ABSTRACT

A COMPARISON OF SOMATOTOPIC ORGANIZATION IN SENSORY NEOCORTEX OF NEWBORN KITTENS AND ADULT CATS

by Edwin J Rubel

To determine the state of functional development in the newborn kitten's somatic sensory system, the organization of mechanoreceptive projections to the sensorimotor cortex was compared to that of the adult cat. Microelectrode mapping procedures were used.

Projections from all contralateral body surfaces to the primary somatomotor cortex (SmI) are present at birth and respond to mechanical stimulation of the receptors. The somatotopic organization of these projections in the newborn kitten is similar to that in the adult cortex with respect to the cortical region receiving projections from each part of the body and to the detailed arrangement of the projections within each of these cortical subdivisions.

The relative sizes of peripheral receptive fields, and the intinsity of stimulation effective for eliciting a response were similar for projections in SmI cortex of both kittens and adults. At both ages receptive field sizes decreased as their locations approached the distal portion of the limbs or rostral part of the face. In adults and newborns, over 75% of the neuronal responses were elicited

by gentle bending of the hairs or light touch to the glabrous skin surfaces.

Other similarities between adult and newborn sensorimotor cortexes included: a) receptive fields of projections to SmI cortex were of fixed, local field type: b) projections to SII cortex responded to mechanical stimulation of the receptors; c) ipsilateral as well as contralateral body surfaces were represented in SII cortex; d) the columnar arrangement of neurons and their receptive fields were apparent in the SmI cortex; e) the coronal sulcus formed a division between the representations of the forepaw and face.

Differences between newborn kittens and adult cats included: a) shorter latency from electrical stimulation of the skin to a SmI cortical response in adults; b) projections to SmI cortex having 'disjunctive' receptive fields were not found in newborn kittens but existed in the adults; c) the diversity of receptive field types found in neurons of the adult postcruciate MsI cortex was not found in newborn kittens; d) newborn subjects displayed less variability in the somatotopic organization of projections and less overlap in the receptive fields of projections to SmI cortex.

It is suggested that the SmI cortex develops as a point-to-point reflection of the distribution of mechanosensitive receptors in the body and that the complexities in this organization seen in the adult cortex occur during postnatal development.

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A THESIS

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

DOCTOR OF PHILOSOPHY

Department of Psychology

1969

G12043
1-30-70

ACKNOWLEDGEMENTS

This research was supported by USPHS Biomedical Support Grant FR07049, NIH Predoctoral Fellowship 31195 and NIH Grant NB05982.

I wish to express my appreciation to: Dean C. L. Winder, Dr. J. H. Wakeley and Dr. L. I. O'Kelly who served as chairmen of the Psychology Dept. and provided financial support throuhgout the course of this study; Dr. Raimundo J. Cabral, John R. Haight, William R. Ives, Phillip S. Ulinski, W. Lee Weller and Roger A. Woudenberg who assisted in the collection of these data; Andrew B. Harton and Emeline G. Haight for aid in the preparation of histological materials; and Paul Herron for the Photographic work.

Special thanks are due to Larry W. Thornton who rendered invaluable assistance in collecting the data from newborn subjects; Dr. Robert L. Raisler who served on the thesis committee; and Dr. Martin Balabin who encouraged and directed my interests in neural-behavioral ontogeny.

Dr. Glenn I. Hatton and Dr. John I. Johnson, Jr. served as co-chairmen of the thesis committee, guided my graduate education and provided help and encouragement throughout its term. To them I am most grateful.

To my wife, Wendy Jean, whose life has been dictated by the birth of organisms, I dedicate this thesis.

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Introduction

The Kitten

There has been a resurgence of interest in the functional ontogeny of the nervous system. Much of this work has been collected in five recent symposia (Bernhard and Schadé, 1967; Hassler and Stephen, 1967; Jilek and Trojan, 1968; Minkowski, 1967; Purpura and Schadé, 1964) and reviewed by Skoglung (1969). Differences between neurons in the neocortex of newborn kittens and adult cats have been demonstrated anatomically (Purpura, 1961; Voeller, Pappas, and Purpura, 1963; Scheibel and Scheibel, 1964), histochemically (Himwich, Pscheidt and Scheigeadt, 1967) and physiologically by Purpura, Shofer and Scarff (1965).

Since the work of Scherrer and Oeconomos (1954) it has been known that when an electric shock is applied to the forepaw of a newborn kitten, an evoked potential can be recorded from the sensorimotor cortex. Similarly, when the optic or auditory nerve of a newborn kitten is electrically stimulated, an evoked potential can be recorded from its corresponding cortical projection area (Marty, 1967). Although these studies do show that afferent connections to the neocortex of the newborn kitten are present at birth, electric shock is a rather atypical and nonphysiological form of stimulation - atypical because it is not commonly found in the environment outside the laboratory and nonphysiological because the receptors are bypassed. (Physiological forms of stimulation, are those for which specialized receptors have evolved to transduce energy changes into neural signals, such as light, sound and pressure.) Studies employing physiological stimulation have shown qualitative and quantitative changes in the gross electrical activity of the cortex as a function of age and cortical development (Ellingson and Wilcott, 1960; Grossman, 1955; Rose, Adrian and Santibanez, 1957; Rose and Lindsley, 1968). These studies indicate the age at which an afferent system is electrophysiologically functional from the receptor to the cortical projection area. However, in the above studies, global forms of stimulation such as bright flashes of light or loud clicks have been used. Thus, they provide no information regarding the ability of an immature nervous system to code the differential qualities of peripheral stimulation within an afferent system.

The Cat

In the past two decades a vast amount of information has been gathered elucidating the neural mechanisms of sensory information coding (Bishop, 1967; Rose and Mountcastle, 1959). Single neurons in the cortical projection areas of each sensory system are specific in the quality and quantity of peripheral stimulation required for activation, and the topographical organization of these neurons is systematic and reliable across animals (Hind, 1961; Hubel and Wiesel, 1965; Mountcastle, Davies and Berman, 1957; Woolsey, 1958).

A fundamental form of sensory coding is the phenomenon of "receptotopic" organization found throughout mammalian sensory systems (Thompson, 1967). This type of coding is reflected in the somatotopic organization of projections to the cerebral cortex of the cat first described by Adrian (1940) and Marshall, Woolsey and Bard (1941). The primary somesthetic area of the cat's cerebral cortex was renamed sensory-motor area I (SmI) by Woolsey (1958) because of its anatomical and functional overlap with the motor-sensory area (MsI). The cytoarchitectural studies of Hassler and Muhs-Clement (1964) and electrophysiological observations by Towe, Whitehorn and Nyquist (1968) have confirmed the hypothesis that SmI and MsI cortices overlap in the region of the postcruciate dimple.

A Difference

Since the historic studies of primate motor cortex by Margaret Kennard (1936, 1938, 1942), it has been repeatedly demonstrated that damage to the neocortex of neonatal animals results in less severe functional deficites than similar lesions to an adult organism. Sharlock, Tucker and Strominger (1963) ablated the auditory cortex of infant and adult cats. Whereas the adult-lesioned animals did not learn a tonal pattern or a tonal duration discrimination, the infant operates were unimpaired. Similarly, Tucker, Kling and Sharlock (1968) found that cats could make photic frequency or intensity discriminations after neonatal ablations of cortical visual areas I, II and III while severe deficiencies were found in adult-operates. Of particular importance to the present investigation is the study by Benjamin and Thompson (1959). These investigators ablated the cortical somatic sensory areas of six day old kittens and adult cats. Six months hence, the adult animals did not learn simple roughness discriminations (e.g. sandpaper vs. cardboard), while the infant-lesioned animals performed as well as normals on all but the most difficult tasks.

Conversely, a few experiments have shown that both the structure and function of cells in the cerebral cortex can be modified by neonatal sensory deprivation whereas deprivation later in life is not as effective (Ganz, Fitch and Satterberg, 1968; Gyllensten, Malmfors and Norrlin, 1965, 1966; Hubel, 1967).

The basis for these forms of 'plasticity' in the nervous system of young animals is not understood, but may lie in the actual redistribution of thalamocortical synaptic connections or in behavioral alterations of 'cue selection'. In order to understand these differences between adult and neonatal organisms, it is necessary to know the extent to which the immature neocortex is coding sensory information.

The Problem

Somatotopic organization appears to be one neural mechanism for coding the locus of peripheral stimulation. To investigate this form of neural coding in an immature nervous system three specific questions were posed.

1. Do projections from the entire body surface to the

primary somatic-sensory cortex (SmI) of the newborn cat respond to physiological stimulation of the receptors?

2. Are these projections somatotopically organized?
3. Is the pattern of organization like that of the adult cat?

To answer these questions, areas of the SmI cortex of newborn kittens (≤ 24 hours post-partum) were electrophysiologically mapped using microelectrodes and these data were compared with detailed maps of adult SmI cortex prepared by similar methods.

In addition to answering the questions posed above, this study provides qualitative information regarding receptive field types and adequate stimulus intensities effective for eliciting a neural response in the SmI, SII and MsI cortical fields of the newborn kitten.

Method

Subject Preparation

Mapping experiments were performed on 16 kittens ranging in age from 6 to 24 hours post-partum (newborns) and 14 adult cats. Both sexes were used. The kittens varied in weight from 86 to 115 grams which is well within the normal range of birth weights reported by Hall and Pierce (1934).

The surgical procedures used for the two groups were quite similar. Preanesthetic doses of promazine hydrochloride (Sparine) (newborns - .15 mg; adults - 6 mg/kg) and atropine sulfate (newborns - .005 mg; adults - 0.1 mg/kg) were administered. General anesthesia was induced by an intraparitoneal injection of pentobarbital sodium (Nembutal) (newborns - 18 mg/kg; adults - 28 mg/kg); the body hair was clipped; a tracheal canula was inserted; and the animal was either suspended by its vertebral arches or supported by bars under its axillary and inguinal regions. Additional doses of Nembutal ($\frac{1}{4}$ original dose) were given as needed to eliminate nociceptive reflexes during the surgical preparation and recording.

The head was secured to a specially designed head holder and the cranium over one side of the anterior neocortex was removed. In some cases the foramen magnum was enlarged for cisternal drainage. After reflecting the dura mater, photographs of the exposed cortex were prepared. In the adult subjects, the brain was kept warm and moist by constructing an acrylic dam around the skull opening and filling it with warm mineral oil (38° C.). In kittens, the brain was covered with a warm agar-saline solution which quickly gelled and served the same purposes, as well as reducing cortical pulsations.

During the surgical preparation and recording, body temperature was maintained at 36-38° C. and the animal was kept hydrated by intraparitoneal injections of 5% dextrose every 3 - 4 hours. More details regarding the surgical procedures are presented in Appendix A.

Two newborn kittens were studied without the influence of barbiturate anesthesia. These subjects were prepared while anesthetized with methoxyfluorane (Metofane). Following surgery, all wounds were infused with procaine, Metofane was discontinued, gallamine triethiodide (Flaxedil) was given to immobilize the kitten, and artificial ventilation was begun.

Recording Equipment

Electrophysiological responses were recorded through glass insulated tungsten microelectrodes (Hubel, 1957; Baldwin, Frenk and Lettvin, 1965). The tungsten electrodes recorded potentials with respect to a stainless steel wire inserted through an exposed muscle of the head or neck. In most cases voltages were passed through 80 Hz low and 10 kHz high filters, amplified, displayed visually on an oscilloscope screen, presented aurally through an audio-monitor and recorded on magnetic tape. A second tape channel was used for synchronized voice commentary. (See Appendix B for further details.)

Mapping Procedures

The mapping procedures closely resemble the "microelectrode method of electrophysiological mapping" described by Welker and Johnson (1965) and Johnson, Welker and Pubols (1968). The microelectrode is lowered to the pial surface under visual inspections. Contact with the pia could be heard over the audio-monitor. The location at which the electrode entered the cortex was marked on an enlarged photograph of the exposed tissue (approximately X10). The electrode was then slowly driven through the cortex with a mechanical microdrive. Every 100 - 200μ the electrode was stopped and the entire body of the animal was mechanically stimulated. When a 'driveable' cortical response was encountered, the 'peripheral receptive field' eliciting this response was carefully delineated. The peripheral receptive field was defined as that area of the body surface which, with minimal mechanical stimulation, reliably evoked a cortical response. A 1 - 2 mm wooden rod, a glass dissecting rod, small lengths of Intramedic tubing of various sizes, or a cat vibrissa were used as stimulating agents to delineate each peripheral receptive field.

The neural response was qualitatively categorized by the minimal effective stimulus as follows:

1. Cutaneous
    a. 'Hair response' - movement of the hairs on the animal's body without deformation of the skin evoked the

response.

b. 'Light skin response' - any slight deformation of the skin on a glaborous portion of the body evoked a response.

2. Deep Pressure

a. 'Normal skin response' - deformation of the skin on a hairy portion of the body or a supra-minimal deformation on a non-hairy portion was necessary to evoke a response.

b. 'Deep response' - stimulation of the underlying tissues such as muscles or joints was necessary to evoke a response.

When the receptive field was determined, it was drawn onto a photograph of the appropriate portion of the body. Written protocols were kept throughout the experiments describing the category of the response, the depth of the electrode where the response was encountered, and the locus of the peripheral receptive field. This information was also put on tape with a sample of the neural response. As the electrode was driven through the cortex any noticeable change in the location of the receptive field was regarded as a new responding locus and the process of receptive field delineation was repeated. When the electrode had been driven through the cortex, it was withdrawn and moved to a new location for another electrode penetration.

In order to map the cortex systematically, successive electrode punctures were made in rows with penetration 0.5 mm or 1.0 mm apart and the rows 1 - 2 mm apart. The anterior-posterior and medial-lateral positions of each penetration within this matrix was recorded on a grid. This procedure left relatively neat rows of electrode penetrations which could be identified histologically and related to the photographic, written and taped records. To facilitate identification of the electrode tracks and the recording sites, small electrolytic lesions were made in some penetrations by passing a current (approx. 40-50 μa for 5 sec.) through the tip of the recording electrode.

At the termination of a recording session, the animal was intracardially perfused with 0.9% saline followed by 10% formalin in 0.9% saline.

Localization of Recording Sites

Following perfusion, the brain was removed; blocked parallel to the rows of electrode punctures; and embedded in celloidin. Serial sections were cut at 25 μ. Alternate sections were stained for cell bodies and myelinated fibers using thionin stain and Weil or Sanides-Heidenhain hematoxylin method.

The course of the electrode tracks through the sections designated the medio-lateral and anterior-posterior location of the responsive area. The exact dorsal-ventral locations cound not be specified but could be estimated by the micromanipulator readings and the position of the electrolytic lesions. The ordinal arrangement of the successively encountered peripheral receptive fields was known with certainty within each electrode penetration.

Measurement of Response Latencies

The latency of cortical responses to peripheral stimulation was determined in one adult cat and several newborn kittens. The latency was measured from the shock artifact to the first unit activity or beginning of the evoked potential. The intensity of the shock was, in all cases, suprathreshold (usually X10) and the frequency of the shocks was varied between .1 cps and 10 cps. These data were also recorded on tape for subsequent varification. It is probable that suprathreshold electrical stimulation, as used here, directly stimulated the afferent nerve trunks or their termination, thereby bypassing the actual receptor sites (Ecknolm, 1967). (See Appendix C for more details.)

Results

1. Response Characteristics

Samples of the electrophysiological responses obtained from SmI cortex in adult and newborn cats are shown in Figures 1 and 2. This sample consists of the first response obtained during or after puncture #3 from each of 6 adults and 7 newborn cats. Thus, the sample is selective in that only first responsive loci in penetrations are shown, but unselected for receptive field parameters since puncture 3 was made in a different cortical location in each preparation, and unselected regarding amplitude. In the adult cats, the primary response used for identification of a cortical locus was a cluster of neural units which could be evoked by mechanical stimulation of the body surface. These unit-clusters probably consist of presynaptic and postsynaptic activity recorded from axon terminals, dendrites and cell bodies surrounding the electrode tip. In the newborn subjects it was not always possible to evoke a distinct unit-cluster in which spike discharges could be identified on the oscilloscope screen. Thus, "neural hash" responses, which were clearly audible over the loud speaker, were often used to define the locus of a cortical response. Whether the responses reflect a difference in the neural elements activated by mechanical stimulation or merely a difference in the size of these elements can not be determined from these data.

Newborn kittens also showed a characteristic lack of spontaneous activity of neurons in the somatomotor cortex. The bottom trace in Figure 2 is from the cortex of an unanesthetized newborn kitten. The relative absence of spontaneous activity is in marked contrast to the neural activity in the sensorimotor cortex of unanesthetized and lightly anesthetized adult cats (Mountcastle, Davies and Berman, 1957; Brooks et al., 1961). Huttenlocher (1967) noted a similar finding in the visual cortex of young cats.

2. Somatotopic Organization

The organization of mechanoreceptive projections to SmI cortex was similar in the adult cats and newborn kittens. The general organization is shown in Figure 3. Projections from the contralateral rear leg, trunk and tail terminate in the medial aspect of the posterior sigmoid gyrus. Projections from the foreleg are found further lateral in this gyrus and receptors in the face, head and neck project to the coronal gyrus. In this study it was found that all areas of the contralateral body surface are represented in the SmI cortex of kittens less than 1 day old and that these projections respond to light mechanical stimulation of the skin or hairs.

