PROPERTIES OF SINGLE UNITS, AND THEIR CORRELATION WITH SOMATOTOPIC ORGANIZATION, IN THE SECOND SOMATIC SENSORY AREA (SII) OF THE CEREBRAL CORTEX OF THE CAT

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John Richard Haight

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This is to certify that the

thesis entitled

Properties of Single Units, and Their Correlation with Somatotopic Organization, in the Second Somatic Sensory Area (SII) of the Cerebral Cortex of the Cat

presented by

John Richard Haight

has been accepted towards fulfillment
of the requirements for

Ph. D. degree in Zoology

John I. Johnson Jr.
Major professor

Date 19 July 1971

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ABSTRACT

PROPERTIES OF SINGLE UNITS, AND THEIR CORRELATION WITH SOMATOTOPIC ORGANIZATION, IN THE SECOND SOMATIC SENSORY AREA (SII) OF THE CEREBRAL CORTEX OF THE CAT

By

John Richard Haight

The properties of single cortical units in cat SII were examined in the light of both the organization of their peripheral receptive fields and types of and conditions under which stimuli were most effective in driving such units. The purpose was to determine if the somatotopic relations of individual cortical units were in any way related to their "physiological" properties such as rate of habituation and adaptation, response latency and the most effective activating tactile stimulus. An ancillary portion of the study dealt with the question of whether the receptive fields of cat SII units were commonly bilateral, as in the monkey, or primarily contralateral, as had previously been reported in the cat.

Normal microelectrode mapping procedures were used. Each isolated cortical unit was also examined as to its stimulus interests and responses to same in as far as this was possible. Experiments were performed under both sodium pentobarbital and nitrous oxide anesthesia in order to see if "light" and "heavy" states of anesthesia had an effect upon the occurence of bilateral receptive fields. Chronic cortical ablations, accomplished some months prior to recording, were done for the purpose of determining whether unit response properties or the bilateral

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representation of peripheral receptive fields would be affected by the absence of portions of the homolateral or contralateral somesthetic cortex.

The results show that:

1. The somatotopic organization of mechanoreceptive fields in cat SII is reversed from the way in which the postcranial regions have previously been portrayed. Axial structures lie medially along the upper bank of the anterior ectosylvian gyrus with apical structures represented laterally on the medial convexity of the gyrus.

2. A definite relationship exists between the way receptive fields are mapped onto the second somatic cortical field and the way that various tactile modalities are arranged in the same area. Trajectories of receptive field clusters are present consisting of a light tactile core and a heavier tactile coat. The representation of these clusters is somatotopically orderly; the representation of individual unit receptive fields within a cluster is also orderly. However, receptive fields arrayed without consideration of these clusters do not necessarily fall into an orderly somatotopic pattern.

3. Ablation of contralateral somesthetic cortex had no effect upon functional properties of SII units nor did such ablation affect the occurence of bilateral receptive fields. Ablation of ipsilateral SI cortex was seen to affect the habituation properties of homolateral SII neurons.

4. Bilateral receptive fields are rare in the mechanoreceptive portions of SII. This lack is apparently not an anesthetic effect but represents a valid species difference when compared with monkeys in whom the majority of SII units are seen to have bilateral receptive fields.

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5. As many as three populations of SII units can be distinguished on the basis of their mean latencies to electrical stimulation. Two of these populations have purely contralateral receptive fields and one has bilateral receptive fields.

6. The tactile interests of cat SII neurons appear to be fairly evenly distributed between light tactile (touch to glabrous surfaces and hair responses) and heavier tactile (pressure, involving skin indentation) modalities. Mixed modalities were consistenly observed but were rare.

It is suggested that the organization of SII cortex, as characterized in this study, is related to the functioning of SII. It is further suggested that the organization of SI cortex be examined using the present techniques. The results from such a study could possibly go a long way toward explaining what, if any, differences are inherent in the organization of the SI and SII cortical fields.

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John Richard Haight

A THESIS

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

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Appreciation is extended to those who, during the course of these lengthy experiments, helped to keep the experimenter awake and the subjects asleep in spite of strong forces tending to operate in the opposite direction. Specifically, thanks go to John Benson, Dan Bratt, Dan Lyons, Marty Preache and Tim Smith.

To my wife, Emeline, who, in addition to all the other things a graduate student's wife must bear, attended to the histological processing of myriad cat brains, I express the profoundest gratitude.

To Professor John I. Johnson who extended his facilities, time and patience must go deepest appreciation also.

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INTRODUCTION

Historical. Since Lord Adrian's description of a dual representation of limb apices in the somesthetic cortex of the cat (1940, 1941), the duality of somatic sensory projections to neocortex has been confirmed in a large number of other mammals, primarily on the basis of physiological rather than anatomical criteria (Adey & Kerr, 1954, marsupial brush tail possum; Benjamin & Welker, 1957, squirrel monkey; Lende, 1963, virginia opossum; Lende & Sadler, 1967, hedgehog; Penfield & Rasmussen, 1950, human; Welker & Seidenstein, 1959, raccoon). These later studies indicated that, contrary to Adrian's conclusions, the second somatic cortical area or SII, as it came to be known (Woolsey & Fairman, 1946), showed a complete, albeit smaller, somatotopically organized representation of the body very much like that observed in the primary or SI cortical receiving area. Furthermore, the earlier studies which used large surface recording electrodes indicated that the somesthetic representation in SII was bilateral, thus distinguishing it from the almost entirely contralateral representation found in SI (Benjamin & Welker, 1957; Pinto Hamuy, Bromiley & Woolsey, 1956; Welker & Seidenstein, 1959; Woolsey & Fairman, 1946; Woolsey & Wang, 1945, for examples). The bilateral component of the evoked SII response survived the ablation of the contralateral somesthetic cortex in its entirety, thus suggesting that the bilateral component would be found at subcortical levels and that it was not entirely, at any rate, a cortical commissural effect (Woolsey & Wang, 1945). Response latencies to tactile stimuli were similar in both cortical areas and SII responses survived the ablation of the homolateral cortex as well. These findings support the contention that SII is subserved directly by a thalamic projection similar to that known for SI (Chow & Pribram, 1956; Clark & Powell, 1953; Walker, 1938; Waller, 1940).

Once the existence of a second somatic sensory area in neocortex had been established, questions of its anatomical relations within the somatic sensory pathways, its behavioral import to the animal and of its physiological properties, properties which presumably could provide information and insight into the meaning of a dual sensory cortical representation for the animal, could be asked. They have, and what follows is a brief review of SII studies whose emphases have been on behavior, anatomy and physiology, respectively.

Behavior. A number of behavioral studies, with somewhat conflicting results, have been reported. These have relied upon the ability of the animal to learn or perform a previously learned discrimination after ablation of all and/or parts of the somesthetic cortex. Some investigators (Allen, 1947; Glassman, 1970) conclude that bilateral ablations of SII permenantly impair the relearning of tactile discrimination tasks whereas ablation of the primary or SI cortex produces only a temporary deficit. Ablation of both cortical areas has roughly the same effect as ablation of SII alone. The foregoing studies were performed on dogs and cats. With monkeys somesthetic discriminations appear to be more severely disturbed when SI is removed (Orbach & Chow, 1959) as opposed to SII. This, however, does not agree with some earlier experiments in which the postcentral gyrus (SI) was removed and only slight impairment noted (Ruch, Fulton & German, 1938).

Further confounding the issue, Zubek's studies (1951, 1952a, 1952b, 1952c) on rats and cats indicate that removal of either SI or SII causes only a temporary impairment in these animals. The rat can overcome, with some difficulty, removal of both areas I and II, but the cat is unable to do so. This latter finding was substantiated by Benjamin and Thompson (1959). The difficulties involved with performing reproducible ablations are notorious, however, and one man's SI may be only a part of another's (see especially, Clark & Powell, 1953). Cytoarchitectonic and physiologic defining criteria are matters of supreme indifference to the suction pipette.

In conclusion it can be said that at the current level of knowledge, a purely "behavioral" approach is not adequate. Such studies have not indicated the hoped for generalization as to what use the various somesthetic cortical areas are put. The behavioral approach requires an additional word of caution. It is not necessary to assume, and may be quite dangerous to do so, that homologous cortical areas in such disparate animals as the rat, cat and monkey must subserve identical functions which would be uniformly manifest in the animals' behaviors. Before further questions as to behavioral significance can be answered properly, it would be desirable to examine the anatomy and physiology of the somesthetic cortices - to ask such questions as which stimuli prove most "interesting" to the area in question and as to how specific sensory modalities and receptive fields are organized within SI and SII.

Anatomy. The first major problem to be solved was the question of how SII was innervated. Rather surprisingly, this question had not been resolved until quite recently. Unlike SI cortex which, when completely ablated, causes severe retrograde degeneration in the ventrobasal complex (Vb) of the thalamus, ablation of SII has little effect upon Vb but does induce some degeneration in the posterior group (Po) of thalamic nuclei. Extensive degeneration in Po is seen only if the homolateral auditory cortices are removed also (Clark & Powell, 1953; Chow & Pribram, 1956; and especially, Rose & Woolsey, 1958). One study purported to find extensive degeneration in Vb after SII ablation (Macchi, Angeleri & Guazzi, 1959) but the difficulty of ablating SII without disturbing the immediately underlying thalamocortical projections from Vb to SI was not taken into account (Guillery, Adrian, Woolsey & Rose, 1966). Direct electrical stimulation in Vb (Guillery, _et al_., 1966) implies strongly that there is a direct projection from Vb to SII in spite of the lack of retrograde degeneration in Vb when SII is removed. An earlier electrical stimulation study (Knighton, 1950) also reported similar findings, but later opinion (Guillery, _et al_., 1966) was that Knighton was stimulating in Po in addition to Vb, thus demonstrating a direct connection from this area too. Findings such as this in somesthetic as well as other sensory cortical areas led Rose and Woolsey (1958) to formulate the schema of _essential_ and _sustaining_ projections. I quote, "We shall consider that a cortical area receives an _essential projection_ from a given thalamic nucleus if destruction of such an area alone causes marked degenerative changes in the nucleus in question. On the other hand, if two cortical areas are considered, and if destruction of neither of them leads to degenerative changes in a thalamic nucleus or to only slight alterations but if a simultaneous destruction of both causes a profound degeneration of this thalamic element, we shall say that both areas receive _sustaining projections_ from this nucleus." From this argument came the thesis that some Vb neurons might project collaterally to both SI and SII. Antidromic stimulation of Vb neurons from the cortical surface have shown that this is the case: 50 to 70% of Vb units that are drivable from both the periphery and from the cortex can be antidromically driven _only_ from SI cortex. Some 30 to 50% can be driven from both SI and SII and a very few (10%) exclusively from SII (Manson, 1969; Rowe & Sessle, 1968). Both of these studies reported that about 30% of Vb neurons encountered could be driven from the periphery but not from either cortical area. More recently, studies involving the placement of electrolytic lesions in both Po and Vb have confirmed, using Nauta techniques, that these thalamic areas do project to SII (Hand & Morrison, 1970; Heath, 1970; Heath & Jones, 1971; Jones & Powell, 1969; O'Donoghue, Morrison & Hand, 1970) and that, in the cat, there is very little overlap in the cortex from these two thalamic centers (Jones & Powell, 1969; Heath & Jones, 1971).

The second somatic area also receives projections from the other somesthetic cortical fields as reported in both the cat and the monkey. SI projects homolaterally to SII (Jones & Powell, 1968a; Pandya & Kuypers, 1969; Spencer, 1950) and commissurally to both SI and SII (Jones & Powell, 1968b; Pandya & Vignolo, 1968 & 1969). SII also sends commissural fibers to its opposite counterpart. All of these projections appear to be homotopically organized (as far as degeneration techniques allow such a claim) and in neither animal do the limb apices project commissurally from SI to the opposite side, only the trunk, upper limbs and head regions. SII, on the other hand, sends projections to the opposite SII from all body regions.

Physiology. Physiological questions have been concerned with the functional differences between SI and SII and whether these differences are preserved across the mammalian orders. If we examine what is currently known about similarities and differences between SI and SII we find:

Similarities.

1. Both areas show somatotopic organization of the peripheral receptive fields onto the cortical surface. Receptive field constancy with respect to time and stimulus and a concern with the lighter tactile rather than nociceptive stimuli are characteristics of these areas, SI wholly so and SII in part.

2. Response latencies in SI and SII are very similar, indicating that information arrives almost simultaneously in both areas, at least from the contralateral components (Carreras & Andersson, 1963; Manson, 1969; Mountcastle, 1957; Welker & Seidenstein, 1959).

3. Somatotopic specializations, *i.e.* the large hand representation in the monkey and the raccoon, appear to be preserved in both areas (Benjamin & Welker, 1957; Welker & Seidenstein, 1959).

4. Both SI and SII show afferent inhibition. Simultaneous stimulation of areas outside the receptive field as well as from within the field is seen to result in less activity than when the receptive field area is stimulated alone (Mountcastle, 1957; Mountcastle, Davies & Berman, 1957; Carreras & Andersson, 1963).

5. There appears to be an axial-distal gradient toward diminishing receptive field size in both areas (Rubel, 1971 plus references cited in 4. above).

Differences.

1. SII is smaller in area than is SI. While point 5. above obtains, the receptive field sizes for a given body area are larger in SII than in SI. Thus, the detailing is apparently greater in terms of receptive field size in SI.

2. Responses to movement of joints are found in SI (Mountcastle, 1957) but not in SII (Carreras & Andersson, 1963; Whitsel, Petrucelli & Werner, 1969).

3. SII receives input from at least two thalamic areas (Vb and Po) whereas SI receives projections from only one area (Vb). Indications are that the Po and Vb projections do not overlap in SII (Heath & Jones, 1971) in the cat. Physiological studies support this contention in both the cat and the monkey (Carreras & Andersson, 1963; Whitsel, *et al.*, 1969).

4. SII has, in the monkey, been shown to have a strong bilateral input. Otherwise its unit properties are of the somatotopically organized, modality-place specific type encountered in the medial lemniscal system. SI, with the exception of the perioral regions, has a strict contralateral input.

5. Anatomically, it is seen that Vb sends essential projections to SI and sustaining projections to SII. Po sends a few essential but mostly sustaining projections to SII and these primarily to the non-somatotopically organized portion (Rose & Woolsey, 1958; Clark & Powell, 1953).

Some of these points are deserving of further amplification. Vb receives an almost strictly contralateral projection from lower centers by way of the lemniscal and portions of the anterolateral somatic sensory pathways (Bowsher, 1958; Chang & Ruch, 1947a; Poggio & Mountcastle, 1960). In most animals there is an ipsilateral component to this projection that is associated with the head, especially in the region of the mouth (see Cabral & Johnson, 1971 for an extreme example). Aside from these oral areas, which are mediated by the trigeminal nerve, the remainder of the body is strictly contralateral in representation (Mountcastle & Henneman, 1952; Poggio & Mountcastle, 1963; Pubols & Pubols, 1966; Pubols, 1968; Rose & Mountcastle, 1952). Further, the representation in Vb follows, in all cases, a strict somatotopy which is preserved in both the SI and SII projection fields (Werner, 1970; Woolsey, 1958, for general discussions).

Po, on the other hand, has been shown to receive bilateral somesthetic projections by way of the anterolateral system (Poggio & Mountcastle, 1960, for review). These projections are not somatotopically organized. Po neurons tend to be labile to the depth of anesthesia, are often driven by more than one stimulus modality and show variation in receptive field size and stimulus threshold over time (Calma, 1964; Poggio & Mountcastle, 1960). These properties are in contradistinction to those of the lemniscal-Vb system. Single unit recordings from SII have shown characteristics which would support a dual projection from both Vb and Po.

