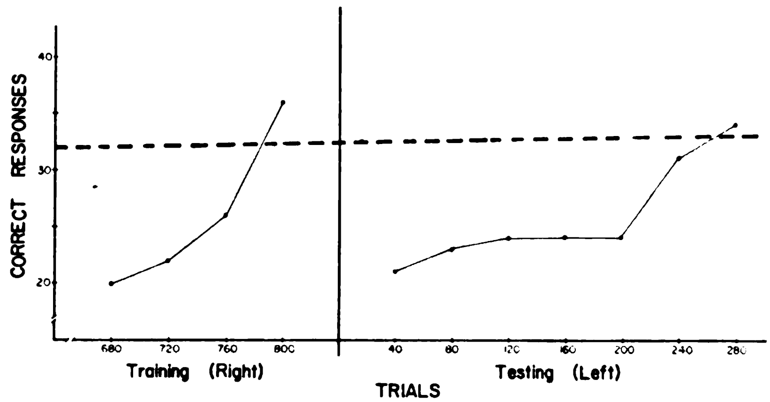
One normal, the sham operated animal, the bilateral SI face animal and the SII forepaw + SI face animal received training and intermanual transfer testing with the temperature discrimination task (37^{o}C vs. 24^{o}C). The animals were trained on the temperature discrimination task to a criterion of 80% and given 40 overtraining trials in a counterbalanced design.

The acquisition of the temperature discrimination learning did not differ for the ablated animals and the controls (figure 29). The SII forepaw + SI face animal and the bilateral SI face animal as well as the control animals showed large intermanual transfer of learning scores (figure 29).

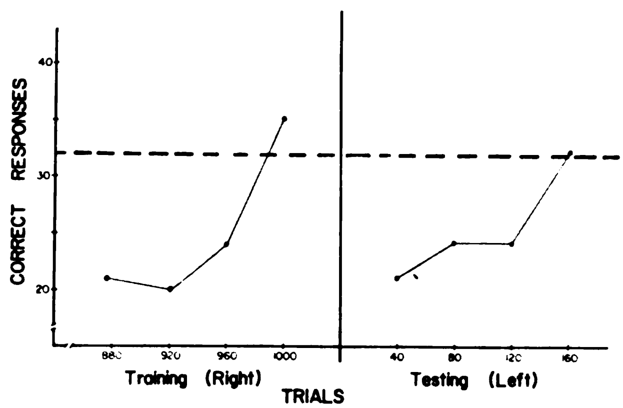
Figure 29.



Correct responses in 40 trial blocks for a sham operated raccoon on a hot/cold discrimination task. The left panel shows the acquisition rate for the right forepaw and the right panel shows the testing for transfer with the left forepaw.



Correct responses in 40 trial blocks for a raccoon with a bilateral SI face ablation on a hot/cold discrimination task. The left panel shows the acquisition rate for the right forepaw and the right panel shows the testing for transfer with the left forepaw.



Correct responses in 40 trial blocks for a raccoon with a bilateral SI forepaw + SI face ablation on a hot/cold discrimination task. The left panel shows the acquisition rate for left forepaw and the right panel shows the testing for transfer with the right forepaw.

DISCUSSION

The results of this pilot study support the hypothesis that the bilateral removal of the SI forepaw, SI face or the SII forepaw and SI face region differentially impairs the intermanual transfer of discrimination learning in raccoons. These results, however, are inconsistent with those of Teitelbaum et al (1968) who found that the removal of the SI forepaw or SII cortical region impaired cats' ability to intermanually transfer discrimination learning. There are several explanations for the differences in the results of these experiments and those of Teitelbaum et al (1968).

Firstly, following the removal of SI forepaw area, there appears to be a very strong species difference between the tactile behavior of raccoons and the tactile behavior of cats and monkeys. The removal of SI in monkeys (Kruger and Porter, 1958; Orbach and Chow,1959), or SI forepaw area in cats (Teitelbaum et al., 1968) did not severely impair the ability of these animals to learn tactile discriminations. In this study, the SI forepaw region has been shown to be essential for raccoons to learn tactile discrimination.

The impairment appeared to be primarily a sensory deficit. The animals were not paralyzed, as they could grip objects, climb up cage bars, and palpate the surfaces in their environment. Although they could see familiar food parcels on the floor of their cage they were rarely able to manipulate it into their mouth with their forepaw because of clumsiness. In this respect, the animals behaved in a manner that supports Kornhuber's (1974) hypothesis which suggests that one of the functions of the SI cortical region is to provide guidance for voluntary motor activities.

Secondly, it is possible that the bilateral removal of SII forepaw + SI face or SI face regions impairs the ability of raccoons to intermanually transfer tactile discrimination learning. The animals used in this study were not pretested for their ability to intermanually transfer tactile discrimination learning. Other studies pretested their subjects to select only those subjects that did well on intermanual transfer of discrimination learning tasks (Teitelbaum et al., 1968). Thus a more homogeneous population was used and the deficits encountered as a result of cortical ablations were more obvious. The small number of available and trainable raccoons prevented the selection process in this study. The way to circumvent this particular problem in future studies is to use reversible cooling of the cortical areas in the raccoon so that each animal can serve as its own control.

Summary. Control and experimental subjects were trained to discriminate rough vs. smooth and temperature tasks in one forepaw and subsequently tested with the other forepaw to determine if saving had occurred. The animals with ablation of the forepaw region in SI were unable to learn the tactile or temperature discrimination. There were no differences between the results of the controls and those of the experimental animals, other than this.

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