The somatotopic organization in each of the these cortical regions depicted in Figure 3 is described in the following sections. These data are representative of what was found in each of the 30 preparations (Table 1).

Table 1

Electrophysiological Mapping Experiments of SmI Cortex

Age	Preparations	Responsive Punctures	Delineated Peripheral Receptive Fields
Newborn	16	199	217
Adult	14	359	501
Total	30	558	718

Organization of Projections from Posterior Body Surface: Leg, Trunk and Tail

Table 2 shows the numbers of successful preparations, electrode penetrations and loci responding to delineated peripheral receptive fields on which the following conclusions are based. Figures 4 - 8 are drawn from this population.

Table 2

Mapping Experiments of Hind Limb, Trunk and Tail Representation in SmI

Age	Preparations	Responsive Punctures	Receptive Fields
Newborn	9	23	42
Adult	8	67	142

Projections from the contralateral leg, rump and tail are located in the medial portions of the posterior sigmoid gyrus. The surface maps shown in Figure 4 reflect the general organization along the medial edge of this gyrus. In these and all subsequent surface maps, only the first receptive field encountered within 1.5 mm of the adult cat's cortical surface or 1.0 mm of the newborn's cortical surface are shown.

Projections from the foot extend anterior up to the posterior bank of the cruciate sulcus while the leg and trunk are represented further posterior and lateral. Further detail regarding the somatotopic organization of these projections is shown in Figures 5 and 6 for adult cats and Figures 7 and 8 for newborn subjects. Distal portions of the contralateral leg are generally represented rostrally, while projections from more proximal surfaces are found successively further caudal in the cortex. Projections from the rump and tail are posterior and ventromedial to those of the leg and foot. Instead of reaching the dorsal surface of the cortex as described by Woolsey (1958), projections from the rump and tail are confined to the dorso-medial bank of the cruciate sulcus (Figures 5, 6 and 7). These projections appear to be organized with the most distal areas of the tail lying ventral to more proximal areas (Figures 5, 6, 8).

In the most rostral portion of this cortical area, stimulation of the digits on the contralateral foot evokes a cortical response. Woolsey (1958) indicates that the digits are represented with D1 most dorso-lateral and D2, D3 and D4 progressively ventro-medial, buried in the banks of the medial longitudinal fissure. Figure 5 (puncture 10) supports this notion of somatotopic organization. Other experiments indicate that the organization of these projections in the adult cat is quite variable in the details of somatotopic organization and does not show a point-to-point correspondence with the organization of the body surface. For example, in the adult map shown in Figure 4, projections from the digits were found posterior and medial to projections from the thigh and knee as well as near the cruciate sulcus. In the newborn kitten less variability is apparent.

Projections from the trunk are organized from medial to lateral on the posterior sigmoid gyrus, lying primarily between the postcruciate dimple and the ansate sulcus. As noted above, projections from the rump lie along the medial bank, while progressivily more rostral body surfaces are represented successively further lateral toward the level of the bifurcation of the ansate sulcus. This relationship is seen in Figure 4.

__Organization of Mechanoreceptive Projections from the Contralateral Foreleg and Forepaw__ Table 3 shows the numbers of successful preparations, electrode penetrations and loci responding to delineated peripheral receptive fields on which the following conclusions are based. Figures 9 - 13 are drawn from this population.

Table 3

Mapping Experiments of Forelimb Representation in SmI

Age	Preparations	Responsive Punctures	Receptive Fields
Newborn	11	72	102
Adult	13	134	280

In both the newborn and adult cat, projections from the contralateral foreleg and paw occupy the lateral aspect of the posterior sigmoid gyrus. The representation of these body surfaces is continuous with the rostral trunk representation at the level of the bifurcation of the ansate sulcus, and extends lateroventral toward the tip of this gyrus. Projections from the upper foreleg and shoulder are represented in the area of the bifurcation of the ansate sulcus while more distal surfaces project to progressively more lateral areas of the cortex. This relationship is illustrated in Figure 9.

Figures 10, 11, 12 and 13 illustrate the organization of the projections from the digits of the contralateral forepaw. While projections from the arm are found on the exposed dorsal surface of the posterior sigmoid gyrus, the digit representation area is close to or buried in the coronal sulcus, which is well developed at birth. The organization of this area is rather simple in the newborn kitten and more complex in the adult cat. In the newborn, digit 5 is represented furthest rostral on the dorsal surface of the gyrus. As the electrode is moved progressively caudal and into the depths of the coronal sulcus, projections from digits 4, 3, 2 and 1 are successively encountered (Figures 10 and 11). In the newborn subjects the tips of the digits, including the claw and sheath, were always found further lateral in the cortex than more proximal regions of the digits. All of the responses obtained in this area were from light stimulation of hairs, pads or claws; the location of the receptive field remained the same with repeated stimulation; each receptive field was continuous and the response followed repetitive stimulations of 3 - 4 per second. Responsive loci meeting all of these criteria are defined as having 'simple' receptive fields. In one newborn cat (68329) the lateral boundary of the digit representation area was delineated. The row of electrode tracts shown in Figure 10 constitutes this boundary. It should be noted that this area does not extend to the ventrolateral pole of the posterior sigmoid gyrus.

In the newborn animal the bottom of the coronal sulcus always separated the forepaw representations from the projections of the face and head. When the electrode tip was on the caudal bank of this sulcus, stimulation of the face elicited a response; whereas stimulation of the forepaw evoked the cortical response when the electrode tip entered cellular areas lying on the rostral bank. The division between the hand and face representations was marked by a small lesion in several of the preparations. Two examples are presented in Figures 10 and 11.

The organization of projections from the contralateral forepaw is more complex in the adult cat. As in the newborn subjects, projections from the forepaw lie along the caudal edge of the posterior sigmoid gyrus extending into the coronal sulcus. Most of these projections meet all of the criteria to be classified as having "simple" receptive fields.

Projections from D5 are usually located furthest rostral and dorsal, while D4, D3, D2 and D1 lie progresively caudal and ventral on the anterior bank of the coronal sulcus (Figure 12, penetrations 20 and 26). Digit 1 appears to have a relatively small representation area while D2, D3 and D4 projections extend to the lateral pole of the gyrus (Figure 13). In these respects the organization of projections from the digits is quite similar to that in the newborn kitten. However, in the adult cortex, projections from the forepaw extend to the tip of the gyrus and overlap with the MsI forepaw representation causing more variability in receptive field organization.

In the cortical region of the adult cats where the SmI and MsI forepaw representations overlap (Welt et al., 1967; Towe et al., 1968) several other types of receptive fields were encountered. In many cases only deep stimulation of the contralateral arm or forepaw evoked a response. These receptive fields were often labile and were often quite large, covering the entire forepaw or foreleg. A further type of receptive field, which I shall designate as 'disjunctive', was commonly found in this area of the adult cortex. 'Disjunctive' receptive fields are identified by lacking the quality of continuity. That is, stimulation of a similar location on two or more digits would evoke the cortical response. In some cases stimulation of glabrous skin on the forepaw evoked the response while in other cases stimulation of two or more claws, claw sheaths, or knuckles evoked the cortical response. Several receptive fields of this nature were found in the posterior sigmoid gyrus of the adult cat. They were always located rostral to the representation of the simple receptive fields of the digits and on the lateral aspect of the gyrus. Figures 9 and 12 show some of the 'disjunctive' receptive fields which were encountered and their cortical location. The present study did not attempt to determine the presence or absence of a somatotopic organization in the cortical representation of the 'disjunctive' receptive field projections.

'Disjunctive' receptive fields were never found in the newborn kitten anesthetized with barbiturate or in the unanesthetized newborn preparations. However, one 'disjunctive' receptive field was found in a 21 day-old preparation.

In the adult cat, as in the newborn, the coronal sulcus separated the representation of the forepaw from projections responding to stimulation of the face (Figure 13), except at its dorsomedial tip. Projections from the foreleg above the wrist were found caudal to the dorsal tip of the coronal sulcus (Figure 12). Figure 16 gives an additional example of this boundary in adult preparations.

Organization of Projections from the Neck, Head and Face

Table 4 shows the numbers of successful preparations, electrode penetrations and loci responding to delineated peripheral receptive fields on which the following conclusions are based.

Figures 14 - 20 are drawn from this population.

Table 4

Mapping Experiment of Neck and Head Representation in SmI

Age	Preparations	Responsive Punctures	Receptive Fields
Newborn	9	31	60
Adult	8	45	69

Mechanosensitive receptors in the neck, head and face of the cat send projections to the coronal gyrus. These projections are primarily from the contralateral side, however the extreme rostral portion of the face and the inside of the mouth are bilaterally represented. The general somatotopic organization is shown in Figure 14. This organization appears to be similar for the newborn kitten and for the adult cat. However, the orientation of the coronal gyrus changes as the brain develops. What was the lateroventral tip of the gyrus in the newborn appears to curve anterior in the adult cat. From Figure 14 it is evident that rostral portions of the face project to anterolateral portions of this gyrus while caudal portions are represented successively more posterior and medial in the adult cat. Furthermore, in the adult, projections from dorsal surfaces of the head are found relatively lateral in this area while more ventral surfaces are found further medial in the bank of the coronal sulcus. (In the newborn, dorsal surfaces of the head are represented posterior to the more ventral surfaces, and rostral skin surfaces are found lateral of more caudal surfaces.) Figures

15 - 20, showing further details of this organization in the adult cat and newborn kitten, suggest the following additional conclusions:

1. The lower lip is represented in the bank of the coronal sulcus while the upper lip is represented progressively toward the exposed surface of the gyrus.
2. At the anterolateral pole of this representation area are found responses from the most rostral portions of the face.
3. Projections from progressively more ipsilateral portions of the face are found as the electrode tip is moved progressively further anterior.
4. The tip of the nose, inside the mough and non-hairy surfaces of the lips are bilaterally represented.

Additional examples of some of these organizational properties can be found in Figures 10, 11, 13 and 21.

3. Preliminary Data Concerning Other Aspects of Somatomotor Cortical Organization

Latencies of Cortical Responses In several preparations the latency from suprathreshold electrical stimulation of the receptive field to a SmI cortical response was determined. Figure 21 shows the means and ranges for these data collected on newborn, and adult cats. Since only one adult cat was used in this study, latencies found by other authors using similar methods are also included. As can be seen from this figure, within any age group, the further caudal the receptive field, the greater the latency. By comparing the latencies to stimulation of the same body area across the age groups, it can be concluded that there is an inverse relationship between chronological age and latency to a cortical response.

Organization of SII In three barbiturate anesthetized kittens mechanoreceptive projections were found in the cortical area just caudal and ventral to the anterior suprasylvian sulcus. The surface map from one such experiment is shown in Figure 22. This area is defined as the second somatomotor area or SII (Woolsey, 1958). Although there are not enough data to show the detailed organization in this area, several features of these projections may be indicated. Projections to SII from all major body surfaces appear to be electrophysiologically functional by 4 hours after birth in the kitten and these projections respond to physiological stimulation of the receptors. The general organization of these projections agrees with the organization described by Woolsey (1958). In the newborn kitten as in the adult, there appears to be a bilateral representation of the body surfaces in this area. In general, the peripheral receptive fields which evoked unit activity in SII were larger than those found in SmI, a relationship also reported in the adult cat (Carreras and Anderson, 1963).

Columnar Organization in SmI Cortex The columnar organization of cell bodies in the primary sensorimotor cortex is vividly apparent in Nissl-stained sections of the newborn cortex. This feature can be seen in Figure 23. The orientation of these columns is always perpendicular to the cortical surface.

The amount of change in receptive field location within any electrode penetration appears to be a direct function of the angular difference between the orientation of cell columns and the orientation of the path of the electrode (or, more simply, the more columns which are traversed, the more receptive fields found). Mountcastle (1957) reported this aspect of receptive field organization in SmI of the adult cat, and this study confirms it in the newborn kitten, where the columns are strikingly apparent anatomically.

Size of the SmI Receptive Fields in Newborn and Adult Cats The size of the peripheral receptive fields relative to the size of the animals was approximately the same for newborn kittens and adult cats. This conclusion can be verified by comparing the sizes of receptive fields in each of the major parts of SmI cortex of the adult cat with those shown for the newborn kittens. These figures also demonstrate the general relationship between size of receptive field and location of receptive field. As noted by numerous previous investigators, and verified here for the newborn cat, SmI cortical projections from distal areas of the body surface have small receptive fields while more proximal areas have relatively larger receptive fields.

Intensity of Adequate Stimuli for Evoking a Response in SmI In both barbiturate anesthetized adult cats and newborn kittens, most of the SmI cortical responses could be elicited by gently bending the hairs in the peripheral receptive field. In the adult cat 75% and in the newborn kitten 81% of the cortical responses could be elicited by brushing the hairs or slight pressure to glabrous portions of the body. These data lead to the conclusion that the adequate stimuli are in the same intensity range for both ages of subjects. In some cases, deep stimulation of the skin, muscles or joints was required to elicit a cortical response. In most of the cortical loci responding only to deep stimulation, the electrode was in the vicinity of the SmI-MsI boundary at the postcruciate dimple (see Figures 4 and 9).

Observations on Postcruciate MsI Cortex in Newborn Kittens

Numerous investigators (see Welt et al., 1967) have studied the response properties of neurons in the postcruciate motor-sensory area (MsI) of the cat brain. This area lies rostral to the postcruciate dimple and is bounded laterally by the coronal sulcus. Hassler et al. (1964) classified this area praecentralaris gigantopyramidalis (Area 4) and our observations indicate that this cytoarchitectural distinction forms the anterior boundary for SmI in both the adult cat and the newborn kitten.

Since it is well known that neurons in MsI are "silent" in barbiturate-anesthetized cats. The two unanesthetized preparations were used to make preliminary observation on this area in the newborn kitten.

Responses elicited from this area in the newborn kitten had the following characteristics:

1. They adapted to stimulation very quickly. Stimulation rates over 1/second were usually ineffective for driving a cortical response.
2. The receptive field was usually difficult to delineate. They were often the "wide-field" variety described by Welt et al. (1967) and often labile.
3. In contrast to studies on this area in the adult cat, in the newborn none of these responses could be reliably driven by stimulation of only the hairs on the contralateral forepaw. Most required deep stimulation while others required deformation of the skin to evoke cortical responses.
4. The most striking feature of these responses was their unreliability. Often, as the electrode penetrated the cortex, it appeared that deep stimulation of the hand or joint movement sometimes evoked a cortical response, however neither the receptive field nor the adequate stimuli could be reliably determined.

All of these aspects of unreliability, noticed in MsI cortex of the unanesthetized newborn kitten, are similar to what has been found in the barbiturate anesthetized adult cat's MsI cortex (Welt, personal communication).

Discussion

These results provide answers to the three questions posed:

1. The projections from all body parts to SmI cortex of the cat _are_ present at birth and _do_ respond to physiological stimulation of the receptors.
2. The somatotopic organization of these projections _is_ like that of the adult cat.

It is clear that this part of the newborn kitten's somatosensory system is coding the locus of peripheral sensory input in much the same way that the adult nervous system handles this task. In view of these results, the similarities of cortical sensory motor organization in newborn and adult cats will first be considered. Next, the differences between what has been found in these cortical areas of the adult cat and our results from newborn preparations will be discussed. Third, a hypothetical explanation of these differences will be presented in conjunction with clarifications regarding the organization of these cortical areas suggested by the study of immature brains. Then the physiological significance of the coronal sulcus will be considered. Finally, the present study will be related to the existing body of literature regarding the functional development of the cerebral cortex.

1. Similarities of adult and newborn cat SmI cortex.

Somatotopic organization The general organization of projections from the body surface in SmI cortex of the adult cat has been well documented (Adrian, 1940, 1941; Amassian, 1951; Celesia, 1963; Cohen, Landgren, Strom and Zotterman, 1957; Livingston and Phillips, 1957; Marshall, Woolsey and Bard, 1941; Patton and Amassian, 1952; Woolsey, 1947, 1958). Each of these studies used evoked potentials at the surface of the cortex as an indication of the neural activity in tissue lying under that cortical locus.

Since metal microelectrodes record the activity of neural elements in a relatively small area around the electrode tip (Welker et al., 1964) and are driven through the cortex, more detail regarding the somatotopic organization within the representation of each body part can be provided. This appears especially important in a convoluted brain such as that of the cat, since much of the cortical tissue responding to mechanical stimulation of the body surface is buried within the depths of the cruciate, ansate and coronal sulci and the medial longitudinal fissure.

In spite of the drawbacks in the evoked potential technique, summary maps presented by Woolsey (1958) and Adrian (1940, 1941) correspond closely to what has been found in the present study. Thus, results regarding the organization of these projections are mainly confirmatory in nature except that some details of somatotopic organization within each main body division have been clarified. These results are also in close agreement with the organization of the exposed portion of the coronal gyrus reported by Darian-Smith, Isbister, Mok and Yokota (1966). They did not attempt to explore the banks of the coronal sulcus, thus many details of the face are ignored. This study also clarifies some of these details.