In the cat (Carreras & Andersson, 1963) it was reported that units in the posterior portions of the anterior ectosylvian gyrus (AEG) tended to have Po properties while units from the more rostral portions of the gyrus displayed Vb characteristics. More interestingly, however, these authors reported a total of nine bilateral and seventeen ipsilateral receptive fields out of a total cortical unit population in AEG of 518. Though a large number of units were examined in this study, the cortical field was not mapped, hence the possible relation of cortical neuronal functional properties in connection with the somatotopic organization could not be determined. A more recent study, using the macaque (Whitsel, Petrucelli & Werner, 1969), showed a somewhat similar division of Po and Vb type activity in SII. The somatotopically organized (Vb derived) portion of macaque SII displayed bilaterally symmetric receptive fields in some 90% of the cases examined, a finding which differs profoundly from that observed in the cat where the percentage of bilateral units was on the order of 10%.

As indicated previously, there is considerable evidence for cortical projections, both ipsi and contralaterally, in addition to the subcortical projections to SII. Electrophysiological studies on these pathways are rare, however. Slow wave evoked potentials arising from stimulation of the ipsilateral SI have been reported in SII (Nakahama, 1959). As nearly as I am able to ascertain, commissural effects pertaining to the somesthetic cortices have not been examined using modern techniques (see also Jones & Powell, 1968b). No neural or unit cluster activity has been reported in either SI or SII arising from any except subcortical areas.

There are indications that SII cortical units might be more interested in movements of stimuli across receptive fields than in punctate or static stimulus conditions (Whitsel, et al., 1969). Unfortunately, there is no real information as to whether this is or is not so in SI, hence this property cannot be used to compare the two cortical areas. In considering the sum of information available, it would seem that SI and SII are more alike than not. Part of the problem might lie in the fact that the mapping studies, for the most part, have not been concerned with the functional properties of the cortical neurons and that the functional studies have neglected the way in which these neurons are arranged in the cortex.

There remains the question of organized, bilateral projections to SII. Experiments in unanesthetized monkeys at both the thalamic (Poggio & Mountcastle, 1963) and cortical levels (Whitsel, Petrucelli & Werner, 1969) show unequivocally that Vb does not have a bilateral input, but that SII does. These responses are almost certainly not derived from Po because Po neurons do not have any of the necessary properties except that of ocassional bilaterality. Earlier Vb and SII studies on anesthetized (pentobarbital) cats (Rose & Mountcastle, 1952; Carreras & Andersson, 1963) are in agreement with the monkey studies except over the issue of bilateral representation in SII. Both Carreras and Andersson (1963) and Whitsel, et al. (1969) mention the possibility that there might be an anesthetic effect responsible for the differential suppression of the ipsilateral SII component in the cat studies. There was a high expectation of finding such a bilateral component in SII based upon the reports of the earlier evoked potential studies (Rose & Mountcastle, 1959, for review; Guillery, Adrian, Woolsey & Rose, 1966; Carreras & Andersson, 1963). In the light of current knowledge about the only possibility for explaining the monkey results would require invoking commissural pathways from the opposite cortex, pathways which have been shown to exist but that have never been examined from the electrophysiological standpoint. If such were to be the case, the cat results might be explained on the basis of an extreme susceptibility to anesthetics (sodium pentobarbital, at any rate) resulting in blockage of these cortical commissural fibers. There is, it should be noted, a report in the literature of an "SII nucleus" in the thalamus of the rat (Emmers, 1965). This finding has not been substantiated in any other animal or in any other laboratory. These findings, Emmer's work aside, force one to conclude that early reports of a lingering bilateral SII slow wave component after ablation of all other somesthetic cortex bring the blame home to a Po projection (Woolsey & Wang, 1945). These authors did report that deepening anesthesia reduced the ipsilaterally derived SII wave, eventually abolishing it. More recent single unit studies show that Po neurons are blocked by deep anesthesia (Poggio & Mountcastle, 1960) and that the Vb pathways are slowed down but never blocked by deepening anesthesia (Poggio & Mountcastle, 1963).

The past and the future. The facts currently available do not permit the construction of a theory of the functional significance of cortical duality though there are dim implications that SI may be concerned with somesthesis from both within and without the body while SII's primary concern is with external stimuli. Physiologically, it seems that in two widely studied animals, the cat and the monkey, whose SII anatomical relations are apparently identical, there might be a widely differing functional import based upon bilaterality or non-bilaterality in SII. Further, though the functional properties in both SI and SII neurons have been studied and though the detailed somatotopic receptive field organization of the periphery onto these cortical areas has long been known, there has as yet been no concerted effort to relate function in either area. Somatotopic organization may prove the key to determining a meaningful relationship among the functional properties of cortical neurons and, eventually, between the two somesthetic cortical areas.

Specific problems concerning SII and this study. An analysis of cortical unit activity in cat SII was undertaken using extracellular microelectrode recording techniques. The study dealt with the following questions:

1. What is the detailed, somatotopic organization of mechanoreceptive projections to cat SII, based upon single unit criteria?

2. Are the functional properties of SII neurons related to the somatotopic organization seen in this area?

3. Are the functional properties of cat SII neurons altered by the chronic ablation of the somesthetic cortices, singly and in combination, both ipsi and contralaterally?

4. Is there a differential anesthetic effect responsible for the suppression of bilateral mechanoreceptive responses in cat SII?

Design of the study. The receptive field organization in SII cortex was determined in all animals studied using conventional mapping techniques (Welker, 1971, for example). Primary emphasis was placed upon the map of the postcranial body regions because of the difficulty in distinguishing the immediately contiguous head regions of SI and SII. In addition to the receptive field data collected at each recording locus, information as to the most effective driving stimulus, the response latency to peripheral electrical stimulation (where possible), the depth into the cortex of the responsive locus and the relative propensities of the units sampled to adaptation and habituation to repeated stimuli were collected. These data, examined at the conclusion of the experiments, allowed an assessment of the points brought out in the first two questions posed above.

In order to deal with the third point a series of unilateral cortical ablations was performed involving the following cortical areas: SI only, SI plus SII and finally, all neocortex except SI. After allowing time for retrograde degeneration to take place - the basis for yet another study - recording experiments were done as follows:

1. In SII ipsilateral to the ablated SI cortex. This was done in order to determine whether the functional properties of SII neurons would be affected by the massive degeneration that this ablation would engender in the ipsilateral Vb. Secondary projections from SI to SII would also be involved in this degeneration.

2. In SII contralateral to the ablated SI. The object of this was to see if SII neuron activity would be altered by removing some of the commissural input from the opposite SI.

3. In SII contralateral to ablated SI plus SII. This was done for the same reasons stated in 2. above except that all of the opposite somesthetic cortex was involved.

4. In SII contralateral to an SI island, all other neocortex ablated. This series was done more for the purposes of looking at thalamic degeneration than in the hopes that there would be an electrophysiological effect upon the opposite SII.

It was also deemed of interest (see point 4. in preceding section) to determine whether cat SII did indeed receive a bilateral input of mechanoreceptive modalities. To this end a group of cats was very lightly anesthetized with nitrous oxide while SII was being mapped in the normal manner. The activity of neurons monitored under these conditions was compared with that seen in a series of animals anesthetized with sodium pentobarbital.

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METHODS

Subjects. With one exception (70352) all cats used in this study were born and raised in this laboratory. In consequence their life histories and general states of health were known. Again, with the same exception as noted above, all experimental procedures were carried out on animals between one and nine months of age. The exception was an adult cat of unknown age.

Recording procedures. The electrophysiological recording experiments were carried out under sodium pentobarbital or nitrous oxide anesthesia. In the latter case surgical preparation was performed under halothane and nitrous oxide combined with the former anesthetic being discontinued approximately one to two hours prior to the onset of cortical recording. In addition gallamine triethiodide (Flaxedil) was used to paralyze the nitrous oxide preparations which were perforce artificially respirated.

Surgical and mapping procedures followed those employed by Rubel (1971) in the cat and by C. Welker (1971) in the rat. Glass coated tungsten microelectrodes (Baldwin, Frenk & Lettvin, 1965) with exposed tip lengths of 20-30 microns were used to record from the cortical units. Fine grain somatotopic detailing in SII cortex was examined using variations of two techniques, that of C. Welker (1971) which employed very closely spaced electrode punctures (on the order of 10-20 per square mm.) and that of Whitsel, Petrucelli and Werner (1969) which sought to traverse many neighboring cortical columns (Mountcastle, 1957) within a given puncture. This was accomplished by a judicious choice of electrode entry angle. The present series of experiments utilized fixed electrode entry angles throughout a given experiment but these were varied from experiment to experiment.

A point of divergence from the usual mapping study techniques lay in the fact that careful record was kept of the stimulus types that proved most interesting the the receptive fields of the isolated cortical units. Observations were also made as to the adaptation and habituation properties of the cortical units as well as their latencies to electrical stimulation when this was possible (Figure 5). In order to accomplish the above it was necessary to isolate reliably single cortical units. The criteria used in determining whether a given cortical response was a single unit or not are amplified below.

Cortical responses, as seen on the oscilloscope screen, were most commonly a series of spikes riding upon a positive going slow wave. Such a series was often a train of spikes all of the same amplitude and fairly evenly spaced in time. These trains usually contained from but one to as many as seven or eight spikes (Figures 1 & 5) and were considered to result from single unit activity. In about one-third of the cases it was apparent that several cortical units were firing within the receiving area of the electrode tip. This was manifest by the multiplicity of spike amplitudes seen riding the slow wave in the oscillogram (Figure 2). If only a few (from two to four or so) units were included in such a cluster, one of these was usually dominant, audibly, as heard over the audio monitor, though not distinguished on the oscilloscope screen. That is to say, the sounds heard over the monitor unquestionably resembled those heard when an obvious single usit was seen on the screen. A certain unmistakable tonal quality was present which convinced me that I was indeed listening to a single neural unit responding to a stimulus even though this was not necessarily distinguishable visually. If more than four or five units were responsive at one time, the result was a "hash" type of

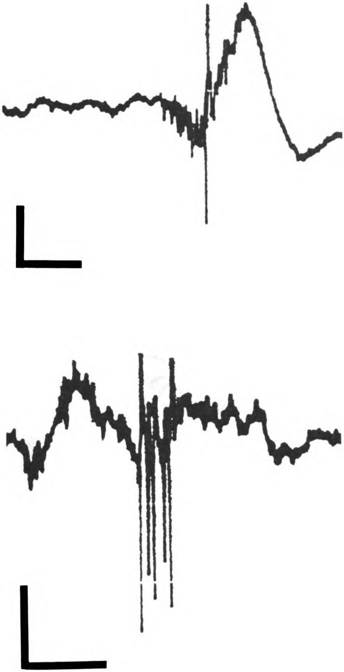


Figure 1. Single unit examples. (TOP) Unit 2A from subject 70315. This unit responded with a single spike to light pressure applied to the pad of the third finger. The response remained a single spike regardless of the stimulus strength. Calibration: 100uV & 10msec/div. (Bottom) Unit 3A from subject 71323. This animal was anesthetized with nitrous oxide. The unit responded to light pressure applied to the proximal volar hand. Calibration: 50uV & 10msec/div.

Figure 2. Multi-unit response. This response consists of at least three single units firing together in response to the stimulus. One of the units (22A from subject 70312) was audibly distinct from the others, though which one that might be is not apparent from this oscillogram. Calibration: 100uV & 10msec/div.

response which was sometimes useful for delineating receptive field areas but precluded the identification of single units or their properties. Often when this happened, I felt secure in claiming that a single unit was being audibly isolated (from a group of five or less), but less secure in any endeavor to identify which of the several visible units was actually being heard. This was because the unit best heard was not always the one with the greatest amplitude. Very often a lower amplitude string of spikes could be driven by appropriate body stimulation, this against a high background noise of non-stimulus related activity. An example of this is shown in Figure 3.

The importance of the preceding paragraph, which unfortunately cannot be augmented with a sound recording, is obvious when it is remembered that the arguments to come are based upon <u>single</u> cortical neuron responses and their stimulus interests. These can be sampled and analyzed only if genuine unitary responses can be convincingly isolated from neighboring responses.

Thus, at the end of a recording session, I had a log of information which would not only allow the eventual reconstruction of the puncture rows in sliced and stained tissue but the following as well:

1. Each receptive field, drawn on a photograph of the appropriate body region.

2. A tape recording together with voice commentary of each cortical unit response to both natural and (where possible) electrical stimulation.

3. A record of the most adequate stimulus for driving each of the cortical units.

4. A measure of the response latencies of many of the units.

5. Measures of the adaptation (response to maintained stimuli) and habituation (response to repeated stimuli) of each isolated unit.

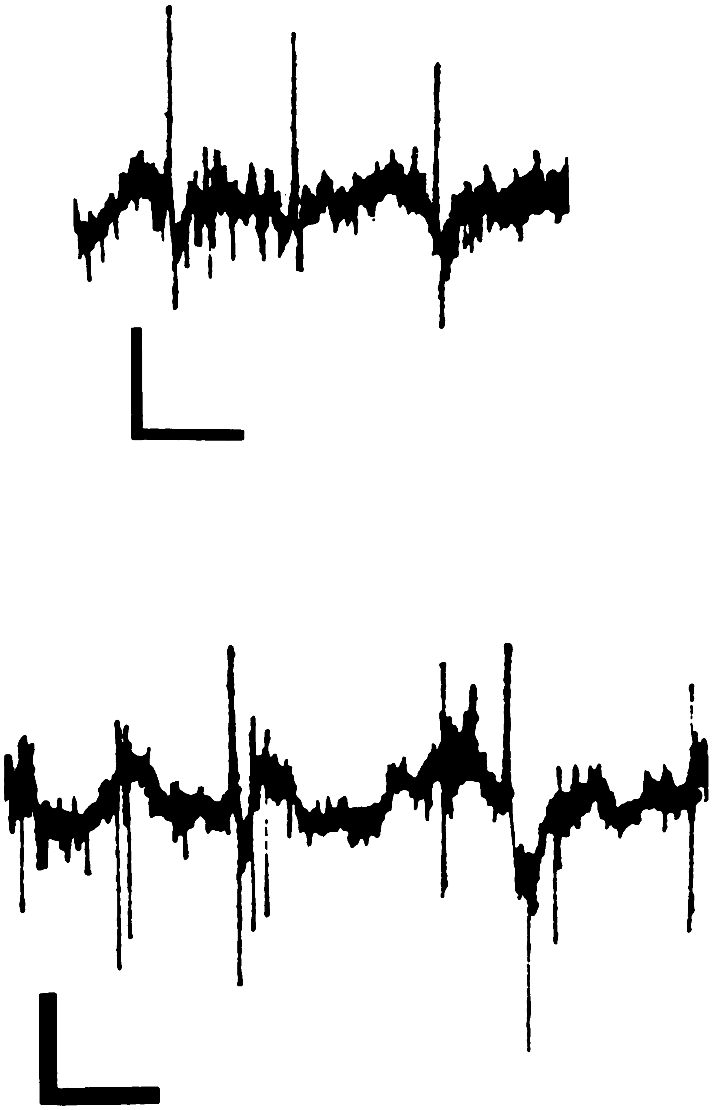


Figure 3. Demonstration of single unit activity in midst of background noise. This is from response 11A, subject 70399. (Top) This oscillogram shows an example of some on-going background activity that was not stimulus related. Calibration 100uV & 20msec/div. (Bottom) Application of the stimulus (squeezing the claw sheath) has resulted in additional activity as shown on this expanded time scale oscillogram. The sheath unit is of smaller amplitude than the background activity, yet it was distinctly audible and visually (in this case) isolated as a single unit. Calibration: 100uV & 10msec/div.

6. A log of special properties or peculiarities of interest concerning any given cortical unit.

Cortical ablations. Unilateral neocortical ablations were performed on seven cats between the ages of 32 and 83 days. The ablations involved the following areas:

1. SI only ablations. (four animals, right hemispheres only) These involved only the posterior body regions of the SI field. The head region (coronal gyrus) was spared. In extent the lesions ran anteroposteriorally from the region of the postcruciate dimple to the ansate sulcus. Mediolaterally, the extent was from the midline fissure to the coronal sulcus. Every attempt was made to spare the underlying white matter.

2. SI plus SII ablations. (two animals, one right and one left hemisphere) Involved was all of the area of 1. above plus the rostral portions of the anterior ectosylvian gyrus. SI head region was again spared but there was encroachment upon the SII head region as there is no topographic demarcation separating SII body from SII head as there is in SI.