The main import of the present study lies in demonstrating that the detailed organization of projections within each major subdivision of the SmI cortex is already laid down in the newborn cat. The specific boundaries of the SmI cortical representation area are discussed in a later section.

Stimulus intensity Since the present study did not attempt to study the stimulus-response characteristics of isolated cortical units in newborn or adult cats, the adequate stimulus was determined by the neural elements within the "driven" cluster of units which responded to the lightest stimulation of the body surface. In view of this classification criteria, it is understandable that very few responses were elicited by only deep stimulation. Yet, it is significant to note that within the SmI cortex of barbiturate-anesthetized adult cats and newborn kittens, the vast majority of cortical responses were driven by very delicate stimulation of the hairs or glaborous skin surfaces (cutaneous). The two "unanesthetized" newborn kitten preparations yielded similar results. These data are in general agreement with investigations of single cells in the hand region of SmI cortex (Brooks and Levitt, 1964; Mountcastle, 1957). However, Morse, Adkins and Towe (1965) reported that 82% of the neurons they studied in SmI cortex of the chloraloseanesthetized cat responded only to skin deformation (deeper pressure). The contradication may be due to the anesthetic effect or the fact the Morse et al. used electrical stimulation of the central foot pad to isolate the responsive cortical units.

Mountcastle (1957) noted that as the recording site on the posterior sigmoid gyrus is shifted from near the ansate sulcus toward the postcruciate dimple "the probability of encountering the given modality types" shifted from units responding to cutaneous stimulation to those requiring "deep" stimulation of the muscles or joints. A similiar relationship was found in the present study for both newborn and the adult cats.

<u>Columnar Organization</u> Mountcastle (1957) first pointed out that within the radial columns of cells which are present in the SmI representation of the contralateral foreleg, all cells in a given column have peripheral receptive fields similar in size, shape and location on the body surface. This columnar organization has been confirmed for several areas of the cat's cortex including SmI (Darian-Smith, et al., 1966; Brooks et al., 1964), SII (Carreras and Anderson, 1963), motor-sensory (Welt et al., 1967) and visual (Hubel and Wiesel, 1965). Our data on the cortex of newborn and adult cats show this organizational quality in all areas of the SmI cortex. The columnar organization becomes especially apparent when the electrode courses down the bank of a sulcus.

In this case the peripheral receptive field location may gradually shift as many as five or six times (Figures 5, 8, 12, 17, 18). While the electrode is traversing several columns, the receptive field shift is almost always ordinal. That is, if digit five is encountered as the electrode enters the cortex and projections from digit 3 are found deeper in that penetration, a receptive field including projections from digit 4 will be found between these points. This orderly shift in receptive field location was so consistently found in all of the preparations, that when two widely separated receptive fields were encountered it was considered an anomaly. Often the histological reconstructions of these electrode tracks indicated that the electrode had crossed a sulcus. In the newborn cat, the electrophysiological aspects of columnar organization were as apparent as in the adult cortex.

In thionin-stained sections of SmI cortex of the adult cat, the columnar organization of cells has been noted by Hassler and Muhs-Clement (1964). This cytoarchitectural characteristic, although apparent in the adult, is more striking in the newbron cat, as in the newbron rat (Caley and Maxwell, 1968).

Receptive Field Organization The sizes of the receptive fields of individual cortical neurons were not determined in the present study. However, some qualitative aspects of the dimensions and organization of receptive fields found should be considered. All of the receptive fields found in the postdimple area of the posterior sigmoid gyrus of the adult cat and the newborn kitten were of the fixed, local field variety described by Welt et al. (1967). That is, these receptive fields had sharp boundaries and were restricted to one portion of the body. In addition, most of the receptive fields found in the adult SmI cortex and all of those found in the kitten were of the "simple" variety described above (i.e. continuous). These results concur with those of Mountcastle (1957) and Brooks and Levitt (1964).

The size of the peripheral receptive fields of cortical neurons is presumably related to both the innervation density on the skin and to an animal's abilities to determine the exact locus of peripheral sensory input (Mountcastle, 1957; Welker, Johnson and Pubols, 1964; Rose and Mountcastel, 1959). In view of these relationships it is important to note that the receptive fields found in SmI cortex of the newborn kitten were of approximately the same relative size as those found in the adult cat. Furthermore, in the newborn kitten, as reported throughout the medial lemniscal system of adult mammals (Mountcastle, 1957; Rose and Mountcastle, 1959; Welker et al., 1964) the size of the receptive fields was inversely related to their 'distality'.

2. Differences between the adult cat and newborn kitten in the organization of somatomotor cortical areas.

<u>Latency</u> The most obvious difference between the newborn and adult SmI cortex is the latency of a neuronal response to

electrical stimulation of the skin. This appears to be a consistent difference, and has been previously reported for the somesthetic, visual and auditory cortex of newborn and young kittens by Scherrer and Oeconomos (1954), Rose and Lindsley (1968) and Marty (1967) respectively, Studies by Ekholm (1967) and Purpura et al. (1965) indicated that growth and myelination of the afferent nerve fibers, and decreases in synaptic delay are all responsible for these postnatal changes.

Complexity Aside from latency changes, the differences between the newborn and adult cat's somatomotor cortex appear to be mainly in the realm of complexity. This difference manifests itself in many ways.

In recording from the kitten SmI cortex, the somatotopic organization was easily distinguished. There appeared to be a point-to-point relationship between receptive field position and cortical location. No anomalies in this organization ever occurred, and the overlap of receptive fields was minimal. As the electrode penetrated the cortex, the receptive field locations may change from digit 4 to digit 3 to digit 2, but this change was gradual in the sense that the digit 3 representation was always between that of digits 4 and 2. An anomalous receptive field location was never interspersed amongst these. In the adult cat however, on several occasions, discontinuities in the somatotopic organization were encountered. An example is shown in Figure 6A, puncture 15.

Two extreme cases of this discontinuity were found in the adult cat. These were ipsilateral projections to SmI cortex from the limbs. One was recorded about 1 mm from the midline and about 6 mm posterior of the cruciate sulcus. In this case light stimulation of the hairs on the ipsilateral knee produced a distinct unit cluster response. In the second case, the electrode was about 2 mm anterior of the bifurcation of the ansate sulcus and a unit-cluster response was elicited by delicate stimulation of the hairs above the central foot pad on either front paw. When the electrode was lowered slightly, only ipsilateral stimulation elicited the response and when it was raised slightly, only contralateral stimulation was effective. In contrast to these two cases, Mountcastle (1957) never found ipsilateral projections to SmI cortex in his extensive analysis of neurons in this area, and Woolsey (1958) reports that aside from the perioral regions, only the contralateral body surface is represented in SmI cortex. However, Nakahama (1958) was able to elicit very small, long latency evoked potentials by ipsilateral radial nerve stimulation. It is also interesting to note that Mountcastle and Powell (1959) reported that a few units in the postcentral gyrus of the monkey (Macaque) responded to ipsilateral stimulation.

In the newborn cat, aside form the ipsilateral representation of the perioral region, only contralateral projections from the body surface were found in SmI cortex. This was true in both the barbiturate-anesthetized and unanesthetized preparations, although ipsilateral stimulation was regularly performed.

Additional evidence for the difference in complexity of receptive field organization is the representation of what has been termed 'disjunctive' receptive fields in the lateral sigmoid gyrus of the adult cat and their apparent absence in newborn kittens. Welt et al. (1967) found single neurons with similiar receptive fields in MsI cortex of the adult cat, however, from their figures it is not possible to determine the exact cortical locus in which they were found, or the extent to which they were found. Johnson et al. (1968) also showed (Figure 16) a receptive field which included the claw of each digit of the hand in the dorsal column nuclei of the raccoon. It is notable that Pubols, Welker and Johnson (1965) did not find 'disjunctive' receptive fields of this type in the dorsal roots of raccoons, coatimundis or cats. It would be of considerable interest to know more about this type of receptive field representation, especially the neural connections forming them.

The boundaries of SmI cortex were much more clearly defined in the newborn than in the adult preparation. In the newborn kittens, the bottom of the coronal sulcus always marked a sharp division between the representation of the forelimb and face, whereas in the adult, the forelimb representation occasionally "spilled over", into the caudal bank of this sulcus at its medial tip. In addition, the rostral boundary of the SmI forelimb representation could be designated in the newborn as the point at which hair stimulation no longer evoked a response and deep pressure was necessary (Figure 9, 67339). It appeared to gradually merge with MsI cortex in the adult cat. The overlap between SmI and MsI cortex is confirmed by the data of Towe et al. (1968) and Brooks et al. (1964).

The most striking example of the difference in complexity lies in a comparison between receptive fields found in MsI cortex of the unanesthetized or chloralosed-anesthetized adult cat and observations on this area in the newborn kitten. A wide variety of receptive fields types have been found in the adult. These include neurons with wide receptive fields covering the entire body, all four limbs or one entire limb; neurons with small fixed receptive fields; and neurons with labile receptive fields. In each of these categories some of the neurons respond to cutaneous stimulation while others respond only to 'deep' stimulation (Brooks et al., 1964; Morse, Adkins and Towe, 1965; Towe, Patton and Kennedy, 1964; Towe et al., 1968; Welt et al., 1967). In the unanesthetized newborn kitten, cortical responses were extremely unreliable; usually driven only by deep stimulation, with receptive fields difficult or impossible to localize, but restricted to the contralateral foreleg. Often these neurons did not follow stimulation as slow as one stimulus every 5 or 10 seconds. The qualities described above for the unanesthetized newborn kitten are quite similar to what is commonly found in MsI cortex of barbiturate-anesthetized adult cats (Welt, personal communication; Rubel, unpublished observations). Thus it appears that the same sources of input to MsI cortex which are rendered quiescent by barbiturate anesthesia in the adult cat, have not yet become electrophysiologically functional in the newborn kitten.

In the next section a hypothetical explanation of these differences in complexity will be briefly outlined and its ramifications for our understanding of this cortical area will be stated.

3. Hypothetical Development of SmI Cortex in the Cat

The main premise of the following hypothesis is that the primary somatic sensory cortex is formed during ontogeny as a point-tc-point reflection of the distribution of mechanosensitive receptors in the animal's body. This organization is brought about by the 'sorting' out of thalamocortical radiations into a precise somatotopic organization as they approach the cortex. The mechanism of this sorting is unknown (*per contra* Sperry, 1967). As these fibers penetrate the cortical grey matter, they create the appearance of cell columns in the cortex. As the axons grow up the columns, they send collaterals to the cells at all levels, thus accounting for the electrophysiologically defined columnar organization (Mountcastle, 1957). It is at approximately this point of development that the kitten is born. The cortex is composed of densely packed columns of cells that are noticeably barren with respect to dendritic and axonal processes (Purpura, 1961), but receiving a detailed description of the distribution of receptors.

During the postnatal period of development, the intranuclear connections at each level of the somatosensory system are elaborated. In the cortex, the growth of dendritic and axonal processes causes a disruption of the vertically aligned cell columns, and forms a dense network of intracortical connections. I suggest that it is these connections which cause the differences in complexity noted above.

Supporting these notions of cortical development are the experiments of Jones and Powell (1968). By observing the terminal degeneration of axons following small cortical lesions, these authors have begun to describe the topography of intracortical connections in the adult cats. They find a dense network of interconnections within each functional subdivisions of SmI cortex, and reciprocal connections between SmI and MsI. It would be of theoretical importance to repeat their studies on newborn kittens to see if these connections are present at birth.

A second line of supporting evidence is furnished by the effects of barbiturates on cellular activity in these areas. It is well known (Woolsey, 1958; Mountcastle, Davies and Berman, 1957) that barbiturates severely depress the spontaneous firing of SmI cortical neurons, and change the receptive field properties of neurons in MsI and SII (see Welt et al., 1967; Carreras and Anderson, 1962). Other authors including Yamamoto and Schaeppi (1961) have suggested that barbiturates are most effective in blocking "polysynaptic neoronal systems" especially in the cortex and brain stem: Their effect is probably in interneurons at each level of an afferent system. These suggestions, along with the observation that there is little or no spontaneous activity in the cortex of unanesthetized newborn cats (Huttenlocher, 1967; and this study) and the observations noted on MsI cortex of newborns, lead to the conclusion that these intracortical connections are not developed in the newborn.

A more direct test of this hypothetical scheme of cortical development would be to determine the effect of localized ablations or local cooling of SmI cortex in adult cats on the receptive field properties of MsI cells. According to the above hypothesis, these procedures should result in an adult MsI cortex with cells that behave like those of the newborn kitten.

I am not suggesting that the total input to MsI cortex in the adult cat is from other cortical sources. This is obviously not the case (Oscarsson and Rosen, 1966). I am suggesting that these sources of input to the somatomotor cortical areas provide for some of the complexities not encountered when investigating newborn subjects and that these sources are responsible for the apparent overlapping of these areas in the adult cat. If these conclusions are sound, then the SmI cortex can be much more easily defined in the newborn cat than in the adult because of the simplicity in its organization and discretness of its boundaries.

4. Physiological Significance of Sulci

Welker and Seidenstein (1959), using evoked potentials recorded from the surface of the cortex, found that sulci in the SmI cortex of the raccoon reliably separate the representations of adjacent body parts. Welker and Campos (1963) extended these findings to several other members of the family Procyonidae. Welker and Seidenstein hypothesized that "cortical sulci are formed at the boundaries of 'physiological' subdivision" and the "the cortex of the gyral crowns is functionally more active than that of the (sulcal) fundi". They indicate that these results could occur during ontogeny by the cortical terminals from densely innervated regions of the skin "pushing upward and outward while sparsely innervated areas are left behind to become the fundi". Conversely, Hand and Morrison (1969) studied axonal degeneration following small electrolytic lesions in the forepaw representation of the ventrobasal complex (VB) of cats. They concluded that the coronal sulcus does not form the lateral boundary of the SmI forepaw representation and that the sulcal fundi are richly innervated by thalamocortical fibers.

The results of the present study support both of the reports mentioned above. In support of Welker and Siedenstein (1959), our results indicate that, in the newborn cat, the fundus of the coronal sulcus forms a true "physiological" subdivision between the forepaw representation and that of the face. In the adult cat this demarcation remains essentially intact although due to the expansions of cortical tissue, the forepaw and face representations may "spill over" onto the adjacent gyrus. Another possible explanation of Hand and Morrison's results is that their electrolytic lesions may have interrupted corticothalamic fibers from the Vb face representation as they course laterally toward the coronal gyrus. In agreement with Hand and Morrison, results of this study indicate that much of the hand and face representation is found in the depths of the coronal sulcus. In raccoons, adult cats and kittens, the cortical grey matter appears deeper at the gyral crowns than in the fundi. However, in the cat and kitten the fundic cortex appears to be richly innervated by thalamocortical fibers and is as "functionally active" as the gyral corwns. In order to explain the apparent differences between these results and Welker and Seidenstein's conclusions, careful microelectrode exploration of the sulci in the cerebral cortex of the raccoon is necessary.

5. Developmental Considerations

Although it has been well established that the primary sensory areas in the cerebral cortex of newborn kittens will respond to electrical stimulation of the afferent nerves (see introduction), relatively few studies have considered the ability of the newborn nervous system to code different qualities of stimulation within a sensory system. Hubel and Wiesel (1963) studied the receptive fields of cells in the striate cortex of two kittens which had had no prior exposure to patterned light. These authors found that receptive field properties of the cells were similiar to those found in the adult cortex. Both "simple" and "complex" fields were reported, cells had definite receptive field orientations, and were aligned in columns with cells of a given column having similiar receptive field orientations. They concluded that "many of the connections responsible for the highly organized behavior of cells in the cortex must be present at birth or within a few days of it." These authors did not look at any other aspect of visual cortex organization, such as retinotopic organization or stimulus-intensity relationships. In direct contrast to these findings is the report by Pujol and Marty (1968). The latter authors used electrical stimulation of the auditory nerve and tonal stimulation to study the development of evoked potentials in the primary auditory cortex of kittens. They noted that very high intensities of tonal stimulation were required to evoke a response in young kittens (2 - 3 days old); that only tones between 500 and 2500 cps were effective; and that a cortical tonotopic organization was not present at this age.

It may be important to note that although these relatively low frequency tones did evoke responses only in the anterior portion in the auditory cortex, the cochlear development at this age indicates that they emerged from the basilar portion. Woolsey and Walzl (1942) indicated that the cortex was organized in a cochleotopic manner with the basilar portion represented rostrally on the cortex and the apex represented caudal. Thus, it appears that the cochleotopic organization may be present in the young kitten and the immature cochlea may have different transduction properties than the adult receptor (see Marty, 1967). Only future experiments using microelectrode methods and local stimulation of the cochlea will answer this question.

The main purpose of this study was to determine if one form of neural coding is present in the cortex of the newborn cat; coding the locus of peripheral stimulation. It has been demonstrated that elements of the SmI cortex are capable of making discriminations regarding the exact locus of delicate mechanical stimulation. This cortical discrimination is performed through a detailed cortical representation of the distribution of mechanosensitive receptors. The results also indicate that many of the response properties of cells in the SII cortex are developed by birth (Carreras and Anderson, 1963).

This study, however, only indicates that one, very basic, form of neural coding is developed at birth, and does not imply that the sensory motor cortex is "adult-like" in structure or function. The contrary is apparently true. The results also suggest many ways in which the adult cortex processes somatomotor information that the newborn kitten is not capable of performing. Of particular interest for future research efforts on the developing somatomotor cortex would be studies of afferent inhibition (Mountcastle, 1957), receptive field intensity coding, frequency coding (Mountcastle et al., 1957), and receptive field types in MsI cortex. Several studies have related enlargements in the neural representation of specific body parts to specializations in the behavior repertory of animals (c.f. Welker, Johnson and Pubols, 1964; Johnson, Hatton and Rubel, 1969). While adult cats appear to spend time using both their forepaws and lips as tactile discriminators, kittens appear quite dependent on the perioral regions. In view of these comparative studies and the behavioral differences, it would be of interest to determine the relative volumes of cortical tissue representing each body subdivision at different ages of development.

In terms of accounting for the differential effects of neonatal and adult damage to the neocortex (Kennard, 1938; Benjamin and Thompson, 1959), the present study offers no explanation. Kennard suggested that an explanation lies in the notion that the behavior of neonatal monkeys is "largely subcortical", (i.e. that cortically dependent sensory-motor behavior patterns are not yet functional). Studies on the neonatal kitten appear to refute this hypothesis. Henry and

Woolsey (1943) indicated that the precruciate motor cortex of newborn kittens is somatotopically organized. From the present study we can conclude that these behavioral differences are not due to major differences in the somatotopic organization of sensory cortex at the time of the ablations. Furthermore, behavioral observations (Rubel, unpublished research) after bilateral removal of the somatosensory cortex suggest that these areas are 'behaviorally functional' in the newborn kitten. In searching for food the lesioned kittens would nestle into the mother like their normal littermates and begin climbing up the fur in search of a nipple. Invariably, however, the lesioned kitten bypassed the nipples and continued climbing over the mother's back. It appeared that these kittens had lost the ability to make the fine discriminations required for finding the glabrous skin surrounding the mother's nipple.

Summary

1. The somatotopic organization of mechanoreceptive projections to the SmI cortex of newborn kittens was compared with that of adult cats. Observation were also made on some functional properties of SII and MsI cortex of newborn kittens.

2. Projections to the SmI cortex from the entire contralateral body surface are present at birth and respond to physiological stimulation of the receptors.

3. The somatotopic organization of projections to the SmI cortex of the newborn kitten is similar to that found

in the adult cat with respect to the cortical region receiving projections from each part of the body and to the detailed organization of projections within each of these cortical subdivisions.

4. The relative sizes of peripheral receptive fields, and the intensity of stimulation effective for eliciting a response were similar for projections in SmI cortex of both newborn kittens and adults. At both ages receptive field sizes decreased as their locations approached the distal portion of the limbs or rostral part of the face. In adults and newborns, over 75% of the neural responses were elicited by gentle bending of the hairs or light touch to the glabrous skin surfaces.

5. Other similarities between adult and newborn sensorimotor cortexes included: a) receptive fields of projections to SmI cortex were of the fixed, local field type; b) projections to SII cortex of newborn kittens responded to physiological stimulation of the receptors; c) ipsilateral as well as contralateral body surfaces were represented in SII cortex; d) the columnar arrangement of neurons and their receptive fields were apparent in the SmI cortex; e) the coronal sulcus formed a division between the representation of the forepaw and face.

6. Differences between newborn kittens and adult cats included: a) shorter latency from electrical stimulation of the skin to a SmI cortical response in adults; b) projections

to SmI cortex having disjunctive receptive fields were not found in newborn kittens but existed in the adults; c) the diversity of receptive field types found in neurons of the adult postcruciate MsI cortex was not found in newborn kittens; d) newborn subjects displayed less variability in the somatotopic organization of projections and less overlap in the receptive fields of projections to SmI cortex.

7. It is suggested that the SmI cortex develops as a point-to-point reflection of the distribution of mechanosensitive receptors in the body and that the complexities in this organization seen in the adult cat occur during postnatal development.

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APPENDICES

Appendix A

Surgical Preparation of Newborn Kittens

A kitten was removed from its home cage and given an intraparitoneal injection of .3 cc (.15mg) promazine hydorchloride (Sparine) plus .1 cc (.005 mg) atropine sulfate. Constant doses were used since weight did not vary excessively. The sparine was given as a preanesthetic medication in order to reduce the dosage needed for complete anesthesia, since the dosage range between achieving a surgical plane and death is slim in the young kitten. The atropine was included to reduce tracheal secretions. At this time the hair was clipped to within 2 mm of the body surface.

In the interim between the pre-anesthetic medication and administering the general anesthetic, the kitten was returned to its home cage with the mother and littermates. Ten to 15 minutes later the kitten was anesthetized with an intraperitoneal injection of pentobarbital sodium (Nembutal) (18 mg/kg of body weight). Additional doses of Nembutal were given, as needed to eliminate nociceptive reflexes during the surgical preparation and recording. Additional doses were $\frac{1}{4}$ the original dosage.

When the animal attained a surgical plane (absence of nociceptive reflexes) a tracheal connula and a rectal thermistor probe were inserted. Towel clamps were then attached onto the vertebral arches just behind the scapula and in front of the pelvis. These towel clamps were used to suspend the animal during the remainder of the experiment. The head was fitted into a specially designed head holder at the desired angle. The head holder consists of dental acrylic molds which fit each side of the kitten head and its ventral surface. These molds were attached to bars connected with the main head holder. To mount the head, each mold was coated with silicone impression rubber (SIR, Precious Metals Res. Corp.) and the head was gently clamped between the molds. The SIR cures thereby holding the head firmly. After the skin was removed over the cranium, jewelers screws were placed through the skull over the posterior portion of each hemisphere (this base was well calcified about 2 mm from the midline). The screws and acrylic head holders were then connected with acrylic, making the entire system solidly attached to the skull, holding it firmly without undue pressure. The cranium over-lying the anterior portion of the left hemisphere was removed with scissors. Frontal sinus bleeding was controlled with bone wax. Following careful removal of the dura, the exposed brain was photographed, and then covered with a warm agar-saline solution (about 1% Ionagar) which quickly gelled. The agar served to insulate the brain from either drying or cooling, and reduced cortical pulsation to a minimum. Between removal of the dura and covering with agar, the brain was kept moist under warm saline or warm mineral oil.

During the preparation and recording, body temperature was maintained at 36 - 38° C with cloth heating tape (Heat-by-the-Yard, Electrothermal Engineering Ltd.), connected to a 12v. battery through a variable resistor. The animal was kept hydrated by a 3 cc intraperitoneal injection of 5% dextrose solution every 3 to 4 hours. The entire preparation, from anesthetic to the beginning of recording lasted about 1½ hours. Figure A1 shows a newborn kitten which has been prepared in the above manner.

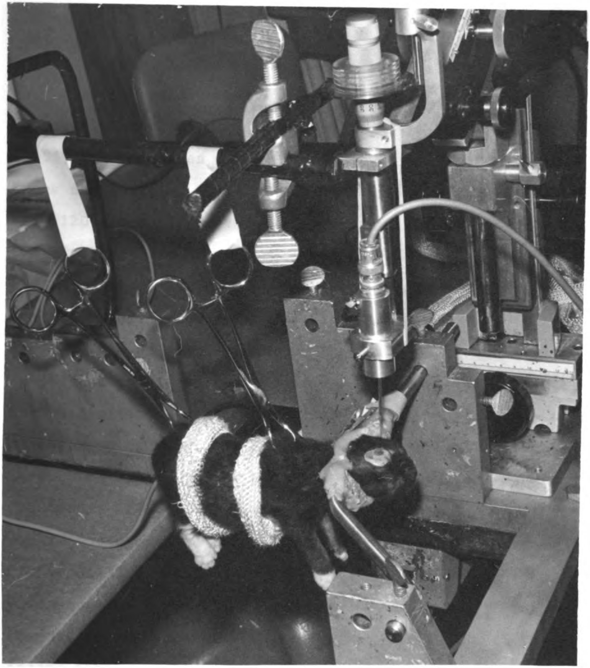


Figure A1. Newborn kitten prepared by the method described.

Appendix 3

Recording Equipment

Electrophysiological responses were recorded through tungsten microelectrodes prepared by the method of Hubel (1956) and insulated with 1 mm (I.D.) pyrex tubing (Baldwin, Frenk and Lettvin, 1965). The uninsulated portion extended 60 - 120 microns from the tip and the 'shaft' portion of the electrode was 30 - 60 microns in diameter. In spite of the high density of neurons in the cortex of a newborn kitten, electrodes with unusually large uninsulated portions ($> 90\,\mu$) proved most successful for reliable recording.

Tungsten electrodes recorded potentials with respect to a stainless steal wire inserted through an exposed muscle of the head or neck. In most cases voltages were passed through 80 Hz low and 10 kHz high filters and amplified (Textronix Preamplifier, model 122). Signals were further amplified, displayed visually on an oscilloscope screen (Textronix CRO, model 502), presented aurally through an audio-monitor (Grass, AM5) and recorded on magnetic tape (Magnecord Stereophonic Tape Recorder, model 1028). The second tape channel was used for synchronized voice commentary. A paper write-out of the neural signals could be obtained, either on-line or subsequent to the experiment, through a Honeywell Visicorder. This recording system is schematicly shown in figure B1.

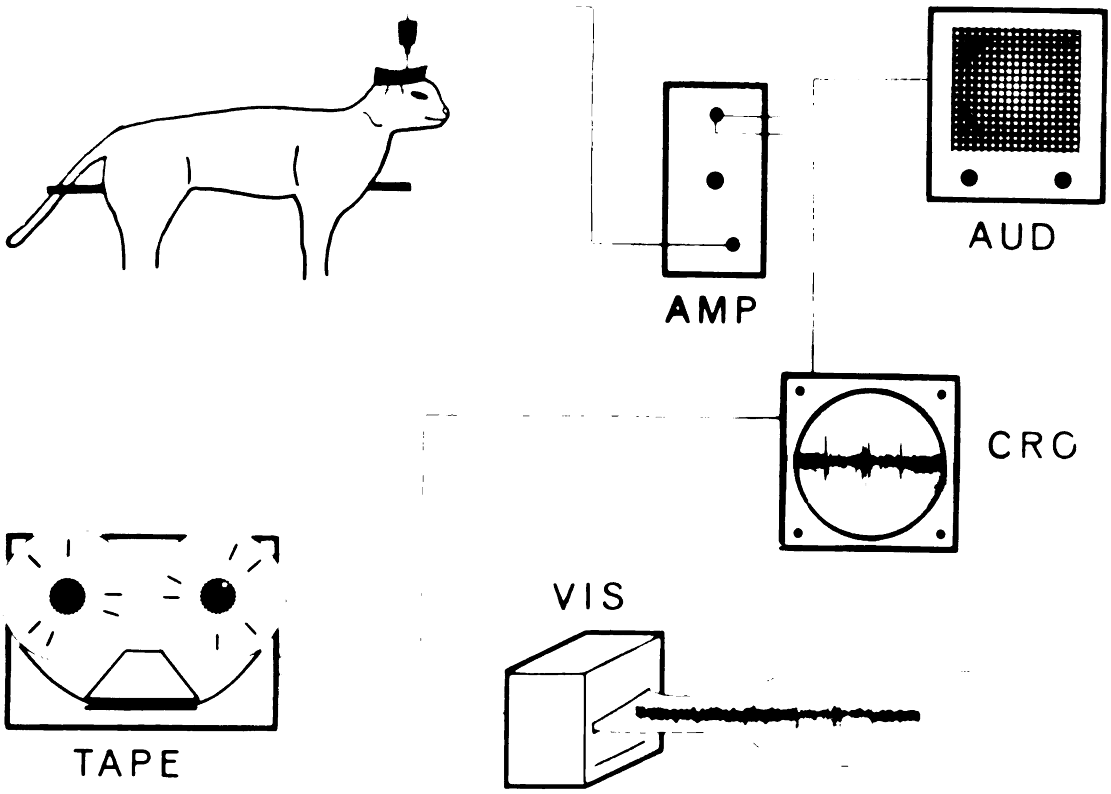


Figure B1. Schematic diagram of recording system, AMP = Preamplifier; AUD = Audio-monitor; CRO = Catode ray oscilloscope; TAPE = Tape recorder; VIS = Visicorder.

Appendix C

Measurement of Response Latencies

In order to determine the latency of cortical responses to peripheral stimulation the following procedures were used in one adult cat and several kittens. After a peripheral receptive field had been delineated, two Grass "Pin-type" electrodes were inserted through the skin approximately in the middle of the receptive field. These stimulating electrodes were connected to the stimulus isolation unit of a Grass (model S4) stimulator which delivered a biphasic 0.1 - 0.2 msec. pulse. The intensity of the shock was, in all cases, suprathreshold (usually X10). The frequency of the shocks was varied between .1 cps and 10 cps. The latency was measured from the shock artifact to the first unit activity or beginning of the evoked potential. These data were also recorded on tape for subsequent varification. It is probable that suprathreshold electrical stimulation, as used here, directly stimulates the afferent nerve trunks or their termination, thereby bypassing the actual receptor sites (Eckholm, 1967).

FIGURES

Figure 1. Sample of unit-cluster responses recorded from SmI cortex of 6 adult cats.

Left to right: Animal number; sample of the neural response elicited by stimulation of the first receptive field location encountered during of after the third electrode penetration; 50μv calibration signal; figurine drawing showing the peripheral receptive field (blackened) effective for eliciting the unit activity. All responses were driven by bending the hairs covering the receptive field. Bottom: 200 msec. calibration with small dots at 10 msec. intervals. All traces un-retouched.

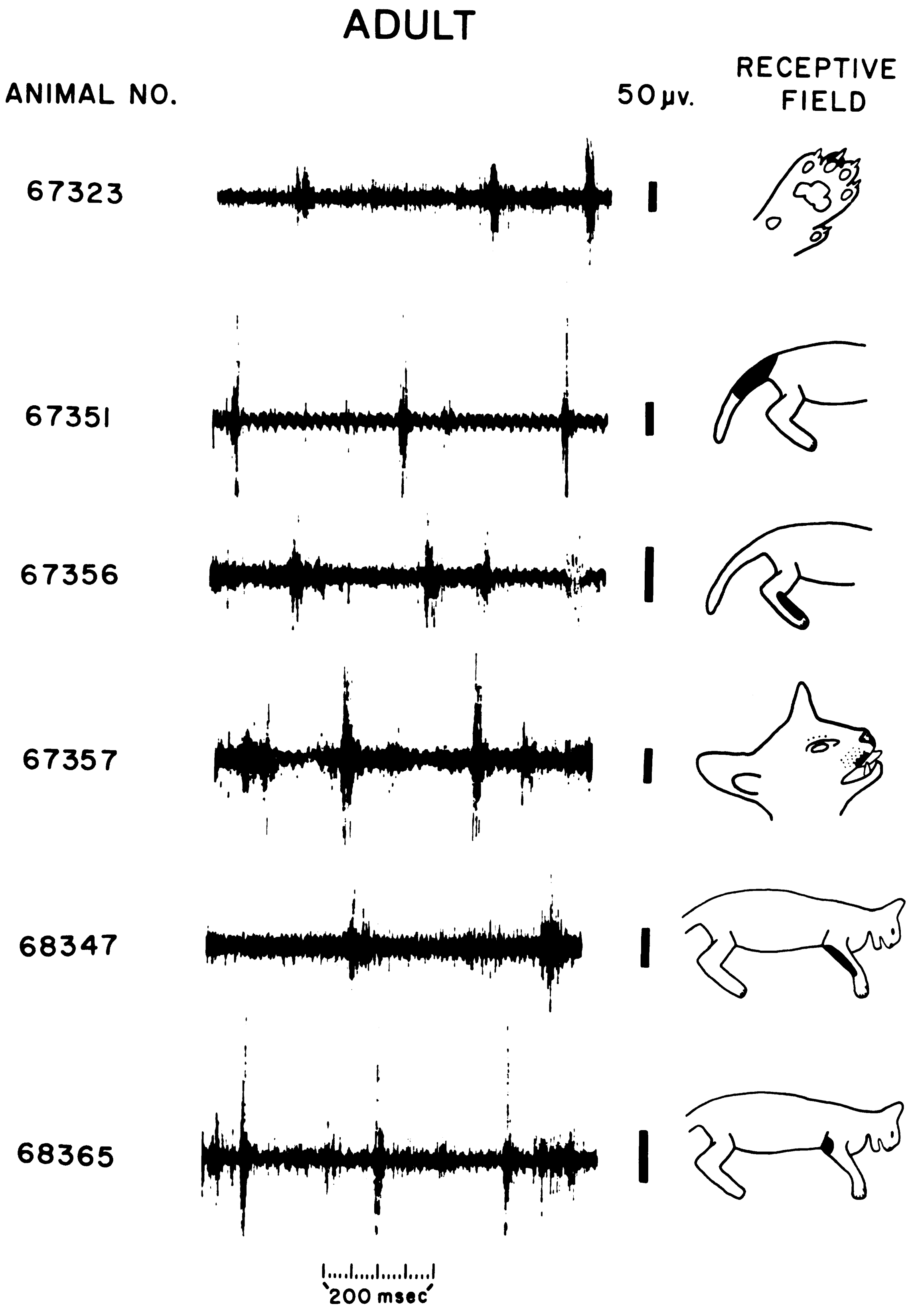

ADULT
ANIMAL NO.
50µv.
RECEPTIVE FIELD
67323
67351
67356
67357
68347
68365
200 msec

Figure 1

Figure 2. Sample of unit-cluster responses recorded from SmI cortex of 7 newborn kittens.