3. SI cortical island. (one animal, right hemisphere) An effort was made to remove all neocortex except that delineated in 1. above. The motor areas anterior to the postcruciate dimple as well as those rostral to the cruciate sulcus itself were removed together with the deep temporal regions and the entire occipital area. The coronal gyrus was also ablated.

All operations were carried out under aseptic conditions using the technique of subpial suction. Recoveries were uneventful except in one case (70397) where a lingering infection destroyed portions of brain tissue outside the immediate ablation area. This animal's recovery was marred by an eye infection whose onset began about one week postoperatively and lasted for approximately 30 days. At the time of the electrophysiological experiment, the animal was apparently normal. The extent of the infectious lesion was not determined until the brain was examined histologically.

<u>Tissue preparation</u>. At the termination of the recording sessions, marking bars were placed in the brain in the plane of the puncture rows. This permitted the tissue to be sliced parallel to the electrode tracks. Following this the animal was deeply anesthetized and inter-cardially perfused with isotonic saline followed by formol-saline solution. The brain was removed from the skull, embedded in celloidin and sliced at 30 microns. The sections were stained alternately for cell bodies (thionin) and myelinated fibers (hematoxylin). As a check upon the extent of the cortical ablations every 9th and 10th section from those areas was stained for cells and fibers respectively. This allowed a determination of the extent and depth of the ablations.

<u>Cortical reconstructions</u>. Large tracings were made of the brain sections containing puncture rows. The punctures were identified using the data obtained during the recording sessions and the electrode tracks and recording loci along those tracks were entered upon the tracings. Each unit response was marked, at the appropriate cortical depth, with a symbol denoting its stimulus modality. Receptive fields were copied onto figurines and arranged in vertical columns corresponding to each puncture and its recording locus. During reconstruction there was a constant interplay between the tape recorded data and the data recorded in the log books. This permitted a constant cross-checking of the results and served as an admirable check upon the investigator's consistency in interpreting data from experiment to experiment.

RESULTS

The experimental sample. A total of fifteen cats provided the cortical unit data for this study. Eight of the subjects were normal and seven had received cortical ablations as outlined in the preceding chapter. The subjects were of mixed sex with ages ranging from eighty days to two years at the time of recording. All but two of the subjects were less than nine months of age at the time of recording. Thus, the majority of the subjects were less than a year of age at the time the data were collected. Both right and left hemispheres were used, more or less randomly, in these experiments.

The second somatic or SII region of the anterior ectosylvian gyrus (AEG) was penetrated a total of 421 times in the fifteen subjects. These penetrations yielded a population of 435 resolvable single cortical units. Of these, 357 were, by virtue of their receptive field properties and position in the cortical tissue as determined by histological reconstruction of the puncture tracks, determined to lie in the postcranial, mechanoreceptive projection area of SII. Table 1 gives the distribution of the unit population. Because of the difficulty in distinguishing

Table 1

Types of Single Neural Units - Numbers and Location

Location of Units	Number of Units
Postcranial mechanoreceptive SII units in AEG	357
Cranial mechanoreceptive units in SI and SII	51
Mechanoreceptive units later shown to be in fiber areas	15
Others	12
Total	435

SI and SII head regions, responses from the cranial areas were excluded from consideration in this study. Fiber responses were generally identified during the recording sessions and excluded at that time. Some fifteen such units managed to creep into the study and were not identified as such until histological reconstruction had been completed. The "other" category consists of postcranial mechanoreceptive responses that were either shown to be from SI or from areas totally outside either somesthetic receiving area. Several of these (seven) were found in the upper bank of the anterior sylvian gyrus.

Anesthetic effects upon single SII mechanoreceptive units. A sample of 33 single units was obtained from two animals that were anesthetized with nitrous oxide during the recording sessions. Of these, 22 were later shown to have been postcranial SII units. A paralytic agent (gallamine triethiodide) was employed with these animals. The remaining thirteen subjects were anesthetized with sodium pentobarbital. No paralytic was used with these.

As far as the functional properties considered in this study are concerned, there were no appreciable differences between the responses obtained under the two anesthetic states. A much higher amount of background activity was noted in the nitrous oxide animals. This occasionally made the isolation of single units more difficult than was the case with pentobarbital anesthetized subjects. Thus, response latencies, habituation properties, receptive field sized and organization, as well as the type of stimulus and the stimulus threshold were unaffected by anesthetic conditions. I failed to find any bilateral or ipsilateral responses in the nitrous oxide animals (0 out of 22 responses) as opposed to the pentobarbital animals (10 out of 335 responses). The difference is probably not significant. As a result of these findings, the remainder of this report will not distinguish between the two types of anesthesia employed except where specifically noted.

Tactile modalities of SII mechanoreceptive units. Careful attention was paid throughout these experiments to the type of stimulation which, when applied to the receptive field under examination, drove the unit optimally. This was generally defined as the minimal mechanical stimulus which could elicit a uniform response from the unit when stimulated repetitively, although, as will be seen, the story is not quite that simple. In general SII units were found to respond either to pressure, involving a noticeable but not violent indentation of the skin or to lighter stimulus modes such as brushing glabrous skin surfaces without visible deformation or by moving body hairs without moving the skin surface. Some units responded to hair stimulation in a focal area surrounded by an area which responded to application of light pressure. Figure 4 demonstrates the tactile modalities as considered in this study while Table 2 gives a quantitative breakdown of the numbers of units responding to the various stimulus modalities.

No units were found which responded to joint movement or unambiguously to stimulation of "deep" tissues. Such latter responses were usually elicitable by using much less vigorous stimulation applied elsewhere on the body surface.

SII units which responded to application of pressure to their receptive fields were mostly of the variety which were driven by light pressure (L). The adequate stimulus was a just noticeable, punctate depression of either glabrous or hairy skin areas. No effort was made to determine thresholds analytically, but it appeared that these units responded to the same stimulus levels over the extent of their receptive

Figure 4. Criteria for establishing tactile modalities.

I. HIGHER THRESHOLD MODALITIES

L Light Pressure

visible indentation of skin

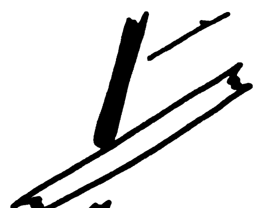
M Moderate Pressure

more pronounced skin indentation

II. LOWER THRESHOLD MODALITIES

T Touch

no indentation, glabrous skin only

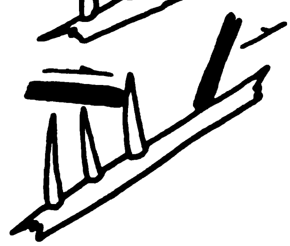


H Hair

no visible movement of skin

TH Touch-Hair

glabrous-hairy border areas



III. MIXED THRESHOLD MODALITY

LH Pressure-Hair

hairy focus with contiguous pressure region

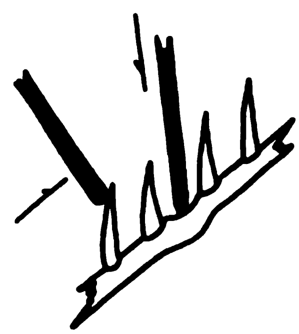


Table 2

Relative Proportions of the Various Tactile Modalities

Modalities	No. of Units	% of Units
I. Higher Threshold Modalities		
Light Pressure (L)	161	45.1
Moderate Pressure (M)	24	6.7
Totals	185	51.8
II. Lower Threshold Modalities		
Touch (T)	44	12.3
Hair (H)	71	19.9
Touch-Hair (TH)	43	12.1
Totals	158	44.3
III. Mixed Threshold Modality		
Pressure-Hair (LH)	14	3.9
Totals	14	3.9
Grand Totals	357	100.0

fields. A sudden increase in threshold marked the receptive field boundary. Moderate pressure (M) units were rarer than L units (see Table 2) but their behavior was similar. The basic difference was that a more vigorous, but by no means violent, tap was required to elicit a response. This resulted in a much more noticeable indentation of the skin. More violent stimuli than those just described were not used in this study. Localization of receptive fields for units that responded to vigorous "thumping" invariably resulted in finding another receptive field, driving the same unit, whose stimulus interests were concerned with non-nociceptive modalities. The conclusion was inescapable that the heavy stimulation was activating a lower threshold receptive field at a distance. This was eventually borne out when electrical means were used to drive isolated units. Placing the stimulating needles outside the low threshold areas failed to elicit a response .

The second major grouping of tactile modalities was primarily concerned with even lower threshold stimuli. Hair (H) units were activated by light brushing of the hair tips or by air puffs delivered parallel to the skin surface. These comprised almost 20% of the mechanoreceptive unit population. A second variety, the touch (T) units, were associated with glabrous skin only which, in the case of the postcranial body regions, involved the pads of the volar hand and foot. These units (12.3% of the total) responded to the lightest of touch, requiring no indentation of the skin for a maximal response. T responses were most often not elicited by punctate stimuli, but by the slow movement of a cat's vibrissa or a paint brush bristle across the receptive field. Though such movement was a very effective stimulus, no directional properties were noted, movement in any direction being equally effective. Yet a further category were the combined Touch-Hair units (TH). Such units always responded to stimulation of a patch of glabrous skin as well as to adjoining hairy skin. The receptive fields of TH units were never disjunct.

The remaining mechanoreceptive units comprised a small but persistent group which possessed both hair (H) and light pressure (L) properties. These LH units had a low threshold (H) modality region in their receptive fields which was surrounded by a higher threshold or (L) area. Again, such receptive fields were not disjunct. As the stimulus was moved away from the central focal area, the unit would no longer respond to light brushing of the hair but would respond to pressure applied to the skin. Further migration of the stimulus resulted in no response at all. The appearance of the unit on the oscilloscope screen, the amplitude and numbers of spikes discharged and its "audible" qualities as discerned from the audio monitor convinced me that the same unit was being stimulated by two distinct tactile modalities.

On occasion SII units would demonstrate shifting stimulus thresholds and migrating receptive field boundaries. Such units, if held for any length of time, generally would stop responding altogether. Succeeding punctures, if nearby, were usually "dead". It gradually dawned upon me that this was due to cortical damage, usually caused by damaged electrode tips. A visible dimpling of the cortical surface upon penetration was a virtual guarantee that cortical depression (of the spreading variety) was in the offing. Spotty, ill-defined receptive fields would result, followed by silence (even in the animals anesthetized with nitrous oxide). Recovery from the depression was alow (one or more hours) and seldom permanent. Another cause of "peculiar" behavior in cortical units apparently resulted from using closely spaced electrode punctures (*i.e.*, on the order of 200 microns or less). Driving the electrode in too deep (desirable from the standpoint of finding the tracks during reconstruction) caused damage at the cortical surface because of the width of the descending electrode's shank. The site of the next puncture was often affected resulting in more "dead" cortex. This problem was solved by controlling the penetration depth to the point where the electrode just entered the underlying white matter, usually a matter of 2 to 3 millimeters. This way the wide part of the electrode did not enter the brain at all. When such precautions were taken, the behavior of SII units remained constant over time. There were no threshold or stimulus modality shifts. The boundaries of the receptive fields were constant. Neuronal properties characteristic of Po projections were not found in the anterior portions of AEG.

Adaptation and habituation properties of mechanoreceptive SII neurons. The vast majority of SII cortical units examined in this study (351 out of 357) adapted rapidly to stimulation (Table 3). That is, upon application of the stimulus the unit would respond with a short burst of from one to eight or nine spikes and then stop even though stimulus pressure were maintained. Though the number of spikes discharged might rise with increasing stimulus strength, units which maintained a discharge as long as the stimulus was applied were quite rare. No units were observed to fire upon release or cessation of the stimulus. The slowly adapting or maintained response units were mostly claw units, responding to the position of the claw within its sheath. Two of the six such units, however, responded to skin pressure.

Table 3

Distribution of Adaptation and Habituation Properties of Postcranial SII Mechanoreceptive Units

Category	No. of Units	% of Units
I. Adaptation		
Fast	351	98.3
Slow (maintained discharge)	6	1.7
Totals	357	100.0
II. Habituation		
Fast	14	3.9
Moderate	42	11.8
Slow	301	84.3
Totals	357	100.0

Habituation, in contradistinction to adaptation, refers to the rate at which a stimulus can be delivered to a receptive field before the unit's following abilities are affected. For the purposes of this study habituation was classed as either: slow - could be driven at rates greater than once per second with no change in the response properties; moderate - drivable at rates less than once per second but greater than once per five seconds; and fast - could not be driven at rates greater than once per five seconds (Table 3). Most units reported in this study were slow habituators. Some displayed moderate habituation while the remaining few habituated quite rapidly. There appeared to be no correlation relating the degree of habituation with tactile modalities, response latencies (see immediately below), type or location of receptive field or anesthetic employed.

One possible experimental effect upon habituation was noted. The two animals whose ipsilateral, postcranial SI cortices had been removed displayed <u>only</u> slowly habituating units in the intact SII cortex (N equals 39 units). All of the remaining animals except one (70352; N equals 8 responses) showed the approximate 85% slow, 10% moderate and 5% fast ratio of habituation categories. The exception noted was a normal (non-ablated) animals from whom possibly too few units were obtained for the exception to be significant.

<u>Response latencies of SII mechanoreceptive units</u>. In view of the long-standing contention that SII receives a dual innervation from both Vb and Po (Guillery, Adrian, Woolsey & Rose, 1966; Heath, 1970; Heath & Jones, 1971), it was decided to examine the SII unit population in terms of response latency to electrical stimulation. Approximately 37% or 132 of the 357 units obtained in this study were driven electrically as well as mechanically and were demonstrably the same unit under both conditions (Figure 5). Closely spaced (two to ten mm) stimulating electrodes were inserted just beneath the skin and square wave pulses of increasing amplitude were delivered until the unit responded, if at all. The stimulating voltage was increased 20-25% over the threshold value for the final latency determination. Figures given in all cases are latencies to the firing of the first spike in the train. This interval was not seen to diminish appreciably with increasing supra-threshold stimuli, though such stimulation often either increased the number of spikes discharged or diminished the intervals between successive spikes in the train. Repetitive electrical stimulation had an effect