Left to right: Animal number; sample of the neural response elicited by stimulation of the first receptive field location encountered during or after the third electrode penetration; 50µv calibration signal; figurine drawing showing the peripheral receptive field (blackened) effective for eliciting the unit activity. All responses were driven by bending the hairs covering the receptive field. Bottom: 200 msec. calibration with small dots at 10 msec. intervals. All traces un-retouched. The arrows point toward the small responses in trace 68329. Bottom trace (69367) taken from unanesthetized preparation. By comparing this figure with Figure 1, note that newborn responses are of lower amplitude and longer duration but otherwise similar to adult responses.

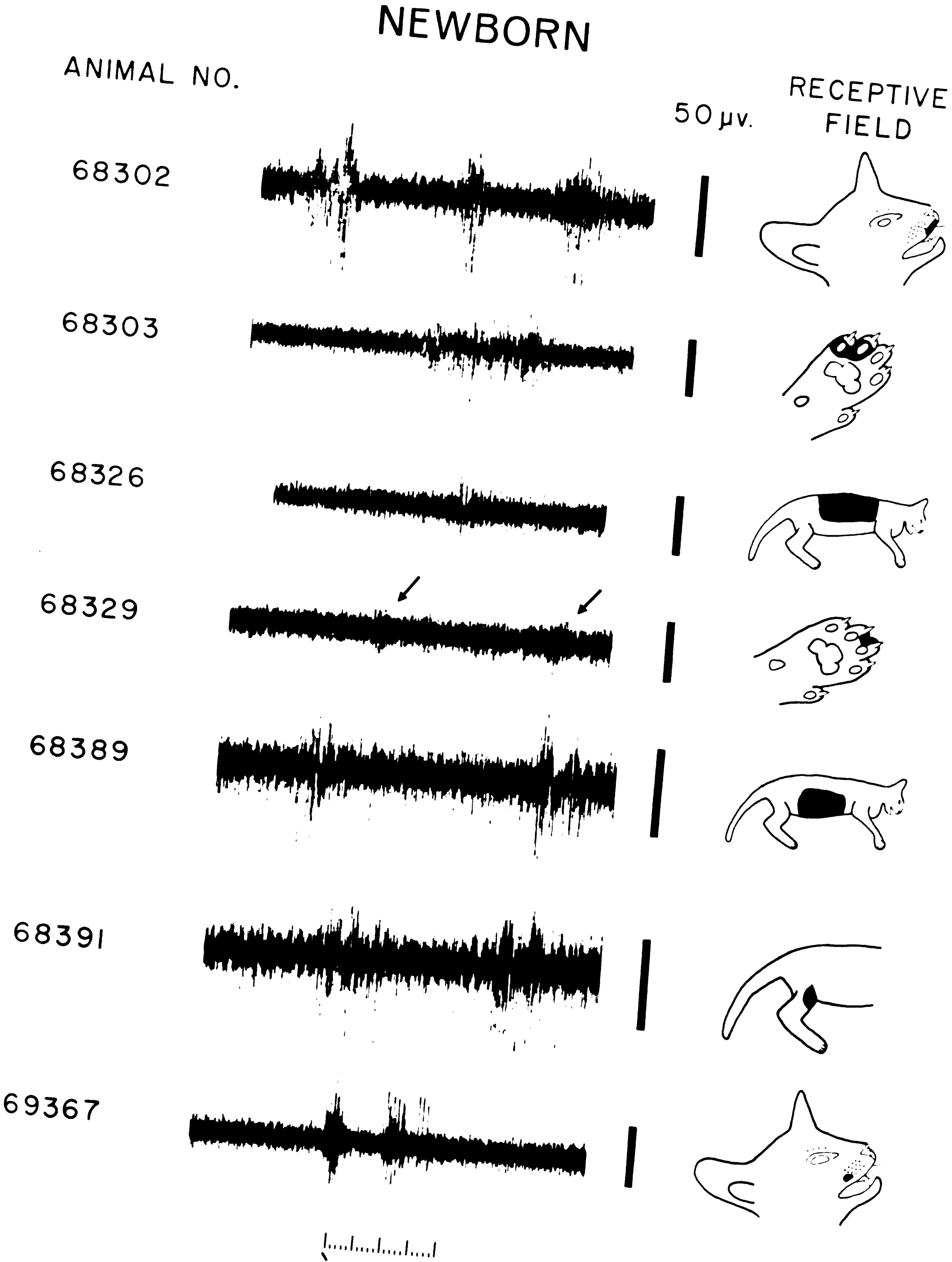

NEWBORN
ANIMAL NO.
50 µv.
RECEPTIVE FIELD
68302
68303
68326
68329
68389
68391
69367
200 msec

Figure 2

Figure 3. General somatotopic organization of mechanosensitive projections to SmI cortex.

Top: Dorsolateral view of the left cerebral cortex of a cat. Middle: Expanded view anterior neocortex with regions of SmI recieving projections from the body surfaces shaded to match shading on figurine of cat body (bottom).

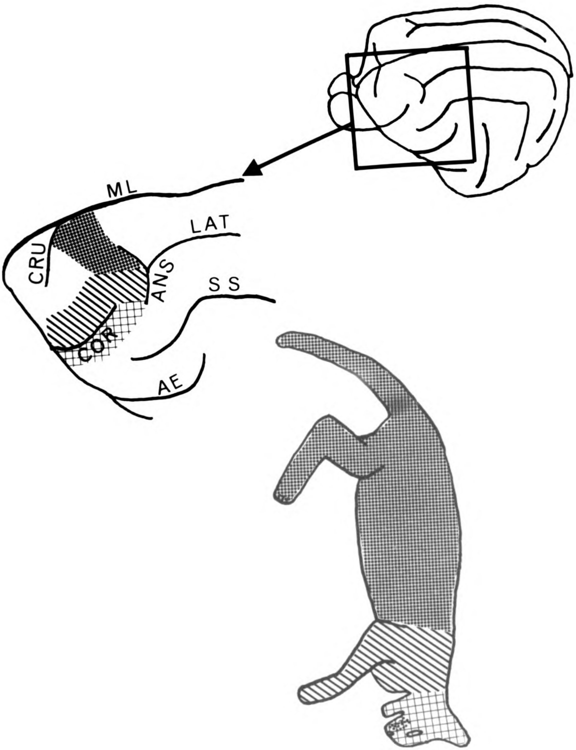


Figure 3

Figure 4. Surface maps of medial aspect of posterior sigmoid gyrus.

At the top are tracings of the left neocortex of an adult cat and newborn kitten, with the areas shown in the expanded tracings (below) outlined. Below: The points where the electrode entered the cortex are represented by open and closed circles on the brain tracing from each preparation. Closed circles indicate that a response to peripheral stimulation was found within 1.5 mm of the surface in the adult preparation or 1.0 mm of the surface in the newborn preparations. Open circles indicate that either no responsive points were found or that the electrode was below these depths when unit activity could be driven by peripheral stimulation. All of these points were histologically verified. The electrode penetrations within each anterior-posterior row are at 1 mm intervals. The peripheral receptive fields and their organization are shown to the right of each brain tracing. Only the first receptive field encountered in each penetration is shown. The blackened areas of the figurines indicate that cutaneous stimulation evoked the neural response while heavily outlined receptive fields indicate that a deeper pressure stimulus was necessary. Open circles correspond to the position of open circles on brain bracings. The approximate position of sulci are indicated on figurine maps by heavy lines. Figurines of volar surface of foot have digit 1 to right and digit 4 to left. ANS = ansate sulcus; CRU = cruciate sulcus; D = postcruciate dimple; ML = medial longitudinal fissure.

Note: Volar surface of the digits is represented rostral of projections from the leg and trunk. Dorsal surfaces of the digits are represented posterior and medial to the volar surfaces. Projections from anterior regions of the trunk tend to be located lateral to the representation of more posterior body regions. In the area of the postcruciate dimple in the adult subject (D), cutaneous stimulation was effective posterior to the dimple while deeper pressure stimuli were needed to drive the neural responses on the anterior side.

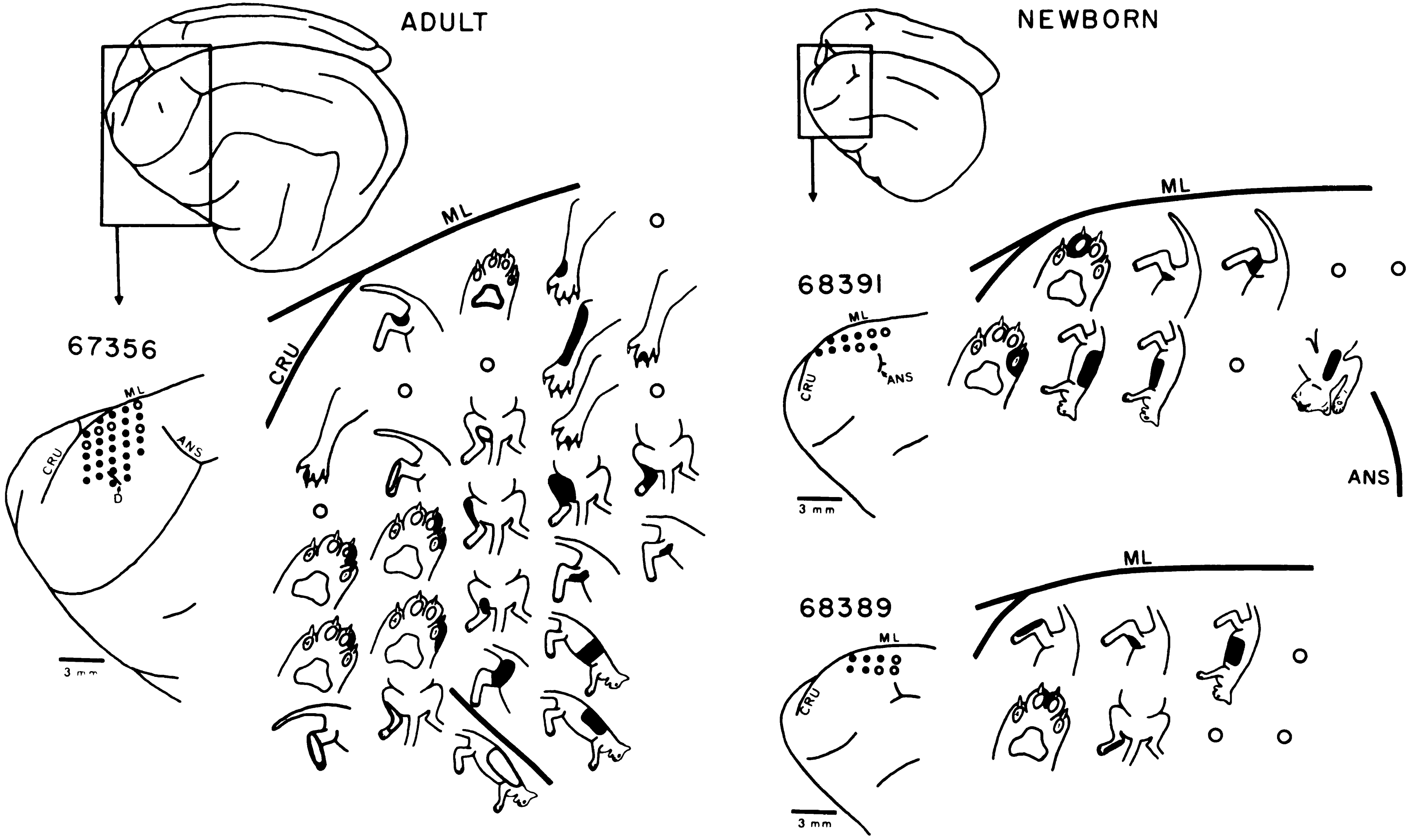


Figure 4

Figure 5. Organization of projections from hind limb, rump and tail - Adult.

Receptive fields found in one row of electrode penetrations near the medial edge of the posterior sigmoid gyrus of the adult cat are shown. Top left: Tracing of the left neocortex from this preparation showing points at which the electrode entered the cortex. Top middle: Schematic view of brain cut transversely through the posterior sigmoid dyrus. Dotted line shows approximate angle at which parasagittal section was cut. Top right: Tracing of parasagittal section through the numbered electrode tracks showing their course through the cortex and the approximate depths at which peripheral stimulation evoked a neural response (dots). The peripheral receptive field evoking a response within each electrode penetration in shown below. The order of the figurines corresponds to the order of the dots in the section tracing. Blackened areas on the figurines depict receptive field in which cutaneous stimulation was effective while heavily outlined areas indicate where pressure stimuli were necessary. In all of the figurines of the foot, digit 1 is at the top and digit 4 at the bottom. The last receptive field in puncture 11 was pressure stimulation on the pads of digits 2 and 3 or light touch to the claw of digit 3. The last two receptive fields in puncture 10 were, respectively, light touch to any claw, and pressure to any of the glabrous pads. ANS = ansate sulcus; CRU = cruciate sulcus. Distance between punctures 12 and 13 was 1.0 mm.

Note: Projections from the digits extend rostral up to the posterior bank of the cruciate sulcus. Distal surfaces of the leg are represented rostral of more proximal surfaces. In puncture 10 digit 1 is represented most dorsal with digits 2, 3 and 4 progressively more ventral. The same organization is apparent in puncture 11. The rump and tail send projections to the dorsal bank of the cruciate sulcus (puncture 13). In punctures 10 and 11 responses to cutaneous stimulation of the dorsal foot are found dorsal to projections responding to stimulation of the claw, or deeper pressure applied to the foot pads.

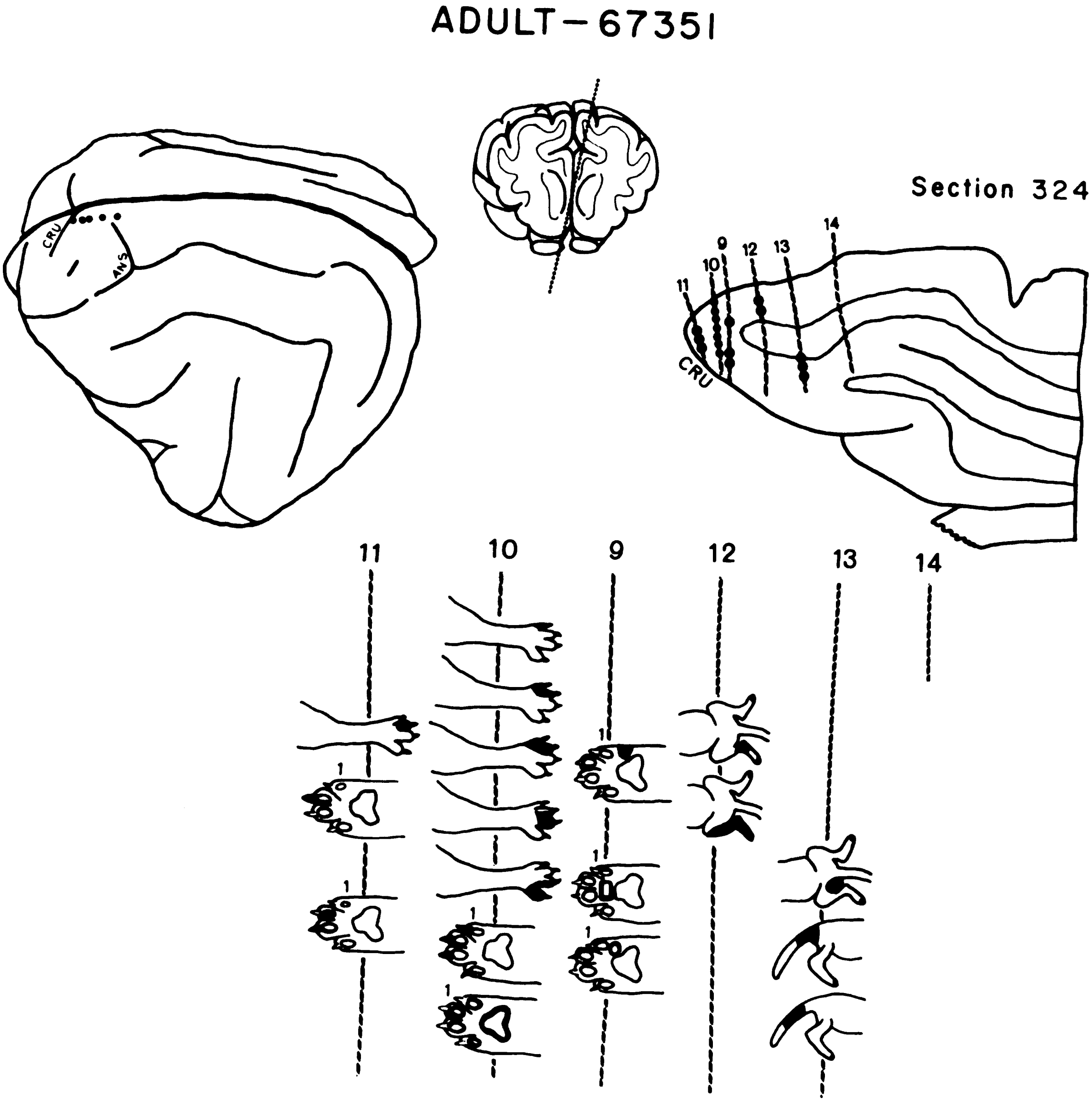

ADULT-67351
CRU
ANS
Section 324
14
9
12
13
10
11
CRU
11
10
9
12
13
14
1
1
1
1
1
1
1

Figure 5

Figure 6A. Organization of projections from hind limb, trunk and tail - Adult

Receptive fields found in one row of electrode penetrations down the medial bank of the posterior sigmoid gyrus of an adult cat are shown. Top left: Tracing of left neocortex from this preparation showing points at which the electrode entered the cortex. Top right: Tracing of a parasagittal section through the numbered electrode tracks showing their course through the cortex and the approximate depths at which peripheral stimulation evoked a neural response (dots and solid diamonds). Solid diamonds are at points where small "marking" lesions were made to facilitate histological identification and localization. The peripheral receptive fields evoking a response within each electrode penetration are shown below. The order of the figurines corresponds to the order of responsive points in the section tracing. Blackened areas on the figurines depict receptive fields in which cutaneous stimulation evoked a response while heavily outlined area (puncture 17) indicates where deeper pressure was necessary. ANS = ansate sulcus; COR = coronal sulcus; CRU = cruciate sulcus. Punctures 14 - 19 were made at 1.0 mm intervals.

Note: The rump, tail and trunk representations are located posterior and ventral to projections from the distal portions of the leg. Distal portions of the tail are represented ventral to the rump and proximal tail projections. Responsive area extends rostrally up to the posterior bank of the cruciate sulcus.

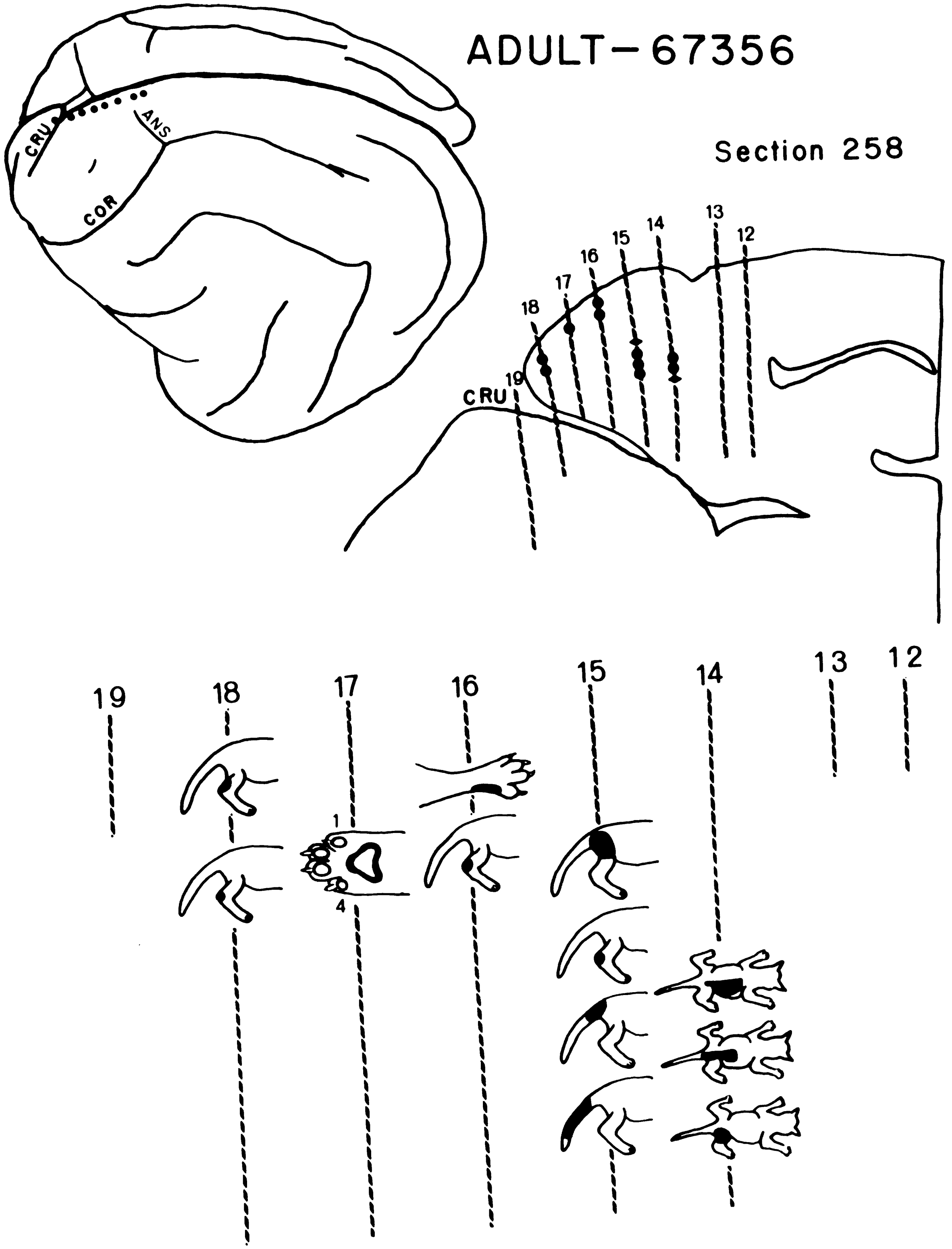

ADULT-67356
Section 258
CRU
ANS
COR
13
12
14
15
16
17
18
19
CRU
19
18
17
16
15
14
13
12
1
4

Figure 6A

Figure 6B. Photomicrograph of section traced in figure 6A. Shows parts of electrode tracks 14 - 19 (Arrows). Thionin stain: approximately X11.

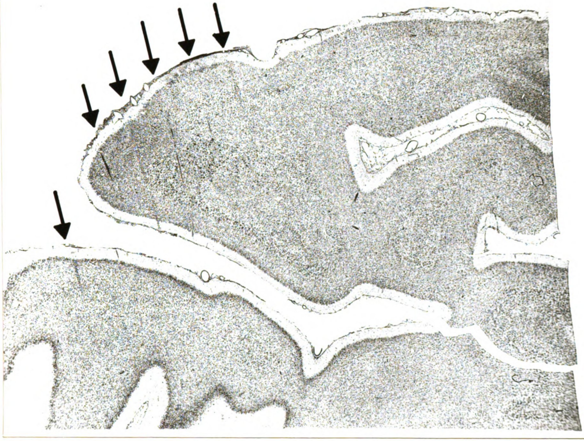


Figure 6B

Figure 7. Organization of projections from hind limb and rump - Newborn

Receptive fields found in one row of electrode penetrations near the medial edge of the posterior sigmoid gyrus of a newborn kitten are shown. Top left: Tracing of left neocortex from this preparation showing points at which electrode entered the cortex. Top middle: Schematic view of brain cut transversely through the posterior sigmoid gyrus. Dotted line shows approximate angle at which parasagittal section was cut. Top right: Tracing of parasagittal section through the numbered electrode tracks showing their course through the cortex and the approximate depths at which peripheral stimulation evoked a neural response (dots). The peripheral receptive fields evoking a response within each electrode penetration are shown below. The order of the figurines corresponds to the order of responsive points in the section tracing. Blackened areas on the figurines depict receptive fields in which cutaneous stimulation was effective. ANS = ansate sulcus; COR = coronal sulcus; CRU = cruciate sulcus; LAT = lateral sulcus; SS = suprasylvian sulcus. Punctures 6, 2, 3 and 4 were made a 1 mm intervals.

Note: As in the adult, the digit representation is found in the posterior lip of the cruciate sulcus. Distal portions of the leg are represented rostral to more proximal portions. Dorsal rump projects to the buried dorsal bank of the cruciate sulcus.

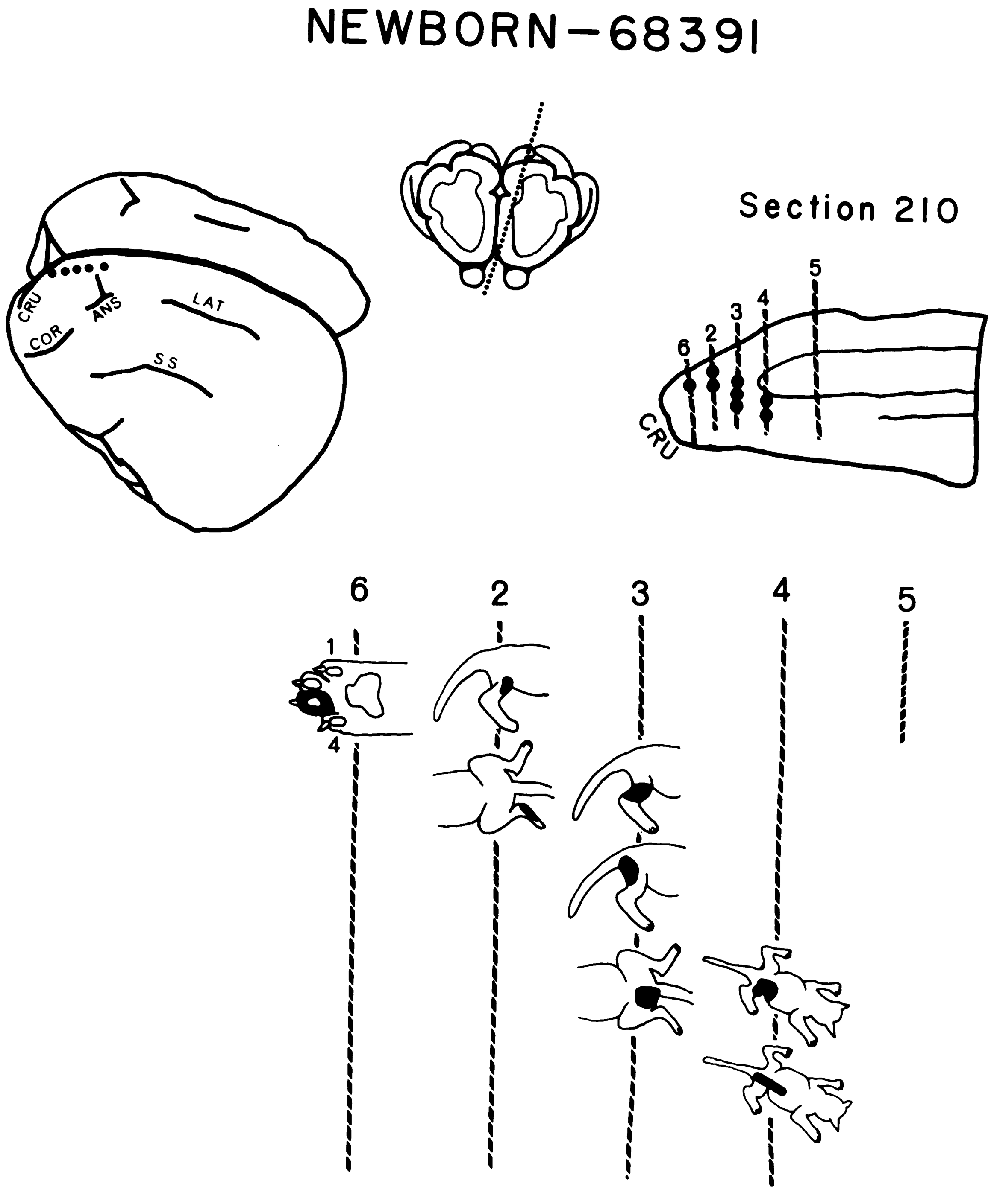

NEWBORN-68391
CRU
COR
ANS
LAT
SS
Section 210
5
4
3
2
6
CRU
6
2
3
4
5
1
4

Figure 7

Figure 8. Organization of projections from hind limb, trunk and tail - Newborn

Receptive fields found in rows of electrode tracks near the medial edge of the posterior sigmoid gyrus of two newborn kittens are shown. Top left for each animal: Tracing of left neocortex showing points at which electrode entered the brain. Top right for each animal: Tracing of parasagittal section through the numbered electrode tracks showing their course through the cortex and the approximate depths at which peripheral stimulation evoked a neural response (dots). The peripheral receptive fields evoking a response within each electrode penetration are shown below. The order of the figurines corresponds to the order of responsive points in the section tracing. Blackened areas on the figurines depict receptive fields in which cutaneous stimulation was effective. ANS = ansate sulcus; COR = coronal sulcus; CRU = cruciate sulcus; LAT = lateral sulcus; ML = medial longitudinal fissure; SS = suprasylvian sulcus. Punctures were spaced at 1 mm intervals.

Note: As in the adults the rump, tail and trunk representations are located posterior to projections from the foot. As the electrode is advanced through the cortex just posterior to the foot representation, the thigh is represented furthest dorsal with the haunch, proximal tail and distal tail represented progressively further ventral. The responsive area extends rostrally up to the posterior bank of the cruciate sulcus.

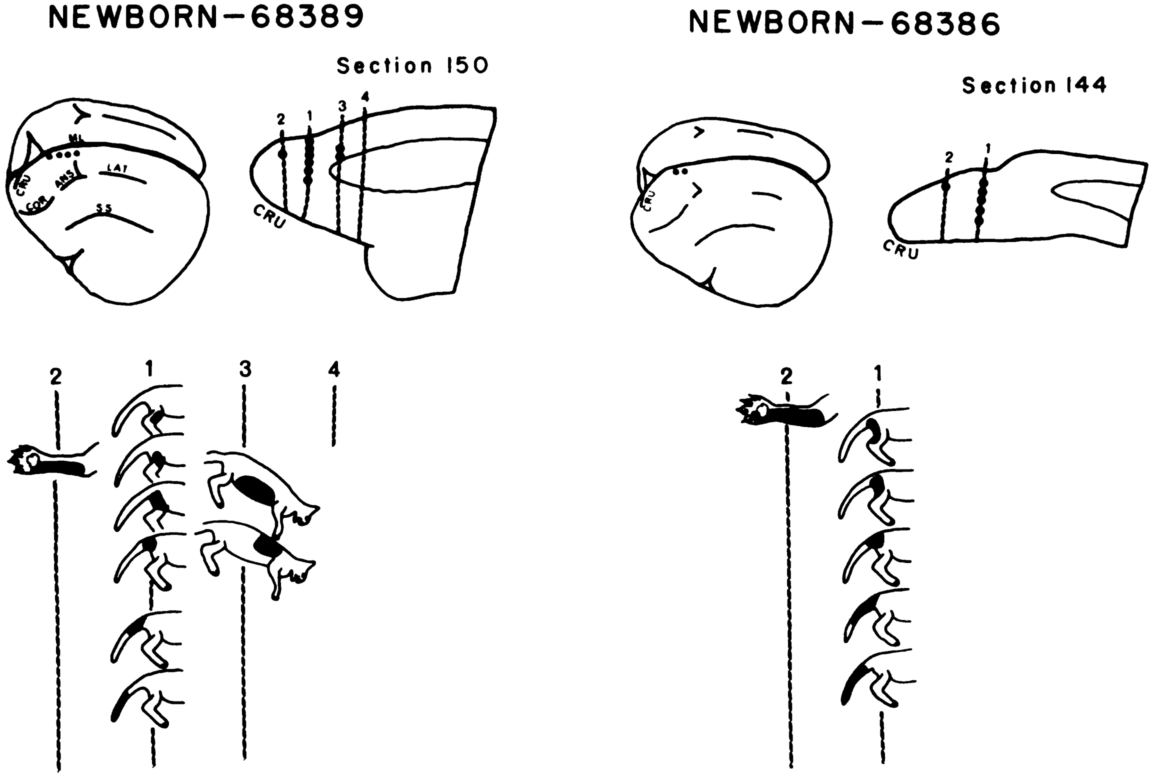

NEWBORN-68389
Section 150
ML
CRU
COR
ANS
LAT
SS
2
1
3
4
CRU
2
1
3
4
NEWBORN-68386
Section 144
CRU
2
1
CRU
2
1

Figure 8

Figure 9. Surface maps of lateral aspects of posterior sigmoid gyrus.