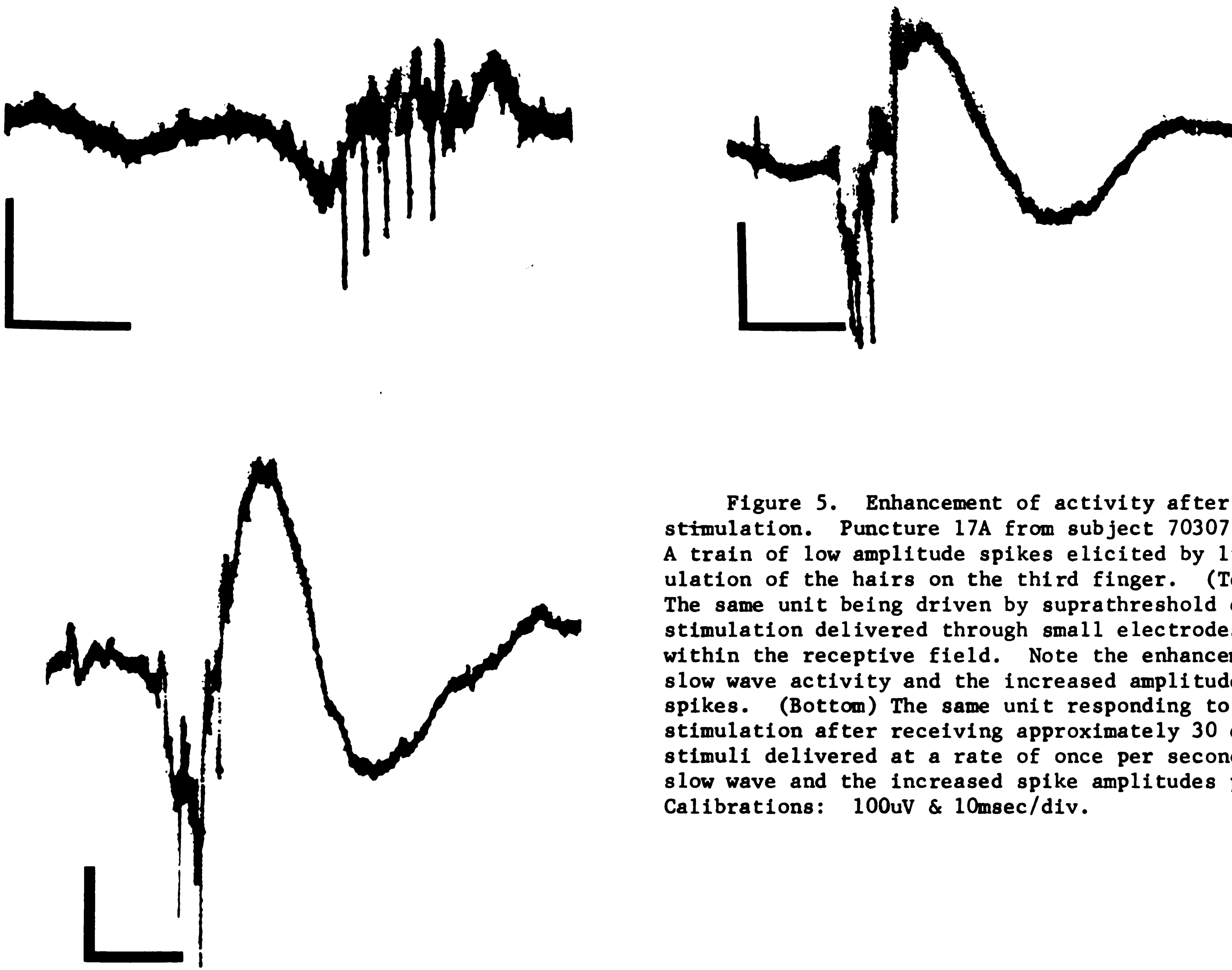


Figure 5. Enhancement of activity after electrical stimulation. Puncture 17A from subject 70307. (Top left) A train of low amplitude spikes elicited by light stimulation of the hairs on the third finger. (Top right) The same unit being driven by suprathreshold electrical stimulation delivered through small electrodes placed within the receptive field. Note the enhancement of the slow wave activity and the increased amplitude of the spikes. (Bottom) The same unit responding to mechanical stimulation after receiving approximately 30 electrical stimuli delivered at a rate of once per second. The large slow wave and the increased spike amplitudes persist. Calibrations: 100uV & 10msec/div.

which was dependent upon the habituation properties of the neuron. As the habituation threshold was reached, the unit would occasionally miss a stimulus, this incidence becoming more frequent as the repetition rate was increased. One consistent feature of the SII units studied was that the isolation of single units was often enhanced by the electrical stimulation. Tactile stimulation following the latency test was routinely performed to make certain that the same unit was being recorded from as had been prior to the electrical driving. Very frequently the demarcation of the unit was obviously superior to its initial occurrence; the signal to noise ratio was improved and the unit was much more audible when listened to over the audio monitor. Enhancement of the slow wave on which the spikes rode was also often noted (Figure 5).

Latencies were determined for cortical units whose receptive fields covered all contralateral areas of the body. For the convenience of presentation these are grouped (Table 4) into Fingers, Hand, Arm and Rear Body, including Tail. In all cases the average response latency of these regions increases as the receptive fields progress distally. Four units were found that had bilateral receptive fields associated with the upper leg and trunk region. For these units the contralateral responses had latencies ranging from 12 to 40 msec with a mean of 24.2 msec while the ipsilateral responses were considerably slower, range: 18-100 msec with a mean of 44.5 msec. Furthermore the mean contralateral response latencies of this group of bilateral units exceed those of the purely contralateral units (mean latency equals 17.2 msec) which are associated with the same body region (hip and upper leg).

Table 4

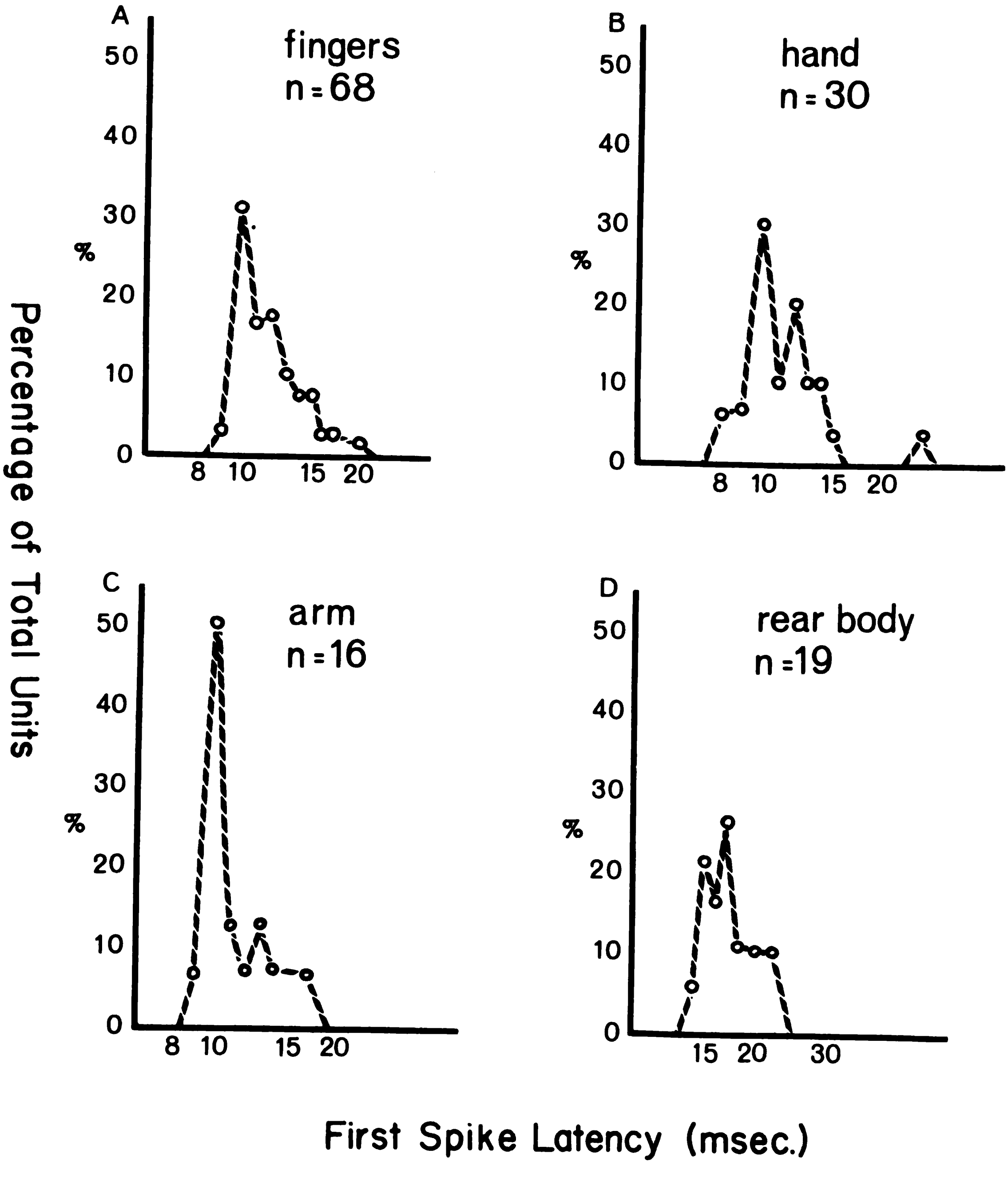
First Spike Response Latencies from Various Body Regions of SII Mechanoreceptive Units to Electrical Stimulation

	Body Region	# of Responses	Range of Responses (msec)	Mean of Responses (msec)	
I.	Strictly Contralateral Receptive Fields				
	Fingers	68	9-20	12.0	
	Hand	30	8-25	11.6	
	Arm	16	9-17	11.3	
	Rear Body & Tail	19	14-22	17.2	
II.	Bilateral Receptive Fields*				
	Hip & Upper Leg	4	12-40	24.2	(contralateral)
	Hip & Upper Leg	4	18-100	44.5	(ipsilateral)

*Data are from the contra and ipsilateral response fields of the same units.

Plotted as probability of response versus response interval (Figure 6) the latency data show that the distribution of responses <u>may</u> be bimodal with the modes on the order of 2.0 msec apart regardless of the body area considered. An attempt was made to correlate this possibile bimodality with the stimuli that best activated the units for which latency data were available. A rough measure was obtained by dividing the response latency populations from all body areas into three groups: a) those whose latencies were less than the first mode, b) those whose latencies lay between the two modal peaks, and c) those with latencies greater than the second mode. The tactile modalities of these units were catalogued and compared across these derived latency classes.
The results (Table 5) indicate that the stimulus interests of SII units are virtually independent of the latency of that unit to stimulation, at least within the limits of the classifications employed in this study. It should be pointed out that these response latencies were obtained under unnatural conditions. Caution should be used in attempting to correlate tactile modalities, obtained by mechanical means, with

Figure 6. First spike response latency distributions from various body regions. The data are plotted as the percentage of responses measured from a given body area versus the $\log_{10}$ of the response latency in milleseconds. Note the tendency toward bimodality.


A
fingers
n = 68
B
hand
n = 30
C
arm
n = 16
D
rear body
n = 19
%
Percentage of Total Units
First Spike Latency (msec.)
0
10
20
30
40
50
8
10
15
20
30

various
es

response latencies, obtained by electrical means. Stimulation of units in the latter mode may well override subtle response differences that might exist between units driven by more natural means.

Table 5

Correlation of Tactile Modalities with Response Latencies of SII Mechanoreceptive Units. Expressed as Percent of Units of a Given Latency Group Displaying Specific Tactile Modalities. (All Figures in Percentages).

Tactile Modality	Response Latency Category		
	I Latency less than first modal peak*	II Latency between the two modal peaks*	III Latency greater than the second modal peak*
Light Pressure	47.2	55.2	38.1
Moderate Pressure	9.4	3.4	4.8
Touch	9.4	15.5	9.5
Hair	20.8	17.2	23.8
Touch-Hair	7.5	3.4	9.5
Pressure-Hair	5.7	5.2	14.3
Totals	100.0	100.0	100.0

*See Figure 6.

Similar techniques were used to compare habituation properties of the SII units and their response latencies. As long as repetitive stimuli were not delivered at a rate near the habituation limit for the unit under examination, there was not any correlation between the rapidity of habituation and the response latency of a unit.

Receptive field properties of SII neurons. As has been reported for SI cortex in the cat (Mountcastle, Davies & Berman, 1957; Rubel, 1971), in the raccoon (Welker & Seidenstein, 1959), in the monkey (Benjamin & Welker, 1957) and in monkey SII (Whitsel, Petrucelli & Werner, 1969), there is a gradient of increasing receptive field size drom distal to axial body areas. The smallest receptive fields are found at the apical limb regions with the largest fields occupying the trunk and upper limbs. The cortical units activated from these receptive fields remain constant in threshold, latency and in tactile modality over time as has been mentioned. Also, the sizes of the receptive fields do not vary in time.

A certain amount of bilateral evoked wave activity was frequently seen having an ipsilateral component both slower in response latency and lower in amplitude as compared with the contralateral response. However, bilaterally or ipsilaterally activated units were quite rare (10 in 357). One purely ipsilateral unit was found; the remainder were bilaterally driven. Bilateral units had receptive fields that were symmetric with respect to the body axis, either continuously across the midline in the case of proximal fields, or disjunct in the case of more distally oriented fields. In terms of receptive field stability and tactile stimulus interests these units were similar to the purely contralateral population of cortical units which comprised the majority of the responses found.

Most of the strictly contralaterally driven SII units had receptive fields that were not disjunct, that is, two responsive areas, separated by a non-responsive area were not generally found. An important exception was concerned with the apical limb areas. The glabrous tactile pads of the hands and feet were often able to activate one unit from several pads. For example, stimulation of one or two finger pads plus the glabrous palm pad would often drive the same cortical unit. These pads are separated by patches of hairy skin which, when stimulated, did not activate the cortical unit at all. In addition glabrous and hairy areas were sometimes included in the same receptive field (TH units).

Finally, about 10% of the receptive fields found were of a "stocking-like" nature, responsive to equal threshold stimulation around the entire circumference of a limb or the trunk. Sometimes an entire limb was involved, at other times only the lower or upper limb, the stocking breaking off sharply at the wrist, ankle, elbow or knee. A few very large receptive fields formed bilateral "body stockings". These stocking fields fit in with the somatotopic organization of the non-stocking fields. The cortical neurons subserving them did not demonstrate anything out of the ordinary in terms of response latency or stimulus threshold or tactile modality. Their habituation properties, however, deserve comment. Often, delivery of a repetitive stimulus to the same point in a stocking field would result in rapid habituation. If, however, the stimulus were delivered rapidly to different areas of the receptive field, the ability to follow remained unimpaired. Nonetheless, the receptive field boundaries remained invariant though excessive stimulation at the field's edge might mislead one into thinking that the receptive area was ill-defined.

Somatotopic organization of mechanoreceptive projections to SII. The organization of receptive fields in SII cortex of the cat follows, for the most part, an orderly somatotopy, similar to that reported in cat SI (Rubel, 1971) and in the somesthetic cortices of a host of other animals (See Chapter I). Axial body areas lie medially along the upper bank of AEG but mechanoreceptive projections to SII do not extend all the way to the fundus of the anterior suprasylvian sulcus (Figure 7). The head faces rostrally with the ophthalmic and maxillary areas lying medially and the mandibular, laterally. SII head region merges into the SI head region occupying the coronal gyrus into which AEG opens. Distal limb areas lie facing laterally with the digits pointed somewhat antero-