At the top are tracings of the left neocortex of an adult cat and a newborn kitten, with the area shown in the expanded tracings (below) outlined. Below: The points where the electrode entered the cortex are represented by open and closed circles on the brain tracing from each preparation. Closed circles indicate that a response to peripheral stimulation was found within 1.5 mm of the surface in the adult preparation or 1.0 mm of the surface in the newborn preparations. Open circles indicate that either no responsive points were found or that the electrode was below these depths when unit activity could be driven by peripheral stimulation. All of these points were histologically verified.

The peripheral receptive fields and their organization are shown to the right of each brain tracing. Only the first receptive field encountered in each penetration is shown. The blackened areas on the figurines indicate that cutaneous stimulation evoked the neural response while heavily outlined receptive fields indicate that stimulation of deeper tissues was necessary. Open circles correspond to the position of open circles on brain tracings. The approximate position of sulci are indicated on figurine maps by heavy lines. ANS = ansate sulcus; COR = coronal sulcus; CRU = cruciate sulcus; D = postcruciate dimple.

Note: Projections from proximal portion of the foreleg are represented medial to those from more distal surfaces in both the newborn and adult cats. Receptive fields on distal surfaces are generally smaller than those on more proximal surfaces. Receptive fields requiring deep stimulation are generally found anterior to "cutaneous" receptive fields. 'Disjunctive' receptive fields (see text p. 19) in the adult cortex are generally found anterior to the 'simple' receptive fields. Projections from the forepaw of the adult cat extend to the lateral tip of the gyrus while in the newborn (68326) unresponsive points were found at the lateral tip of the gyrus. The receptive field found just medial to these "nil" punctures was probably from MsI cortex rather than SmI, since it only responded to very deep stimulation and was found relatively far anterior in the posterior sigmoid gyrus.

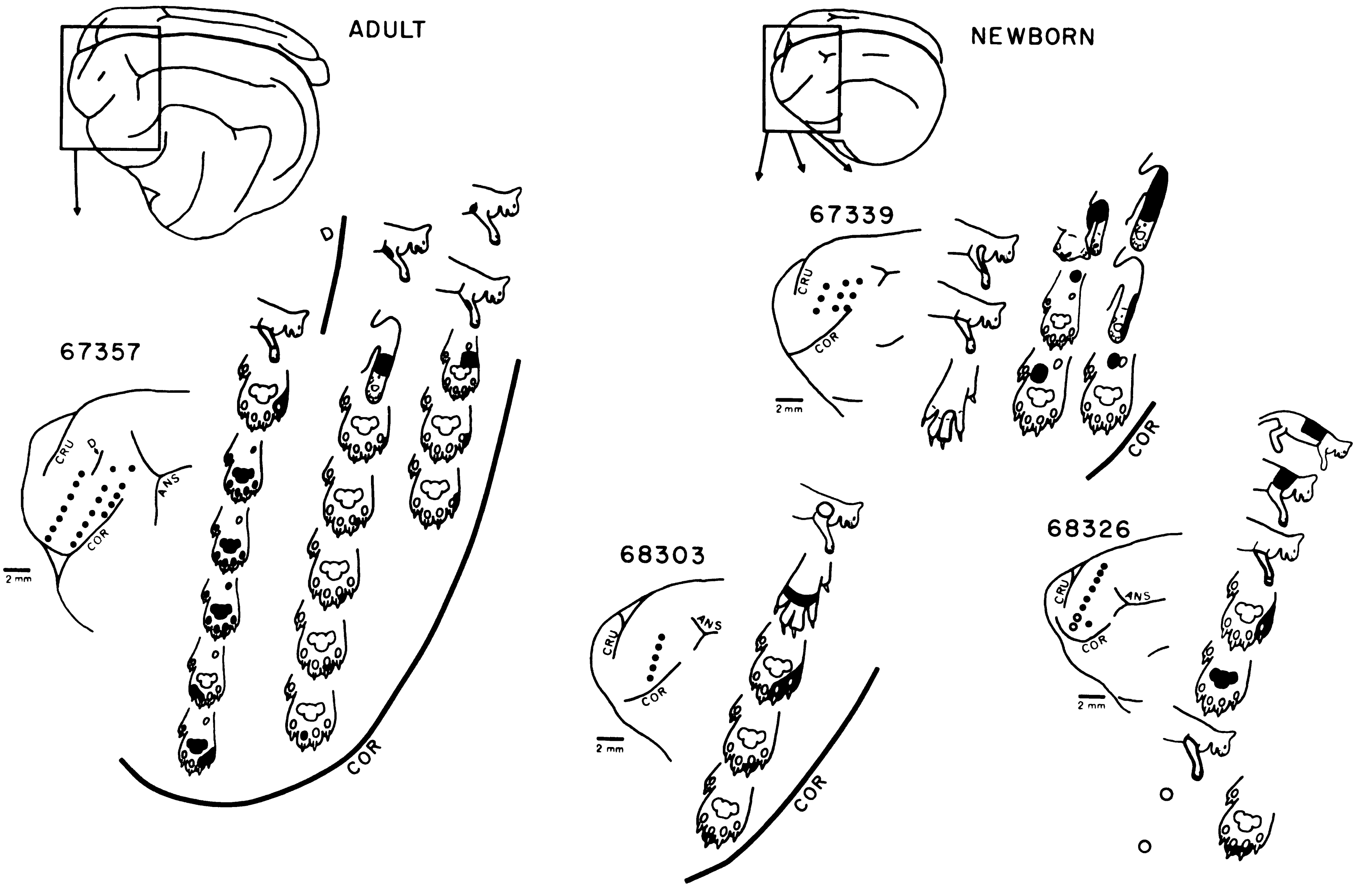

ADULT
NEWBORN
67357
CRU
D
ANS
COR
2 mm
D
COR
67339
CRU
COR
2 mm
COR
68303
CRU
ANS
COR
2 mm
COR
68326
CRU
ANS
COR
2 mm

Figure 9

Figure 10A. Organization of projections from forepaw - Newborn.

Receptive fields found in one row of electrode penetration through the forepaw digit representation of the lateral aspect of the posterior sigmoid gyrus of newborn kitten are shown. Electrode penetrations on the posterior sigmoid gyrus 1 mm lateral to these (open circles) were unresponsive. Top left: Tracing of left neocortex from this preparation showing points at which the electrode entered the cortex. Top middle: Schematic view of brain cut transversely through the posterior sigmoid gyrus. Dotted line show approximate angle at which parasagittal section was cut. Top right: Tracing of parasagittal section through the numbered electrode tracks showing their course through the cortex and the approximate depths at which peripheral stimulation evoked a neural response (dots). Open diamonds are at points where small "marking" lesions were made to facilitate histological identification. The peripheral receptive fields which evoked a response within each electrode penetration are shown below. The order of the figurines corresponds to the order of responsive points in the section tracing. Blackened areas on the figurines depict receptive fields in which cutaneous stimulation evoked a response. Ac = anterior commissure; Cd = caudate nucleus; COR = coronal sulcus; CRU = cruciate sulcus; PS = presylvian sulcus; SS = suprasylvian sulcus. Punctures are spaced at 0.5 mm intervals.

Note: As the electrode is moved from anterior to posterior on the posterior sigmoid gyrus (tracks 5, 10, 11, 12, 13, 14), receptive fields progressively nearer to digit 1 are encountered. Lesion made in track 14, just above a response to digit 2 stimulation (open diamond), indicates that the bottom of the coronal sulcus separates the forepaw representation from the head representation. Tracks 14 - 16 indicate that dorsal surfaces of the head are represented posterior to ventral surfaces.

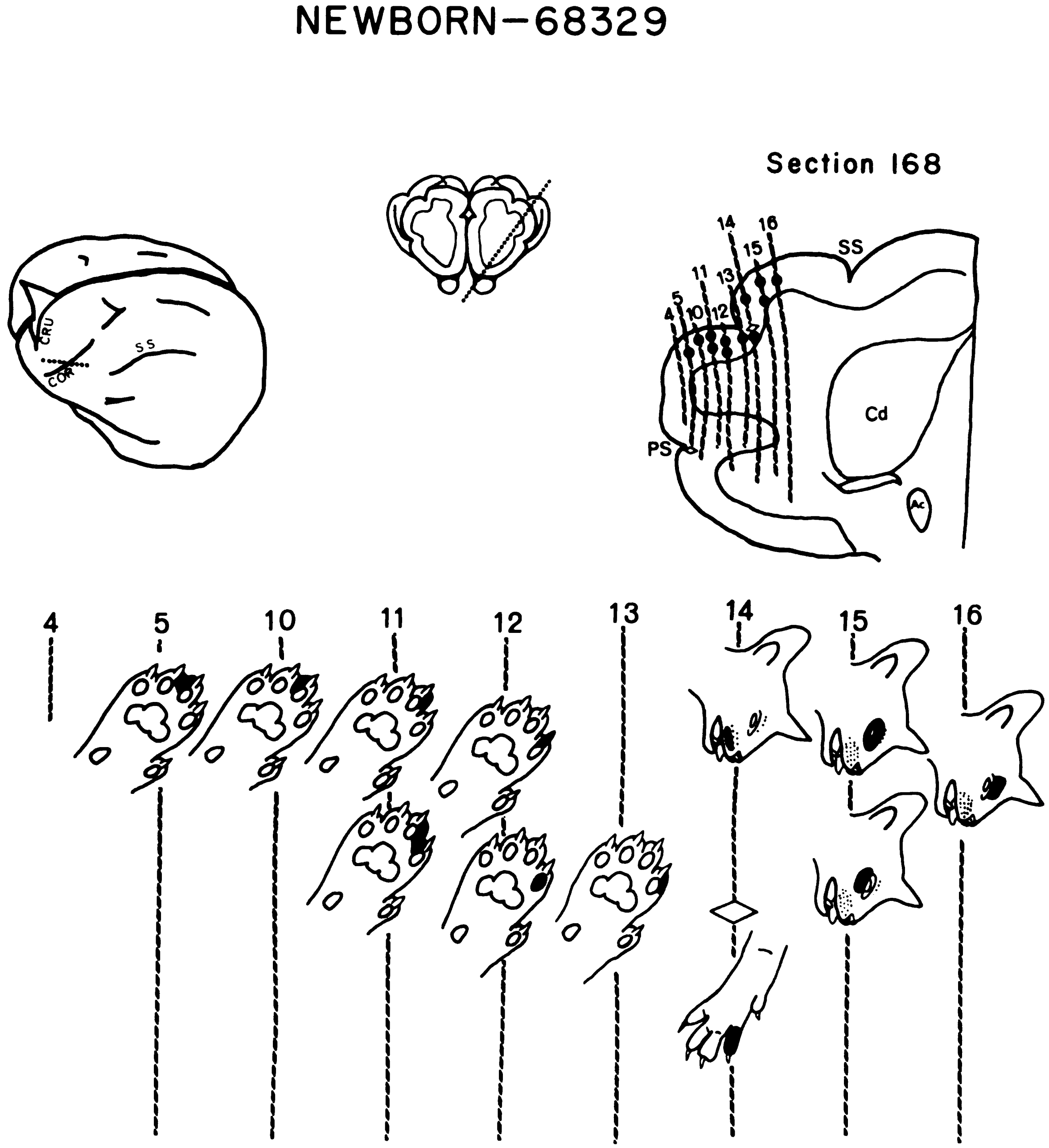

NEWBORN-68329
Section 168
CRU
COR
SS
14
16
15
SS
11
13
5
4
10
12
Cd
PS
Ac
4
5
10
11
12
13
14
15
16

Figure 10A

Figure 10B. Top: Thionin-stained section shown in figure 10A. Parts of electrode tracks 5 and 10 - 15 can be seen. Bottom: Sagittal section through the posterior sigmoid gyrus of an adult cat at approximately the same level as the section above. Both sections approximately X12.

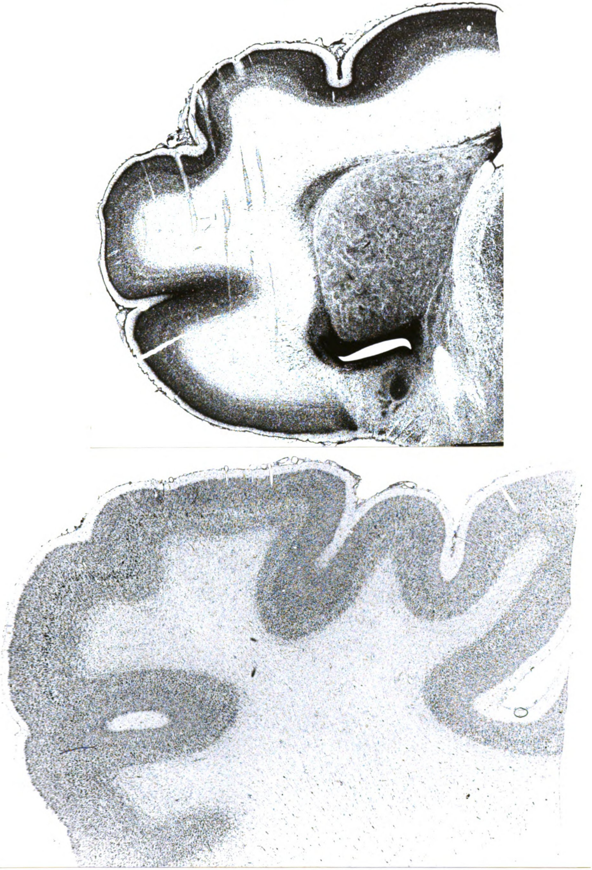


Figure 10B

Figure 10C. Top: Hematoxylin-stained section adjacent to that shown in fig. 10A and 10B (top). Bottom: Hematoxylin-stained section adjacent to the one shown in fig. 10B (bottom). Note that in the newborn brain (top), the stain is taken up by the cell bodies and the cortical radiations are unmyelinated, while in the adult brain myelinated fibers are stained. Both sections approximately X12.

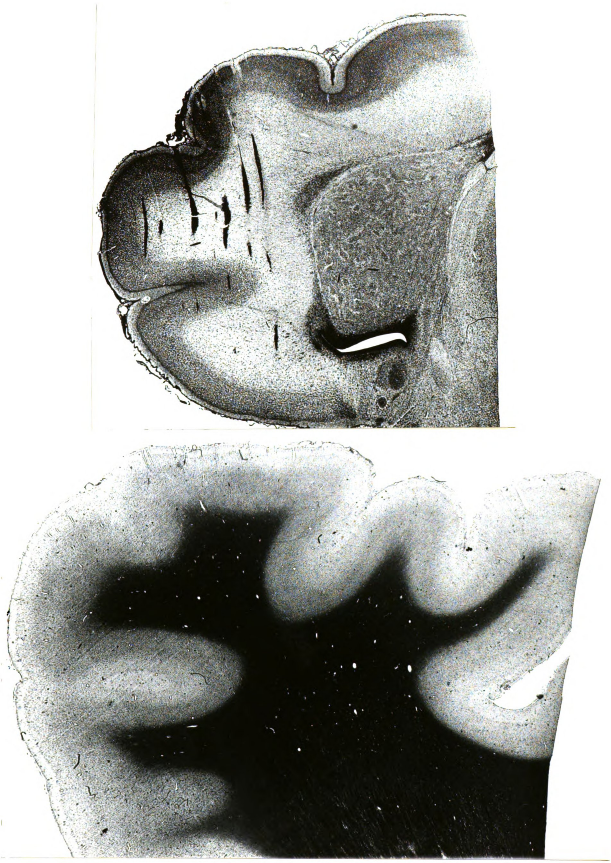


Figure 10C

Figure 11. Organization of projections from forepaw - Newborn

Receptive fields found in one row of electrode oenetrations through the forepaw digit representation cn the lateral aspect of the posterior sigmoid gyrus of another newborn kitten are shown. This row of punctures is slightly medial of those shown in figure 10A. Top left: Tracing of left neocortex from this preparation showing the points at which the electrode entered the cortex. Top middle: Schematic view of brain cut transversely through the posterior sigmoid gyrus. Dotted line shows approximate angle at which parasagittal section was cut. Top right: Tracing of parasagittal section through the numbered electrode tracks showing their course through the cortex and the approximate depths at which peripheral stimulation evoked a neural response (dots). Open diamonds are at points where small "marking" lesions were made to facilitate histological identification. The peripheral receptive fields evoking a response within each electrode penetration are shown below. The order of the figurines corresponds to the order of responsive points in the section tracing. Blackened areas on the figurines depict receptive fields in which cutaneous stimulation evoked a response while heavily outlined area (puncture 14) indicates where deeper presure was necessary. COR = coronal sulcus; CRU = cruciate culcus; Cd = caudate nucleus; Ac = anterior commissure. Punctures 10 - 16 are at 0.5 mm intervals.

Note: As the electrode moves from anterior to posterior on the posterior sigmoid gyrus (tracks 10 - 15), receptive fields progress from digit 5 (track 10) to digit 1 (tracks 14 and 15). The lesion in track 15 was made midway between the response from the neck (above diamond) and the response to the first digit (below diamond). The position of this lesion again indicates that the bottom of the coronal gyrus separates the forepaw and head representations.