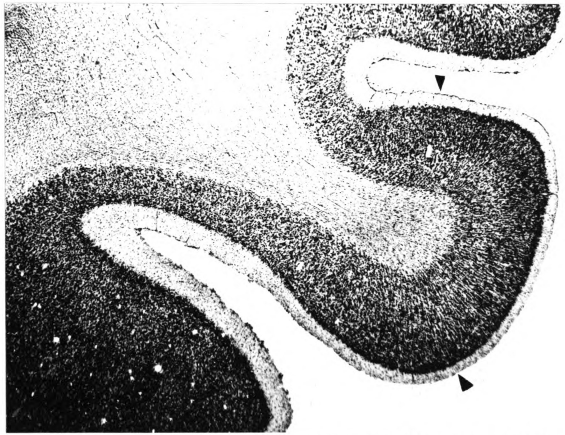


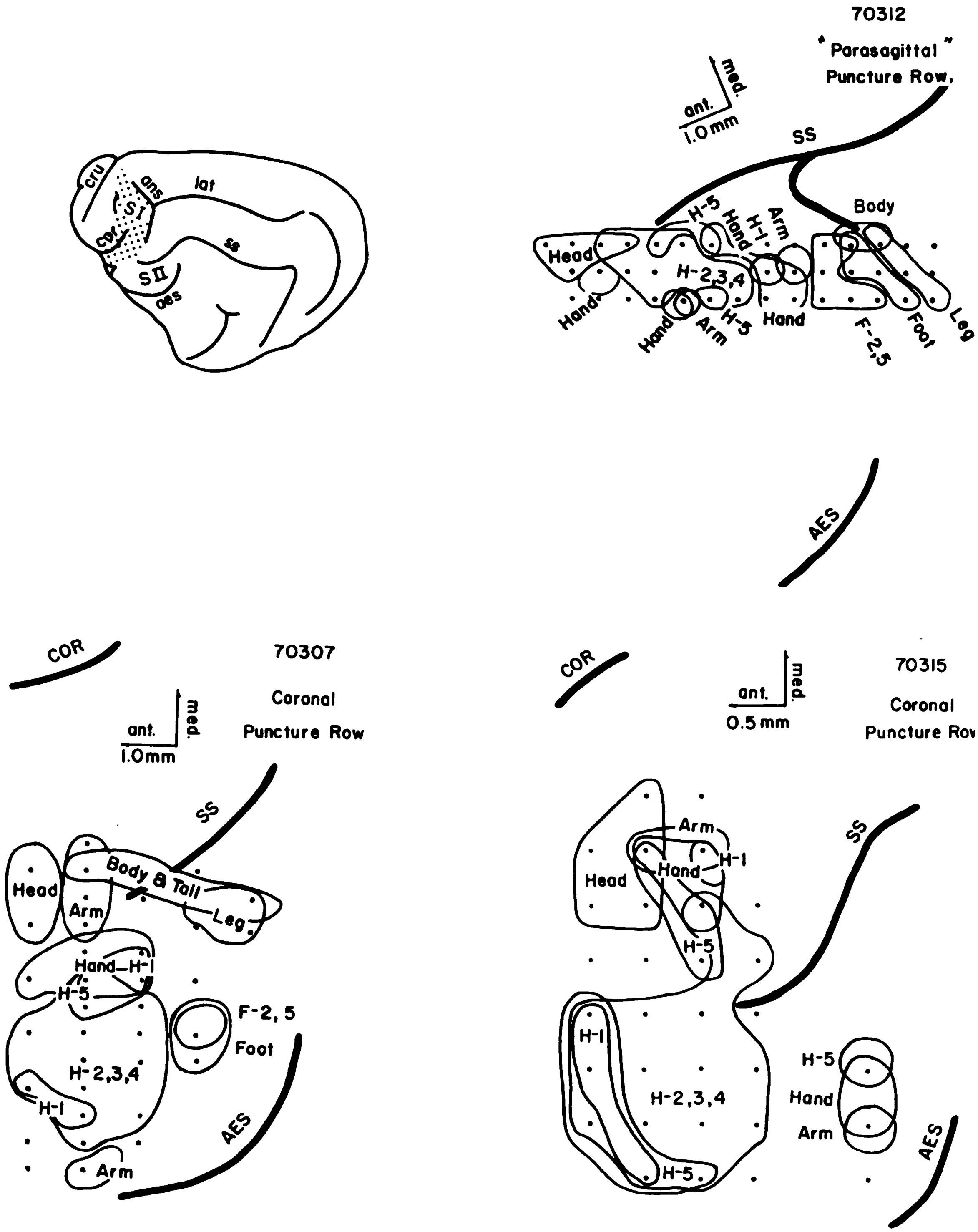
Figure 7. A thionin stained coronal section through the anterior ectosylvian gyrus showing the medial (left) and lateral (right) boundaries of SII. From subject 68324, a normal histological control.

laterally. Lateral to, but not extending to the anterior limit of the hand and finger representation are found projections from the external or ulnar arm (Figures 8B & 8C). This is a fairly prominent feature of the map and has, perhaps, been responsible for some of the confusion about the orientation of proximal structures in cat SII in the past (Berman, 1961). Projections from the limb apices are not found in the lower bank of AEG and, in fact, are seldom seen to extend much beyond the medial convexity of the gyrus (Figure 7). Low threshold auditory responses were not observed within the area of SII occupied by mechanoreceptive projections to either the fore or hind limb areas.

By far the largest portion of the postcranial SII region is devoted to projections from the hand and fingers. Representation of the rear leg region, while considerable, is much less impressive that that of the fore limb. The head, though not mapped in great detail in this study, also appears to have an extensive representation, rivaling that of the forepaw. Axial structures were very sparsely represented, though some responses were found from all body areas except the belly.

Studies prior to this one which have dealt with the organization of projections to the somesthetic cortices have invariably reported a high degree of somatotopy. That is to say, that projections from a given body region are reflected in an orderly, topologically consistent manner onto the cortical surface. Thus, a puncture locus which showed activity from the third contralateral finger would be expected to have as neighbors units on or very near that third digit. With the exception of some trigeminal projections to intraoral regions (Bombardieri, 1971; Cabral & Johnson, 1971 have discussed this problem in Vb) the projections from a given body region flow smoothly and continuously onto the cortical field. Occasionally problems have arisen over the way in which the

Figure 8. Location of somesthetic cortex in the cat together with maps of the somatotopic organization of SII from three subjects. (A-Upper left) A diagram of the left cerebral hemisphere locating both SI (dotted) and SII somatic sensory cortical areas. (B-Upper right) From experiment 70312. All punctures containing units which responded to stimulation of a given body area are closed within a line. Thus all "head" responses are enclosed as are all foot responses and so on. Puncture locations are marked by dots. H-5 is the fifth digit of the hand; F-2 the second digit of the foot, etc. (C-Lower left) From experiment 70307. Note that the most axial structures lie medially but that there is an extreme lateral lying arm projection as well as the more medially situated one. (D-Lower right) From experiment 70315. These data are acquired from more closely spaced punctures. Note the overlap of the internal and external digits of the hand. Abbreviations: AES, anterior ectosylvian sulcus; ANS, ansate sulcus; COR, coronal sulcus; CRU, cruciate sulcus; LAT, lateral sulcus; SS, suprasylvian sulcus.



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SII
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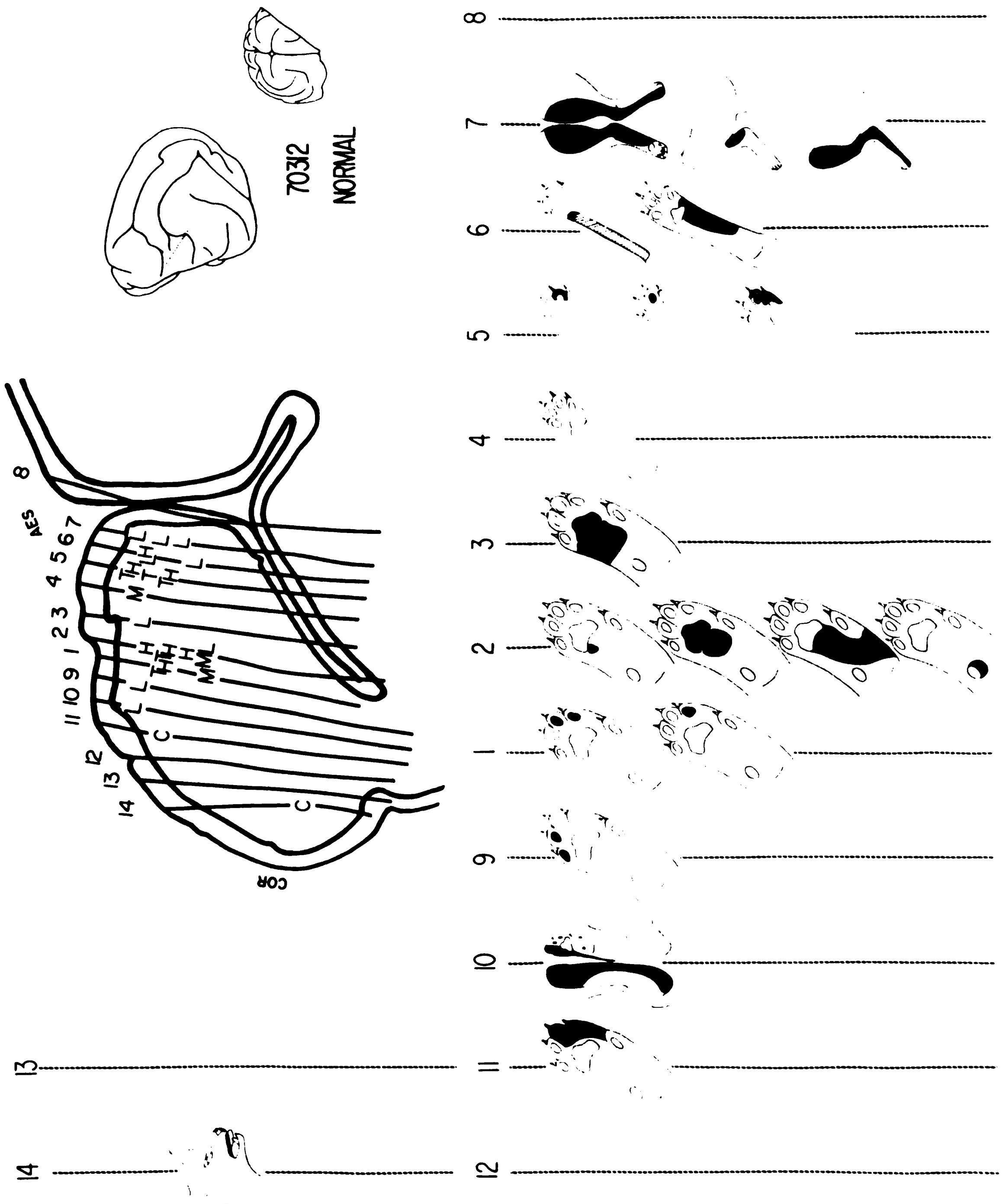
70312
"Parasagittal"
Puncture Row.
ant.
med.
1.0 mm
SS
Body
Head
H-5
Hand
H-1
Arm
H-2,3,4
Hand
Hand
Arm
H-5
Hand
F-2,5
Foot
Leg
AES
COR
70307
Coronal
Puncture Row
ant.
med.
1.0mm
SS
Head
Arm
Body & Tail
Leg
Hand
H-1
H-5
F-2, 5
Foot
H-2,3,4
H-1
AES
Arm
COR
70315
ant.
med.
0.5 mm
Coronal
Puncture Row
Arm
H-1
Hand
Head
H-5
SS
H-1
H-2,3,4
H-5
H-5
Hand
Arm
AES

head and forelimb maps are related (Pubols & Pubols, 1971 most recently) but other recent mapping studies (Whitsel, Petrucelli & Werner, 1969) have shown that there is no discontinuity between the head and neck-body-shoulder representations. Further discussion of this point will be reserved until the next chapter.

The map of postcranial SII in the cat obeys the standard rules in all areas except the forepaw and its digits. Here the projections appear to be somewhat less than orderly. Figure 8D shows a detailed map of the forepaw region from one animal (70315). It can be seen that the outer fingers, numbers one and five, appear to _either_ side of the mesial digits, numbers two through four. Further, these central digits do not necessarily appear in 2-3-4 or 4-3-2 order, but rather in mixed sequence. This apparent lack of simple somatotopy was consistently observed in all animals studied. Closer examination of the data suggested that there might be a sub-organization in the forepaw region which might be better resolved if a series of experiments were done using even closer puncture spacing than heretofore had been the case. Hence, a mapping series using 0.2 mm puncture spacing instead of the previously standard 0.5 and 1.0 mm spacing was done. The idea of a sub-organization was verified and forms the subject of the next section.

The relationship of tactile modalities and receptive field organization in SII. The data contained in the roughly parasagittal row of reconstructed electrode tracks shown in Figure 9 demonstrate the substance of the findings reported in this section. Due to the lateral position of this puncture row, the division between the forelimb and hindlimb is pronounced with the hand and foot forming separate "pockets" as represented on the cortex. The angle at which the electrode entered the gyrus contrubutes more to the appearance of these "pockets" than does any

Figure 9. Reconstruction of a parasagittal puncture row (Subject 70312). This section lies near the lateralmost extent of the mechanoreceptive portion of SII. Tactile modalities are indicated in the schematic brain section at approximately the level within the puncture that they were found. Receptive fields are indicated below and to the left of the brain section. Note that there appear to be two "pockets", one devoted to the forearm and the other to rear leg projections and that the higher threshold tactile modalities (L and M) appear to surround the lighter tactile modalities (T and H). The hatched portion of the receptive field in puncture 6 represents the L or light pressure portion of this mixed modality response. To the right of the figure are shown a tracing of the left cerebral hemisphere of this animal with the orientation of the puncture row shown in small dots. To the right of that figure is a "cut" away diagram showing the angle at which the electrodes entered the cortex. Abbreviations: AES, anterior ectosylvian sulcus; COR, coronal sulcus.

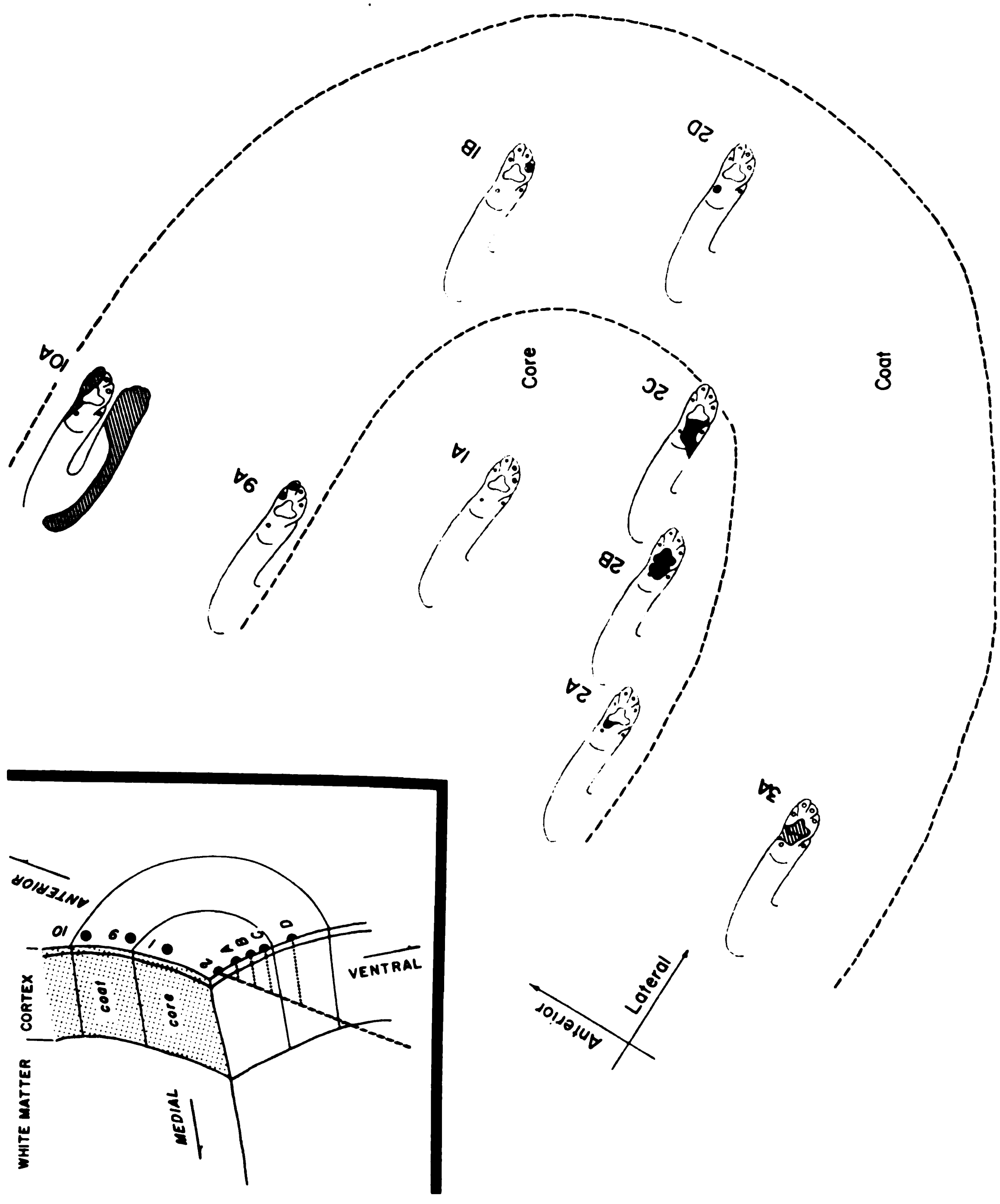

70312
NORMAL
AES
COR
8
7
6
5
4
3
2
1
9
10
11
12
13
14

real type of functional organization. The electrodes, as can be seen from the right hand inset, entered the brain at close to a 45^{o} angle, an angle which, nonetheless, was somewhat less than that formed by the axis of AEG with the median sagittal plane. The result was that the bottommost recording loci (*i.e.*, those deepest within a given puncture) are more lateral to those nearer the surface - and are not really at any greater distance from the surface of the gyrus because of its curvature. The point being made here is that the lower boundaries of the "pockets" are _not_ areas of heavier or pressure tactile modalities as might be first supposed by looking at Figure 9 but are, rather, simply the junctions of the cellular cortex with the underlying white matter which, due to the lateral placement of the section shown, is not visible in Figure 9. It was, however, this _apparent_ surrounding of light tactile modalities (H,T & TH) by the heavier ones (L & M) that drew attention to the possibility that this might be a general feature of organization in SII. A search was made for other instances of light tactile cores surrounded by heavier tactile coats, a search that was amply rewarded.

As it turned out, this also was an explanation for the lack of somatotopy in the hand region. Returning to Figure 9 and taking the entry angle of the electrode into account one can see that the organization of the core-coat is more cylindrical than "pockety". Putting the example from Figure 9 into a more schematic form (Figure 10) we see that this one puncture row has enough data to define approximately one-half of two separate such core-coat complexes, one associated with each limb. This was a fortunate circumstance made possible because of the orientation of the electrode tracks to the gyral curvature as discussed above.

Figure 10. Illustration of core-coat tactile modality arrangement for a portion of the puncture row illustrated in Figure 9. (Upper left) a diagramatic cut through the dorsolateral wall of AEG. Viewer is looking toward the rostral pole of the brain. A further section is taken at the level of puncture 2 in order to show the entry angle of the recording electrode and how, in consequence of that angle, deeper lying recording loci are lateral to those above. In this case, due to the lateral position of the punctures in the brain, ventral is roughly equivalent to lateral.

The main portion of the illustration shows the receptive fields brought to the surface of the cortex. The dotted lines indicate the approximate boundaries of the inner core of light tactile modalities and the outer coat of heavier or higher threshold tactile modalities. Solidly drawn receptive fields indicate light tactile responses while diagonal lines indicate the heavier tactile responses. Responses 1B, 2D and 9A are "heavy tactile". The diagonal lines do not show because the receptive fields are small. Abbreviation: AEG, anterior ectosylvian gyrus.



10A
9A
1A
1B
2A
2B
2C
2D
3A
Core
Coat
Anterior
Lateral
ANTERIOR
VENTRAL
CORTEX
WHITE MATTER
MEDIAL
coat
core

Considering only the hand projections, most anteriorally is seen a light tactile core consisting of projections from the volar hand. The receptive fields are ordered in the form of a central stripe ranging from the apices of digits two and three to the junction of the wrist and hand. Four distinct single units representing as many receptive fields comprise this region. Within the core the more distal body parts lie antero-medially with the proximal parts aimed posterolaterally. This is in exact accordance with what the map would predict (Figure 8). If, on the other hand, the receptive fields comprising the heavier tactile coat region are examined, it is seen that the progression of receptive fields is quite different from that seen in the core. The core is enveloped such that it is surrounded by receptive fields which physically surround the core whether they form a part of the natural progression of receptive fields or not. Though this seems a logical enough scheme, it violates the "laws" of somatotopy in that many receptive fields are found that do not quite belong where they are.

Reference to Figures 11, 12 and 13 will clarify this point. In Figure 11 is seen a thionin stained parasagittal section through the arm and hand area of AEG. Electrode tracks and the orientation of the cortical columns (Mountcastle, 1957) are visible. A reconstruction of this section is seen in Figure 12. Eleven electrode tracks are visible, seven of which contain data. Taking into account the columnar arrangement of the cortex, the recording loci can be arrayed in an absolute antero-posterior sequence. For instance, puncture 3B lied posterior to 3A as does 4B to 4A. In puncture 8, however, the uppermost loci are posterior. Also in puncture 8 the puncture is less parallel to the columns. This usually results in more recording loci (more columns traversed) and also in more closely spaced loci.

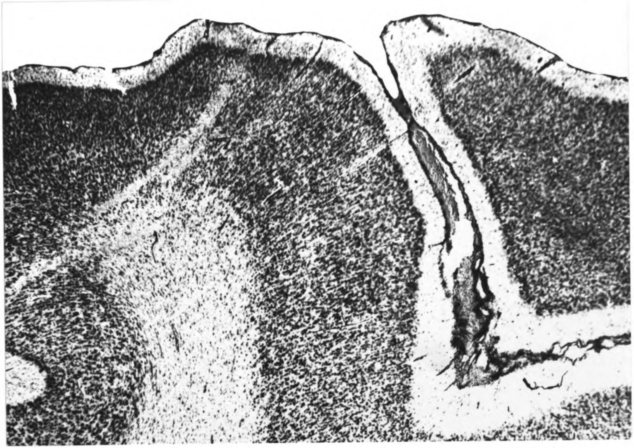


Figure 11. A thionin stained "parasagittal" section through AEG showing portions of a row of electrode tracks. Note the cortical columns in relation to the puncture rows. Data from experiment 71321. Anterior is to the left.

Figure 12. Reconstruction of puncture row illustrated in Figure 11. Symbols same as in Figure 9. Cortical columns are indicated as fine lines. In relation to the colums it can be seen that puncture 8A is anterior to punctures 8B and 8C but that punctures 3A and 4A are posterior to punctures 3B and 4B respectively. Note that the boundary loci, 8C and 6A are heavy tactile, bordered by empty punctures. Abbreviation: SS, suprasylvian sulcus.

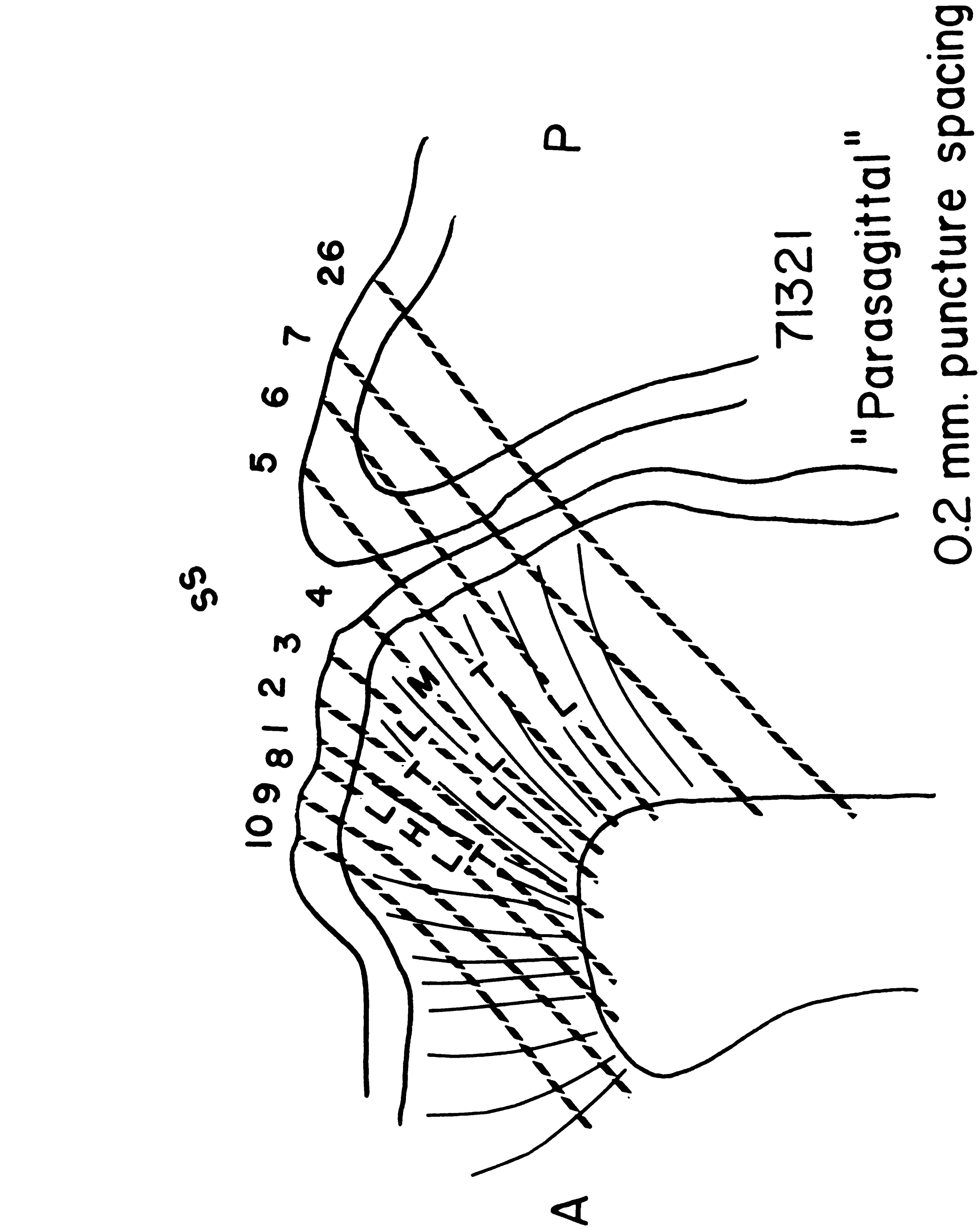
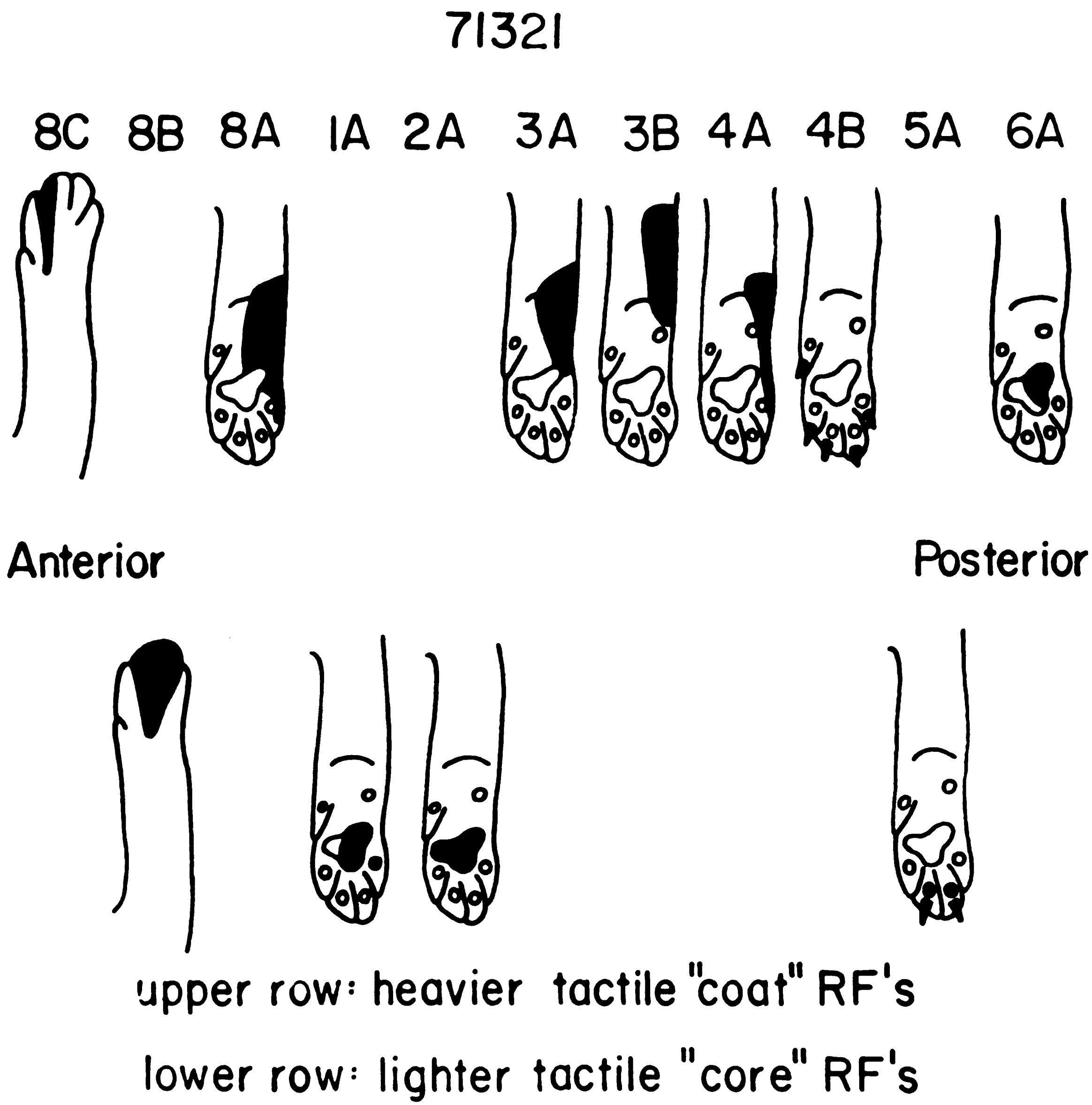

A
P
SS
10 9 8 1 2 3 4 5 6 7 26
7I321
"Parasagittal"
0.2 mm. puncture spacing

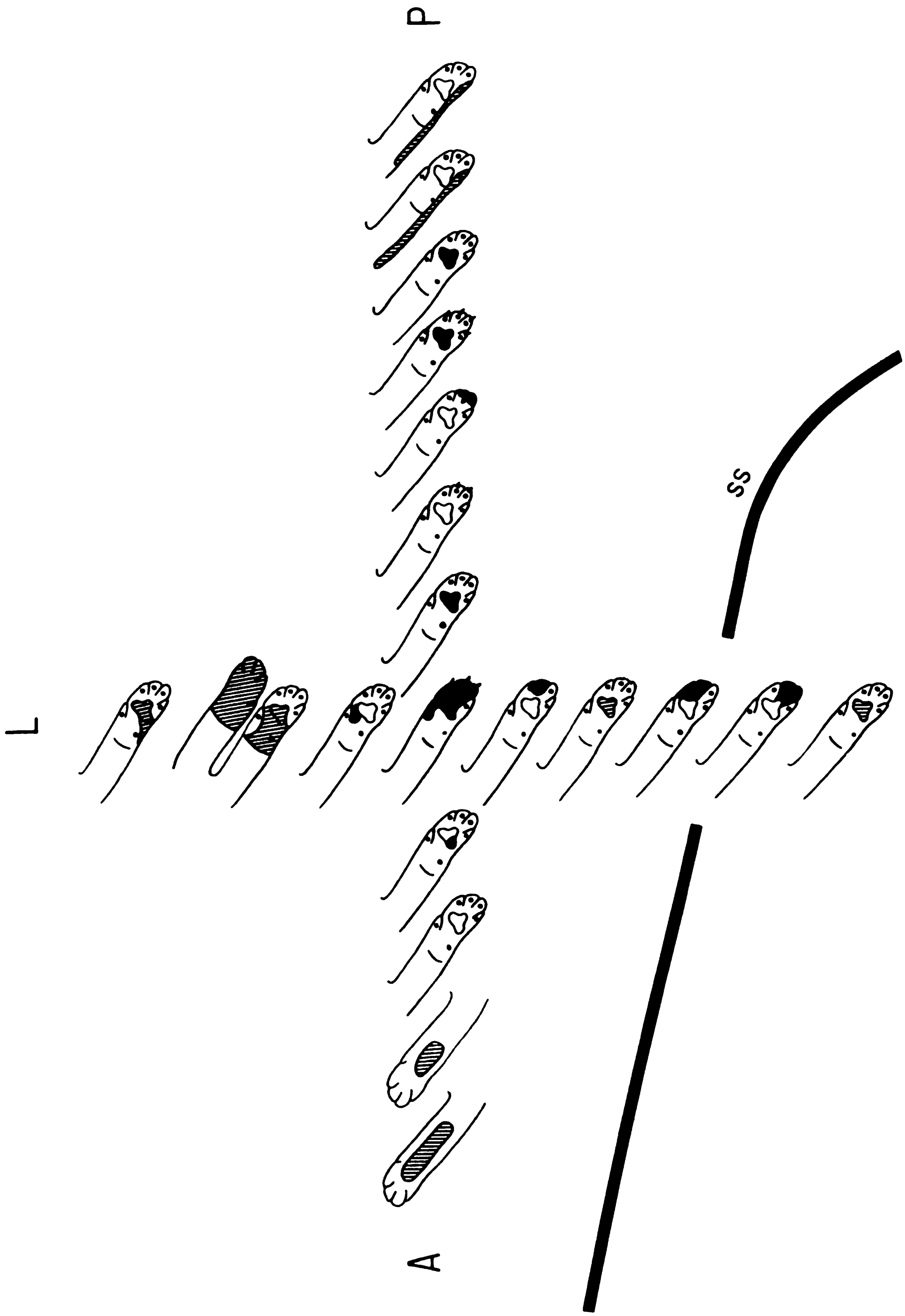
Figure 13. Core-coat tactile modality arrangement derived from data presented in Figures 11 and 12. As noted in Figure 12, loci 8C and 6A are bounded by blank punctures. Observe how the coat receptive fields tend to bracket the lighter tactile cores. Another interesting point is illustrated by the sequence 8A-1A-2A-3A-3B. The progression of receptive fields runs proximal - more distal - back to proximal - even more proximal. The next sequence of loci (4A-4B-5A-6A) has an even less proximal starting point than seen with the first sequence. The core region is comprised of projections from the digit apices while the posterior bounding heavy tactile locus (6A) occupies the same position that the light tactile core of the first sequence did. Abbreviation: RF, receptive field.


71321
8C 8B 8A 1A 2A 3A 3B 4A 4B 5A 6A
Anterior
Posterior
upper row: heavier tactile "coat" RF's
lower row: lighter tactile "core" RF's

Finally, in Figure 13, are seen the receptive fields of the recording loci. No data were found posterior to 6A or anterior to 8C, hence this row traverses the extent of the hand representation at this rather lateral level. In doing so the punctures demonstrate a common finding in this study. Units forming the very edges of boundaries of the map of SII were almost always responsive to the heavier tactile modalities. Figure 13 is arranged into two rows of receptive field figurines. Uppermost are those fields which were best activated by the application of pressure. The progression of receptive fields in this row is volar hand-digit apices-external hand-ulnar forearm. This is followed by a break in the progression which then returns (puncture 3A) to the proximal volar hand, begins to creep distally to encompass the fifth digit and thence around to the digit dorsums. The lower row of receptive fields, corresponding to the lighter or touch and hair tactile modalities progresses from the medial volar hand to the external volar hand and terminates on the dorsal digits. If the light tactile fields <u>and</u> their heavier tactile coats are considered as <u>units</u>, what is seen is simply a light tactile focus, surrounded by its coat, which progresses from the medial digit pads to the lateral hand and moves onto the dorsal digits. Also, the progression of receptive fields <u>within</u> a core-coat unit is orderly. It is only when one attempts to order the progression of the upper row of receptive fields alone or both rows together without taking into account the tactile modalities that there appears to be an organizational breakdown.

Several attempts were made to "cross" a core-coat complex with perpendicular puncture rows. The results from a portion of one such crossing are shown in Figure 14. A problem arises when two dimensions are considered because it is only possible to determine the orientation

Figure 14. A crossed core-coat in two dimenstions (experiment 71322). A coronal puncture row was crossed in the approximate center of a "core" with a parasagittal puncture row. Shown here is one large (approximately 1.4 mm diameter) core-coat complex together with one smaller, uncrossed complex. The light tactile core (solid black) is derived and internal aspect of the hand. The heavy tactile coat region (hashed) completely surrounds the core on all sides, dorsally, proximally and laterally. Abbreviations: A, anterior; L, lateral; P, posterior; SS, suprasylvian sulcus.

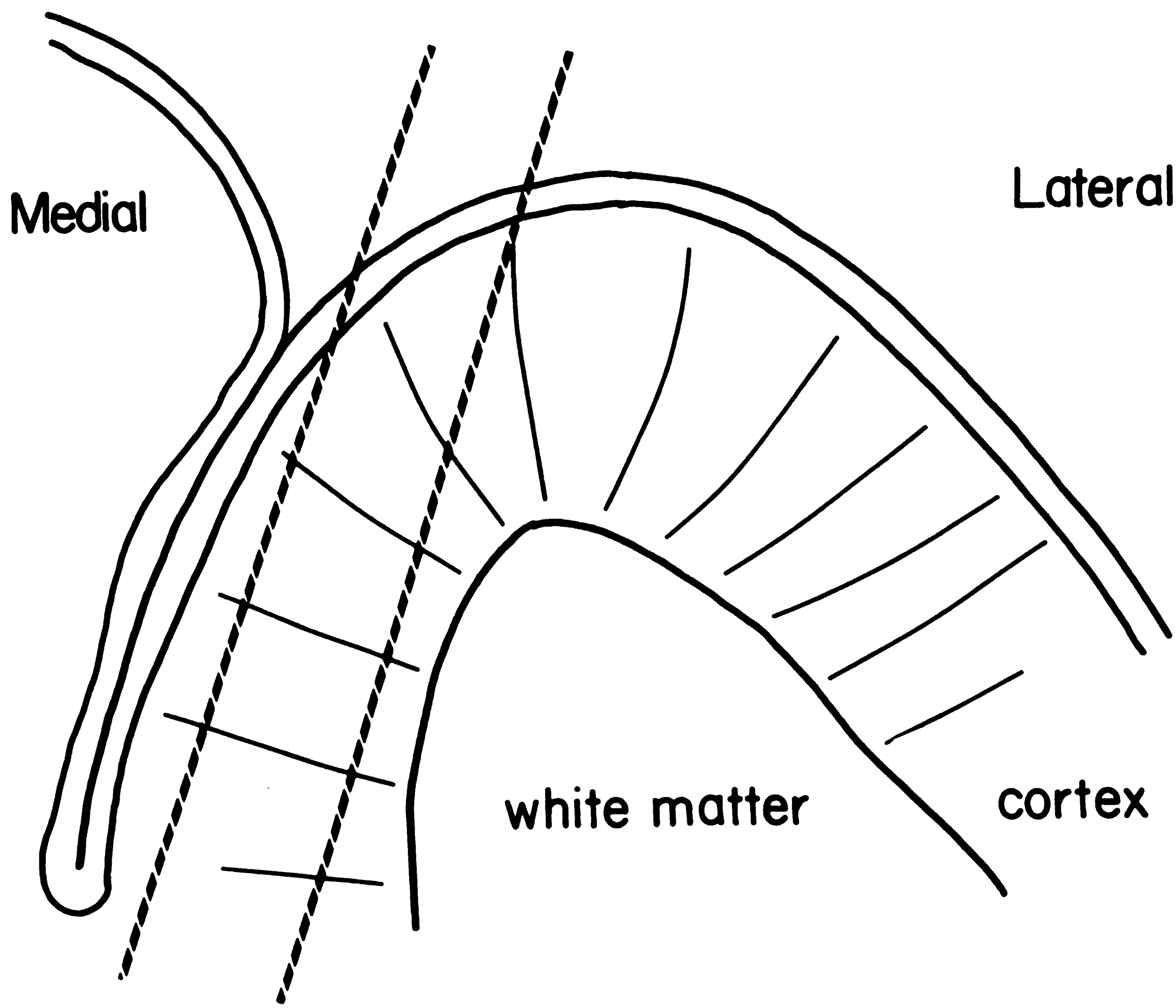

P
L
A
ss

of punctures to cortical columns in one plane at a time. The example shown in Figure 14 was chosen because the parasagittal puncture row lay just lateral to the point where AEG suddenly dropped into the anterior suprasylvian sulcus. This allowed an accurate prediction of the orientation of the punctures and cortical columns (Figure 15). The curvature of the cortex assured that the recording loci nearest the cortical surface would always be lateral to those below in the same puncture. Thus, it is with a high degree of confidence that the orientation of receptive fields in the coronal puncture row of Figure 14 is presented.

The larger of the two core-coat complexes shown in Figure 14 is crossed, though probably not exactly through its center. Parasagittally, the coat ring has a diameter of approximately 1.2 mm, coronally, 0.8 mm, making this one of the larger such complexes. The light tactile core (receptive fields shown in solid black) is concerned with the claws and and volar digits and palm. The heavy tactile coat surrounds the core on all sides, dorsally, proximally, medially and laterally. A second, uncrossed complex is seen medial to the first, lying within the suprasylvian sulcus.

Using these closer (0.2 mm) puncture spacings, a total of twelve core-coat complexes were determined in three animals, one of which was anesthetized with nitrous oxide. Four of the complexes were successfully crossed as shown in Figure 14. The functional organization of SII suggested by the 0.5 mm spaced puncture rows is even more pronounced when closer spacings are carefully employed. A sub-organization relating tactile modalities with the receptive field organization has been demonstrated. Treated as a homogeneous projection of receptive fields, the map of SII

Figure 15. How absolute sequences of receptive fields, both within and among punctures, are established using the columnar organization of neocortex. Medial to the convexity of the gyrus shown, recording loci near the cortical surface will always lie lateral to those located deeper within the puncture. In an extreme case it would be quite possible for a recording locus in one puncture to lie medial to a locus in a neighboring puncture even though that puncture lay <u>lateral</u> to the first.


Medial
Lateral
white matter
cortex

fails to show orderly somatotopy except in the most general sense. If the map is viewed as a mosaic of functional subsets as outlined in this section, a degree of order can be imposed upon the mechanoreceptive projections, especially in the hand area which otherwise defies analysis.

DISCUSSION AND SUMMARY

Somatotopy and functional considerations in somesthetic cortex. Though considerable attention has been given to the somatotopic organization of the somesthetic cortices, these studies have but rarely considered such organization using single unit criteria. Many of the older studies mapped cortex using surface evoked potentials. The more recent studies have used microelectrodes but still generally have recorded from several units at once (Rubel, 1971). The unit cluster (Figure 2) activity thus obtained can be used to determine the orientation of receptive fields on the cortical surface but the inability to separate out single unit activity precludes any attempt at determining, except grossly, what the functional properties of the cortical units subserving given receptive fields might be. The recent papers by Carol Welker (1971), Werner and Whitsel (1968) and Whitsel, et al. (1969) dealing with the rat and the monkey, respectively, appear to comprise the entire single unit mapping literature. This is not to say that single unit studies in somesthetic cortex are lacking. Such certainly is not the case. The preponderance of these studies have dealt with the functional and receptive field properties of single cortical units without considering their neighborly relationships. For instance, a number of studies have catalogued the tactile response properties of cortical units in a manner similar to that employed in the present study. The pericruciate motorsensory area of the cat (Welt, Aschoff, Kameda & Brooks, 1967), the coronal gyrus or SI face area of the cat (Morse, Adkins & Towe, 1965), the hindlimb SI area of the cat (Levitt & Levitt, 1968), the anterior ectosylvian gyrus or SII of the cat (Carreras & Andersson, 1963; Morse & Vargo, 1970), as well as the general SI cortex of cat (Mountcastle, 1957; Mountcastle, Davies & Berman, 1957) show modality specific responses that have been remarked upon by the investigators cited. To the present author's knowledge no one has yet reported a quantification of the degree of tactile stimulation and the resultant cortical response though, for example, this had been reported earlier in a study of response properties of Procyonid rhinaria (Barker & Welker, 1969) at first order levels using the von Frey technique (Woodworth & Schlosberg, 1960). Direct electrical stimulation of peripheral fields (Towe, Patton & Kennedy, 1964), or of dissected out peripheral nerves (Andersson, Landgren & Wolsk, 1966), while permitting precise control of the stimulus can afford little insight into the question of exactly what that stimulus might really be as far the the responding cortical unit is concerned. For the purposes of the present discussion, studies which rely solely upon electrical stimulation will not be considered.

Summarizing briefly, research on somesthetic cortex has been concerned with one of two things. Either the somatotopic organization of receptive fields has been examined at the expense of considering the other properties of individual cortical neurons, especially as concerns stimulus modalities - or the converse situation has obtained. Even those studies which carefully mapped using single unit criteria did not consider, except in passing, the tactile stimuli which are of interest to the receptive fields and their allied cortical termini. The contribution of the present study is that it has considered both of these features of cortical organization, albeit not with a great deal of quantification, by examining receptive field organization and tactile responses together. In the process of accomplishing this the conclusions of some previous investigators have been upset and others substantiated. These will be dealt with in turn.

Functional properties of SII neurons: comparisons with other studies. The AEG units sampled in this study correspond to those found in zones B and C of Carreras and Andersson (1963), that is to say, the portion of SII devoted to their "modality-place specific" units which comprises the somatotopically organized part of AEG. This area has been shown to receive most of its innervation from Vb (Jones & Powell, 1969). Single unit studies on SII neurons are few (Carreras & Andersson, 1963; Morse & Vargo, 1970; Whitsel, et al., 1969). Two of these studies plus the present effort were done on cats, Whitsel, et al. used monkeys. Three different anesthetics have been used in the cat studies (Table 6), sodium pentobarbital, alpha-chloralose and nitrous oxide. The monkey study utilized unanesthetized preparations. The present author finds little difference in SII unit behavior between animals anesthetized with pentobarbital and nitrous oxide. Results obtained under chloralose anesthesia (Morse & Vargo, 1970) appear to be similar to those reported by both the present author and by Carreras and Andersson (1963). All studies report that the majority of SII units respond to surface stimulation involving the hairy and glabrous surfaces of the body. None of the studies report finding units responsive to joint rotation. Deeper lying responsive areas, located in fascia and periostea were reported by Carreras and Andersson who verified their presence by dissecting the receptors out, thus proving that they did not lie on the surface. Such units comprised only 6.4% of their modality-place specific neuronal population. Approximately 6.7% of the SII units encountered in the present effort were of the moderate pressure variety (Figure 4 & Table 2). These units might form a population similar to that described as "deep" by Carreras and Andersson. These authors, however, state that their "deep" population all display slowly adapting

Table 6

A Comparison from Four SII Single Unit Studies

Investigator	Subject	Anesthetic	Forepaw Latency Range (msec.)	% of Total Number of Units with:		
				Bilateral Receptive Fields	Light Tactile Modalities	Heavier Tactile Modalities
Haight (1971)	Cat	Nitrous Oxide Pentobarbital	8-25 $\bar{x} = 11.9$	2.8	44	52
Carreras & Andersson (1963)	Cat	Pentobarbital	8-30	5.8	N/A	N/A
Morse & Vargo (1970)	Cat	Chloralose	6-30 $M_o = 13.0$	11.8	58	42
Whitsel, et al. (1969)	Monkey	None	N/A	90.0	87	13

N/A, not available from published data.

properties to stimulation, a point not in agreement with the properties seen for moderate pressure units in the present study.

Also described by Carreras and Andersson is a population of SII units having one or more of the following properties: 1) changing stimulus thresholds, 2) indefinite receptive field boundaries, 3) ipsi or bilateral receptive fields and 4) large, stockinglike receptive fields. These units made up 12% of their mechanoreceptive unit population. The present study found that 11.2% of the mechanoreceptive unit population is either stockinglike, ipsilateral, bilateral, or any combination of these. Present findings do <u>not</u> support the idea of non-modality-place specific neurons in the anterior portions of AEG. It is felt that such behavior on the part of an SII unit indicates cortical damage, either to the unit or to its synaptically associated surround (see pages 27-28). Evidence for this contention is recruited by the finding that successive penetrations within 0.2 to 0.5 mm of a puncture that showed migrating field boundaries and variable thresholds were almost invariably equally ill-behaved, or even totally silent. On two occasions a long parasagittal row of closely spaced punctures was made (subjects 71321 & 71322). Though units isolated in this row of punctures were normal in every respect, all punctures in closely spaced rows lateral to the original row displayed erratic unit activity. If care was taken not to drive the recording electrode too deeply into the cortex, thus avoiding marginal and other cortical layer damage, the unit activity obtained was of invariant receptive field size and threshold. This discussion is not to deny the existence of non-modality-place specific neurons in AEG, however. Both in the cat and the monkey the posterior portions of SII were reported to be populated with such non-specific neurons. I maintain that such responses do not form an appreciable portion of the somatotopically organized anterior area of AEG and that when such units do appear, one must suspect the possibility of tissue damage.

It is difficult to discuss the question of adaptation and habituation in a functionally meaningful manner when anesthetized preparations are used. The present study reports that most mechanoreceptive units (98%) are rapidly adapting. This is in agreement with the findings of Whitsel, *et al*.(1969) in monkey SII (90%), of Carreras and Andersson (1963) also in cat SII (89%) and of Morse and Vargo (1970) who find that close to 100% of the cat SII units are fast adapting. Habituation is taken by the present author to refer to the rate at which nearly identical stimuli can be delivered to the receptive field of a neuron and produce the same response with each stimulation. This is not, then, the absolute following rate which is usually much higher. Present findings indicate that there is alteration in response properties of cat SII neurons if repetitive stimulation rates exceed 10-12 per second. Carreras and Andersson, on the other hand, report 15-20 per second while in the unanesthetized monkey, Whitsel, *et al*. claim 10 per second or less. In the anesthetized cat SI cortex it was reported that while the absolute following rates often exceeded 30 per second, habituation effects were noted at stimulus repetition frequencies as low as 10 per second (Mountcastle, Davies & Berman, 1957). The two cortical areas, SI and SII, would seem to be similar in this regard. Anesthesia appears to have little effect also. In contrast, Vb neurons, in both anesthetized and unanesthetized monkeys were examined and found to be profoundly affected in terms of absolute following rate depending upon the state of anesthesia. Following rates in excess of 100 stimuli per second were observed in the unanesthetized case, slowing to the order of 10 per second under barbiturate anesthesia (Poggio & Mountcastle, 1963). The difference in habituation properties between the two states is not as great, though it is not possible to give figures because these authors did not carry out their unanesthetized habituation recovery curve to the 100% level as they did for the unanesthetized case. Extrapolating from the appearance of their plotted data (their Figure 5) it seems that the two 100% reliable repetition points of the two curves might coincide, indicating that, in Vb also, anesthesia has little effect upon habituation.

This study also concurs with the observations of Whitsel, et al. (1969) that there are SII units more interested in motion across the receptive field than in simple punctate stimuli. In the SII of the unanesthetized monkey such motion detectors predominated in both hairy and glabrous areas while in the barbiturated cat only the fields associated with glabrous skin (approximately 25% of all units examined) so responded. Another interesting similarity concerns the units which habituated rapidly when repeatedly stimulated in the same place on the receptive field surface. In both the anesthetized cat and the awake monkey the observation was made that such habituation could be lessened or even avoided if the same spot were not struck each time, but rather the stimulus were moved from place to place on the receptive field.

A concluding comment with respect to anesthetic effects upon mechanoreceptive SII units is that these effects might not be as profound as previously thought. The present study considered the behavior of SII neurons under two states of anesthesia, one relatively "deep", the other extremely "light". Very little difference in the activity of the unit populations was observed. It must be remarked, however, that this study did not directly compare the behavior of single neurons under different anesthetic states, only populations of neurons were so compared. A similar criticism can be leveled at most studies which purport to compare anesthetic effects.

Response latencies as reported in this study (Tables 4 & 6) are in agreement with those reported from similar body regions by several other workers (Carreras & Andersson, 1963; Morse & Vargo, 1970). Contralateral response latencies appear to be unaffected by the anesthetic employed and, further, they are not appreciably different from those reported in SI (Mountcastle, Davies & Berman, 1957; Rubel, 1971). This condition has been reported from the earliest "evoked potential" days (Woolsey & Wang, 1945) amd forms strong evidence that similar pathways innervate the two cortical areas.

The distribution of response latencies from various body regions (Figure 6) is asymmetric with most units firing with short latency to stimulation while a consistent few form a long latency "tail". Thus, there seems to be a "fast" and a "slow" population from each body area though the demarcation between the two populations is not distinct. The suggestion is there, however, as each body region's distribution shows a tendency toward bimodality. Attempts to correlate the unit latencies with other functional properties such as tactile interests, habituation properties, receptive field size, and so on, failed. Bilateral units were observed to respond with greater ipsilateral latencies than contralateral. Further, the contralateral latencies of the bilateral population were consistently greater than the latencies of units whose receptive fields were purely contralateral (Table 4). The latency findings indicate that there may be as many as three classes of SII mechanoreceptive unit, two of which form a "fast" and "slow" latency division of that population having strictly contralateral receptive fields and the other, even "slower" group pertaining to the bilaterally innervated cortical units.

Cortical ablation effects and the question of bilateral receptive fields in cat SII. A number of subjects received chronic cortical ablations as outlined in the second and third chapters of this study. Electrophysiological recordings were made from these animals in the hope that some light could be shed on the question of bilaterality and cat SII neurons. Such recordings showed that removal of all or part of the opposite somesthetic cortex had no effect upon the functional properties of SII neurons. Remembering that in the course of this entire study only nine bilateral and one purely ipsilateral receptive field was found, it becomes obvious that little can be said about bilaterality of representation of receptive fields on the basis of neocortical integrity. However, of these nine units, four were derived from animals missing portions of their opposite cortices. Three such units came from animals whose entire postcranial SI had been removed while the other bilateral unit came from an animal whose cortical mantle except for postcranial SI had been ablated. Two additional animals were recorded from whose entire opposite somesthetic cortex had been removed. No bilateral responses were found in these although the single ipsilateral response did come from one of them (Table 7). About the only point that can be made from these findings is that bilateral and ipsilateral projections to the anterior portions of AEG are rare. It is interesting to note that in animals whose contralateral somesthetic cortices (SI and SII) had been removed, no bilateral activity was seen, just the one ipsilateral response. The sample size is such that any comment on possible commissural rather than subcortical routes for explaining bilaterality would represent wishful thinking rather than fact. It is worth repeating here that bilateral slow wave activity was common in cat SII under all conditions, cortex intact or not.

Table 7

Distribution of Contralateral, Ipsilateral and Bilateral SII Receptive Fields in Normal and in Neocortically Ablated Cats

Type of Ablation & Number of Subjects.	Bilateral RF's	Ipsilateral RF's	Contralateral RF's
Normal Animals (8)	3	0	188
Contralateral SI removed (2)	3	0	53
Contralateral SI & SII removed (2)	0	1	35
Contralateral SI island (1)	1	0	34
Ipsilateral SI removed (2)	2	0	37
Totals	9	1	347

Other studies have also described ipsi and bilateral receptive fields in cat SII (Table 6). These all show, using three different anesthesias, that such receptive fields are not common in cats. This is in marked contrast to the findings reported in the unanesthetized monkey SII where some 90% of all units found displayed bilateral receptive fields. It begins to appear that this may be a species difference rather than an anesthetic effect as suggested by Whitsel, et al.(1969) and hinted at by Carreras and Andersson (1963).

Two animals were used in the present study whose ipsilateral SI cortices had been removed. This ablation apparently affects the habituation properties of the homolateral SII neurons. In most other subjects a persistent fraction of SII units (15%) showed a tendency toward rapid or moderate habituation (see page 28). This was not the case with the homolaterally ablated SI animals (2 subjects, 39 SII units).

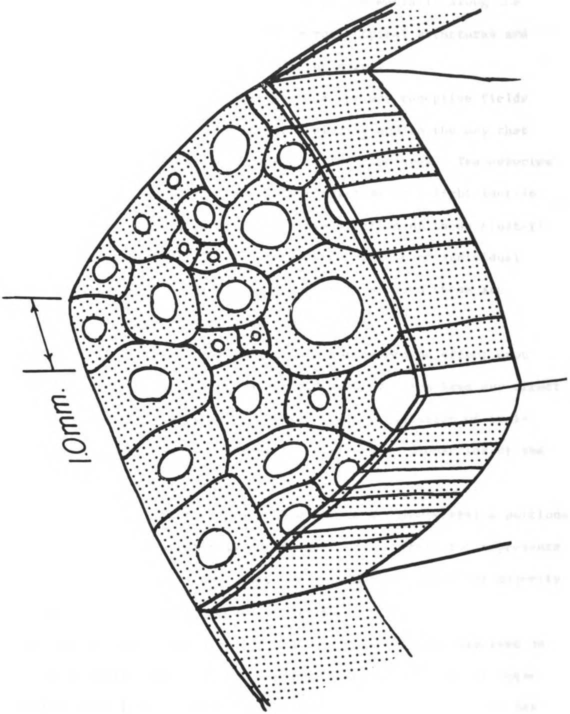
All were slowly habituating. Whether this finding is due to the known corticocortical projections joining SI to SII (Jones & Powell, 1968a) or to degeneration effects in Vb due to the removal of substantial portions of its essential projection field is not known. This question is left to a future study. One more point of possible interest here is the question of afterdischarges. Not uncommonly (approximately 10% of the units sampled) SII units would discharge with an appropriate latency to either electrical or mechanical stimulation, fall silent for a period ranging from 15 to several hundred milleseconds, and then fire an additional burst. The latencies of the afterdischarges were quite variable under conditions of constant stimulus even though the initial discharge was uniform in latency upon delivery of repetitive stimuli. A similar finding has been reported in cat SI (Mountcastle, Davies & Berman, 1957). Several interpretations are possible here. The first, and perhaps simplest is that a given cortical unit may receive projections by more than one pathway, an idea that has been reviewed and elaborated upon at some length by Andersson (1962). Such a system of multiple pathways, having the same origin and terminus, could well be responsible for a delayed afterdischarge, assuming that the secondary pathway involved more synapses and/or slower conduction velocities. A second explanatory model relies upon the centrifugal projections from the sensory cortex back to the subcortical relays in the thalamus (Rinvik, 1968), medulla and spinal cord (Kawana, 1969). The initial activation of a cortical unit would then be relayed back to subcortical levels, presumably having either an inhibitory or an excitatory effect. This latter could possibly account for the observed afterdischarge. Yet a third possibility involves interneurons exerting a local excitatory rather than inhibitory effect as suggested by Wall (1967) in the spinal dorsal horn or by Eccles (1966) in Vb. Neither of these two latter schema are particularly convincing in accounting for the rather long latencies exhibited by the afterdischarges (up to 500 msec and more) seen in this study. Further comment will have to await further experimentation.

Somatotopic organization of SII. Two reports prior to the present one have purported to show the somatotopic organization of cat SII (Woolsey, 1958; Berman, 1961). Both of these authors claim that axial structures are represented laterally in AEG with the distal body parts pointing medially into the suprasylvian sulcus. The present author feels that there can be no question about the orientation of the body map onto AEG (Haight, 1971) and that said orientation is opposite to that claimed earlier. Distal structures lie laterally with axial body parts represented within the suprasylvian sulcus (page 38). It may be possible to explain the earlier findings, however, on the basis of a peculiarity in the lower forearm representation already noted in the present study (Figure 8). First, a comment on technique is in order. Early investigations of somatotopic organization in cortex relied upon surface potentials evoked by stimulation of the body surfaces. This method, while effective, does not allow a fine degree of resolution in relating neighboring receptive fields. Secondly, there is a prominent extension of the forearm region, as has been mentioned, to the very lateral portions of the map in SII. In fact, the hand representation is surrounded on three sides by the arm representation. Thus, as Berman (1961) shows, there is an arm projection field lying laterally to the hand and finger fields, a projection field which wraps around the hand and finger map along the posterior edge of SII hand area and eventually connects with the remainder of the arm and body which are represented medial to and not lateral to the hand map. This is applicable to the ulnar forearm area. Similarly, the radial forearm projections envelop the anterolateral aspect of the hand map, though this projection is not nearly as prominent as the first mentioned. Thirdly, a considerable variation in gyral patterns exists in cats. Often this variation is responsible for "burying" all but the hand and lower arm representations of SII deep within the suprasylvian sulcus, thus removing axial structures from the range of surface recording electrodes. Such axial structures form a small part of the total map area and could easily be overlooked if one were using only surface potentials for mapping. This third point was probably responsible for Adrian's (1940, 1941) failure to observe SII potentials for more proximal body areas. There is little doubt that accurate portrayal of the somatotopic organization in cortex requires the microelectrode recording technique. This allows the examination of neighboring cortical columns (Mountcastle, 1957; Werner & Whitsel, 1968; Whitsel, et al., 1969) and, thus, the detailed organization of receptive fields upon the cortical sheet (see also Werner, 1970).

A recent study in cat SI (Rubel, 1969 & 1971) which used unit cluster criteria for delineating receptive field organization makes the statement that, ". . . if digit five is encountered as the electrode enters the cortex and projections from digit three are found deeper in that penetration, a receptive field including projections from digit four will be found between these points." (Rubel, 1969, page 31) Either matters are not that simple in SII or Rubel's multiunit recording technique did not allow him to detect inconsistencies in the receptive field organization of cat SI. SII in the cat, at any rate, fails to follow the rules. Inconsistencies abound, especially in the hand area and these formed, for some time, a formidable interpretative obstacle. More in desperation than inspiration it was decided to examine tactile modalities and receptive field organization together. The results were unexpected and striking. There is an orderly level of organization of receptive fields in hand SII - _if_ tactile modalities are taken into consideration. The heavy-light tactile modality alternation (schematically portrayed in Figure 16) when taken as integral units rather than as a series of adjoining receptive fields show an orderly and convincing portrayal of the body surface onto the cortex. This portrayal takes the form of the "trajectories" described by Werner and Whitsel in monkey SI (1968).

Having resolved the fine structural irregularities in the SII map, the question remains as to how this organization relates functionally to the animal. What is not known at present is whether a similar or different type of organization obtains in SI cortex or in Vb thalamus. Assuming that the fine grain somatotopy is different in the two cortical areas, this could go a long way toward explaining the functional operation of these two areas. As stated in the introductory chapter, there is very little basis at present for such speculations. The behaviors of neurons in Vb, SI and SII appear to be more similar than not. The differences that do exist, with the exception of the repeatedly noted absence of joint responses in SII, are not of a variety that encourage any meaningful functional speculation. The present study has suggested that the impasse might be broken simply by employing two long used investigational techniques in conjunction - that of somatotopic mapping and that of examining unit properties. Any further attempts at attributing functional import to the present findings will have to await the results from similar investigations upon SI and Vb.

Figure 16. Hypothesized mosaic of core-coat modalities and receptive fields in cat SII. The cores (clear areas) and the coats (dotted areas) extend through the entire thickness of the neocortex. The complexes are of varying size, ranging from the order of 1.5 mm diameter maximum to 0.4 mm minimum.


1.0mm.

Summary. The somatotopic organization of mechanoreceptive fields in cat SII is reversed from the way in which postcranial regions have previously been portrayed. Axial structures lie medially along the upper bank of the anterior ectosylvian gyrus. Apical structures are represented laterally on the surface of the gyrus.

A definite relationship exists between the way receptive fields are mapped onto the second somatic cortical area and in the way that various tactile modalities are arranged in the same area. Trajectories of receptive field clusters are present consisting of a light tactile core and a heavier tactile coat. The representation of these clusters in SII is somatotopically orderly; the representation of individual unit receptive fields in SII is not necessarily so when these are considered apart from the core-coat organization.

Ablation of contralateral somesthetic cortex had no effect upon functional properties of SII units nor did such ablation have any effect upon the occurence of bilateral receptive fields. Ablation of ipsilateral SI cortex was seen to affect the habituation properties of the homolateral SII neurons.

Bilateral receptive fields are rare in the mechanoreceptive portions of SII. This lack is apparently not an anesthetic effect but represents a valid species difference when compared with monkeys where the majority of SII units have bilateral receptive fields.

As many as three populations of SII units can be distinguished on the basis of their latencies to electrical stimulation. Two of these populations have purely contralateral receptive fields, the other has bilateral receptive fields.

The tactile interests of cat SII neurons appear to be fairly evenly divided between light tactile (touch to glabrous skin surfaces and hair responses) and heavier tactile (pressure, involving slight skin indentation) modalities. Mixed, light-heavy modalities are present but rare.

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