NEWBORN-68326

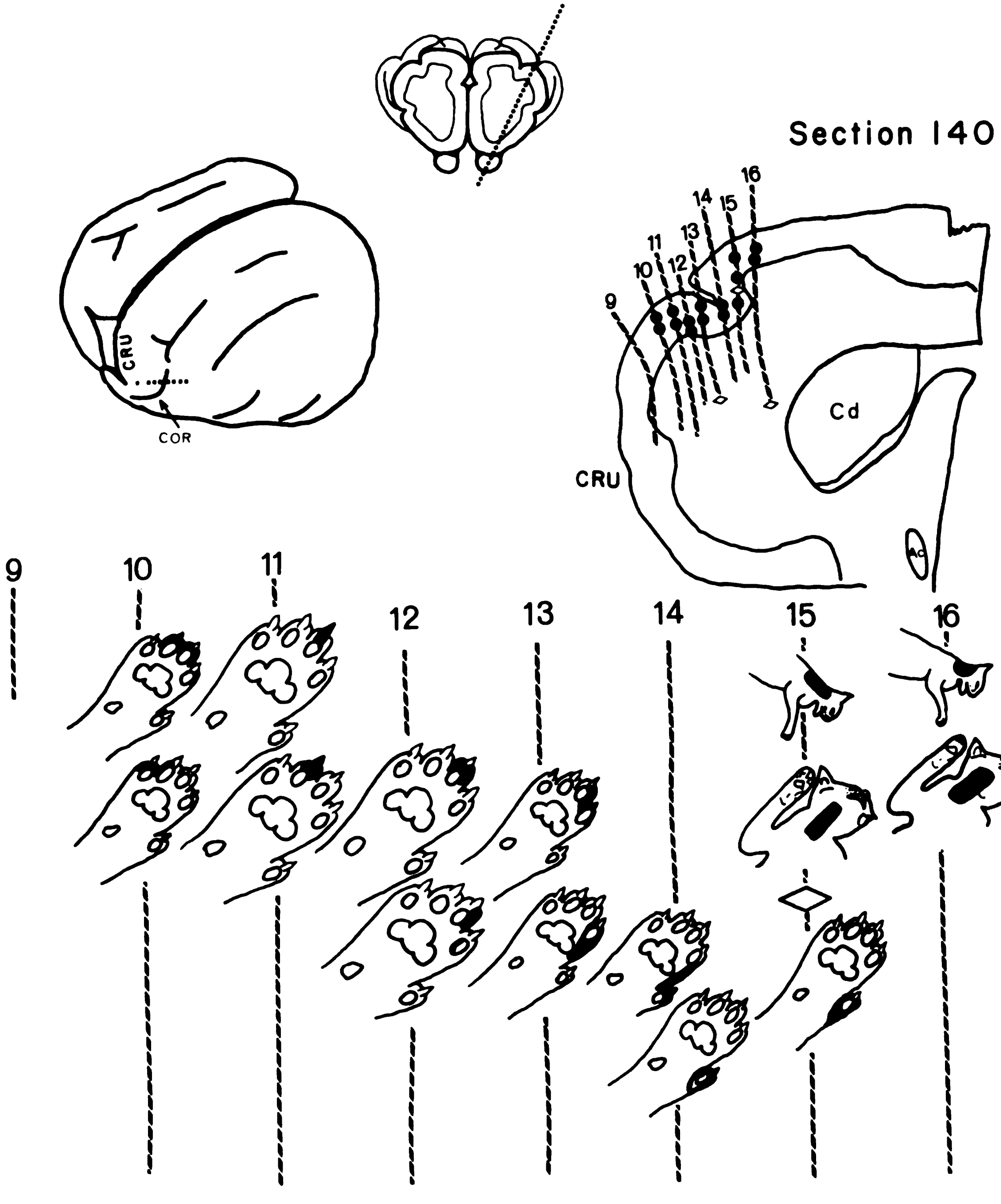


Figure 11

Figure 12. Organization of projections from forepaw - Adult.

Receptive fields found in one row of electrode penetrations through the forepaw digit representation on the lateral aspect of the posterior sigmoid gyrus of an adult cat are shown. Top left: Tracing of left neocortex from this preparation showing the points at which the electrode entered the cortex. Top middle: Schematic view of brain cut transversely through the posterior sigmoid gyrus. Dotted line shows approximate angle at which parasagittal section was cut. Top right: Tracing of a parasagittal section through the numbered electrode tracks showing their course through the cortex and the approximate depths at which peripheral stimulation evoked a neural response (dots and solid diamond). The solid diamond (puncture 23) indicates that a small "marking" lesion was made at a point responsive to peripheral stimulation while the open diamond (puncture 20) indicates that the lesion was made at an unresponsive point. The peripheral receptive fields evoking a response within each electrode penetration are shown below. The order of figurines corresponds to the order of responsive points in the section tracing. Blackened areas on the figurines depict receptive fields in which cutaneous stimulation evoked a response while heavily outlined area (puncture 23) indicates where deeper pressure was necessary. ANS = ansate sulcus; COR = coronal sulcus; CRU = cruciate sulcus; PS = presylvian sulcus; SS = suprasylvian sulcus. Punctures 20-24 were made at 1 mm intervals.

Note: In punctures 20 and 26, as the electrode tip approached the fundus of the coronal sulcus, receptive fields moved from digit 5 to digit 1. Digit 1 representation was found at the bottom of the sulcus. Posterior to the medial tip of the coronal sulcus, (puncture 27) projections from the foreleg above the wrist were encountered. Responses found in punctures 22, 23 and 24 may be part of the MsI forepaw representation. 'Disjunctive' receptive fields were found in puncture 22. In puncture 25, after the electrode was advanced through the coronal sulcus, projections from the ipsilateral side of the tongue were found in the anterior aspect of the coronal gyrus.

ADULT–68347

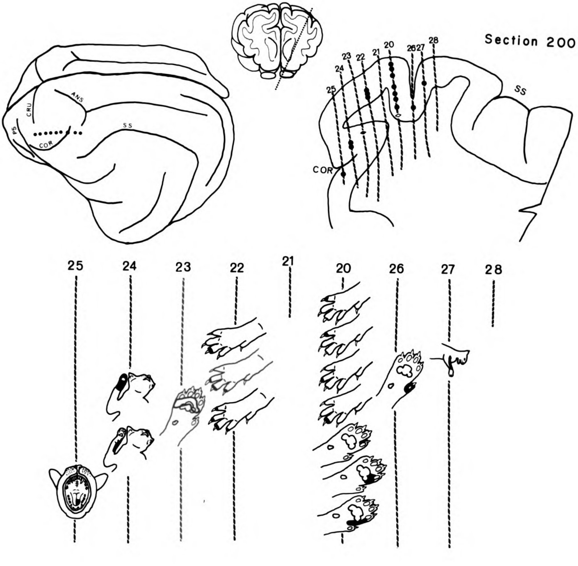


Figure 12

Figure 13. Organization of projections from forepaw and face Adult.

Receptive fields found in one row of electrode penetrations through the forepaw digit representation on the lateral tip of the posterior sigmoid gyrus on an adult cat. Top middle: Schematic view of brain cut transversely through the posterior sigmoid gyrus. Dotted line shows approximate angle at which parasagittal section was cut. Top left: Tracing of neocortex from this preparation showing points at which the electrode entered the cortex. Top right: Tracing of parasagittal section through the numbered electrode tracks showing their course through the cortex and the approximate depths at which peripheral stimulation evoked a neural response (dots). Open diamonds are at points where small "marking" lesions were made to facilitate histological identification and localization. The peripheral receptive fields evoking a response within each electrode penetration are shown below. The order of the figurines corresponds to the order of responsive points in the section tracing. Blackened area on the figurines depict receptive fields in which cutaneous stimulation evoked a response. COR = coronal sulsus; CRU = cruciate sulcus; PS = presylvian sulcus; SS = suprasylvian sulcus. Punctures 29 - 32 were made at 1 mm intervals.

Note: Projections from digits 3 and 4 extend to the lateral tip of the gyrus. Projections from the 4th digit (puncture 32) were found anterior to those from digit 3 (punctures 29, 30, 31). Whenever the electrode entered the coronal gyrus (puncture 34 and bottom of punctures 29 - 32), projections from the face are encountered, indicating that the coronal sulcus separates forepaw and face representations. As the electrode is moved progressively anterior in the coronal gyrus, receptive fields approach the animal's midline and finally only ipsilateral projections are found (puncture 32).

ADULT-68347

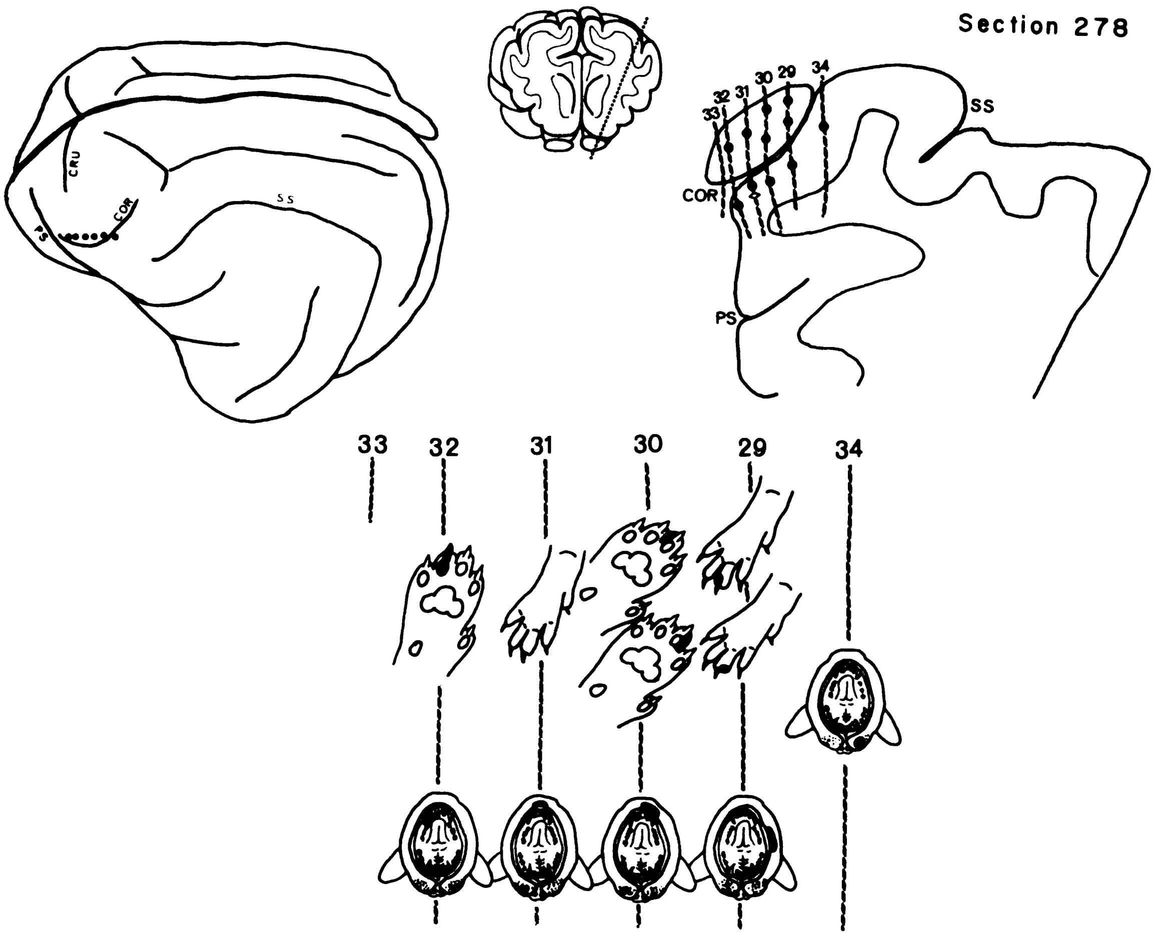


Figure 13

Figure 14. Surface maps of coronal gyrus.

At the top are tracings of the left neocortex of an adult cat and newborn kitten, with the areas shown in the expanded tracings (below) outlined. Below: The points where the electrode entered the cortex are represented by open and closed circles on the brain tracing from each preparation. Closed circles indicate that a response to peripheral stimulation was found within 1.5 mm of the surface in the adult preparation or 1.0 mm of the surface in the newborn preparation. Open circles indicate that either no responsive points were found or that the electrode was below these depths when unit activity could be driven by peripheral stimulation. All of these points were histologically verified.

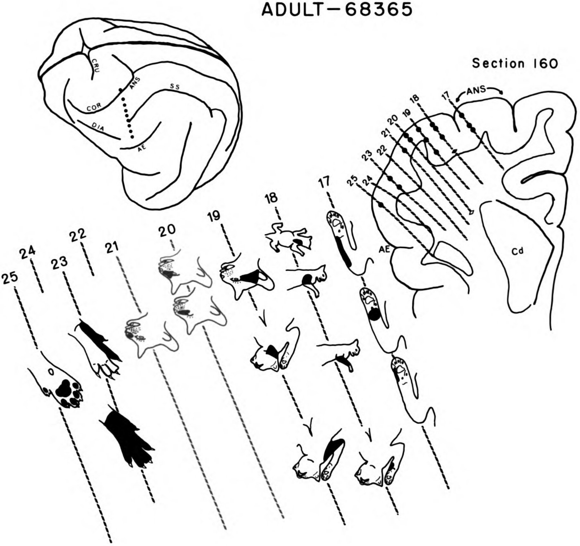
The peripheral receptive fields and their organization are shown to the right of each brain tracing. Only the first receptive field encountered in each penetration is shown. The blackened areas on the figurines indicate that cutaneous stimulation evoked the neural response while heavily outlined receptive fields indicate that stimulation of deeper tissues was necessary. Open circles correspond to the position of open circles on the brain tracings. The approximate position of sulci are indicated on figurine maps by heavy lines. COR = coronal sulcus; DIA = diagonal sulcus; SS = suprasylvian sulcus.

Note: Anterior surfaces of the face are represented rostral and ventral of the more posterior surfaces. Dorsal surfaces of the head project to more ventrolateral cortical loci than ventral surfaces. Projections from the forepaw, found near the suprasylvian sulcus in the adult are in SII cortex.

Figure 15. Organization of projections from head - Adult

Receptive fields found in one row of electrode penetrations through the coronal and anterior ectosylvian gyri of an adult cat are shown. Top left: Tracing of left neocortex from this preparation showing points at which the electrode entered the cortex. Right: Tracing of coronal section through the numbered electrode tracks showing their course through the cortex and the approximate depths at which peripheral stimulation evoked a neural response (dots and solid diamond). The solid diamond (puncture 18) indicated that a small "marking" lesion was made at a point responsive to peripheral stimulation while the open diamond (puncture 20) indicates that the lesion was made at an unresponsive point. The peripheral receptive fields evoking a response within each electrode penetration are shown below the brain tracing. Blackened areas on the figurines depict receptive fields in which cutaneous stimulation evoked a response. AE = anterior ectosylvian sulcus; ANS = ansate sulcus; Cd = caudate nucleus; COR = coronal sulcus; CRU = cruciate sulcus; DIA = diagonal sulcus; SS = suprasylvian sulcus. Punctures 18 - 25 were made at 1 mm intervals.

Note: At this level, the representation of the head does not include projections from the lips or mouth. Projections from the foreleg are found on both sides of the ansate sulcus. Projections from dorsal surfaces of the head are seen in punctures 19, 20 and 21. Rostral portions of the head are represented lateral in the cortex of more caudal portions. As the electrode is moved into the anterior ectosylvian sulcus, SII forepaw projections are encountered (punctures 23 and 25).



ADULT—68365
CRU
ANS
SS
COR
DIA
AE
Section 160
17
ANS
18
19
20
21
22
23
24
25
AE
Cd
17
18
19
20
21
22
23
24
25

Figure 15

Figure 16A. Organization of projections from face - Adult

Receptive fields found in a row of electrode penetrations through the coronal gyrus, 2 mm anterior to those in the previous figure (15) are shown. Top left: Tracing of left neocortex showing points at which electrode entered the cortex. Right: Tracing of coronal section showing electrode tracks and the approximate depths of responsive points (dots and solid diamonds). The solid diamonds mark points at which small "marking" lesions were made. The peripheral receptive fields are shown below the brain tracing. The order of figurines corresponds to the order of responsive points in the section tracing. Blackened areas depict receptive fields in which cutaneous stimulation evoked a response while heavily outlined areas indicate where deeper pressure was necessary. ANS = ansate sulcus; Cd = caudate nucleus; COR = coronal sulcus; DIA = diagonal sulcus. Punctures 11, 10, 9, 13 and 14 were made at 1 mm intervals.

Note: At this level of the coronal gyrus, projections from the vibrissae dominate. In puncture 9 the bottom two loci were found in the bank of the coronal sulcus and were responsive to vibrissae stimulation while the top response received projections from the dorsal surface of the nose. Anterior and dorsal surfaces (puncture 9) tend to be represented in the cortex lateral of more posterior and ventral surfaces (puncture 11). The coronal sulcus appears to separate forepaw projections from the face representation. SII forepaw projections are found near the suprasylvian sulcus (punctures 13 and 14).

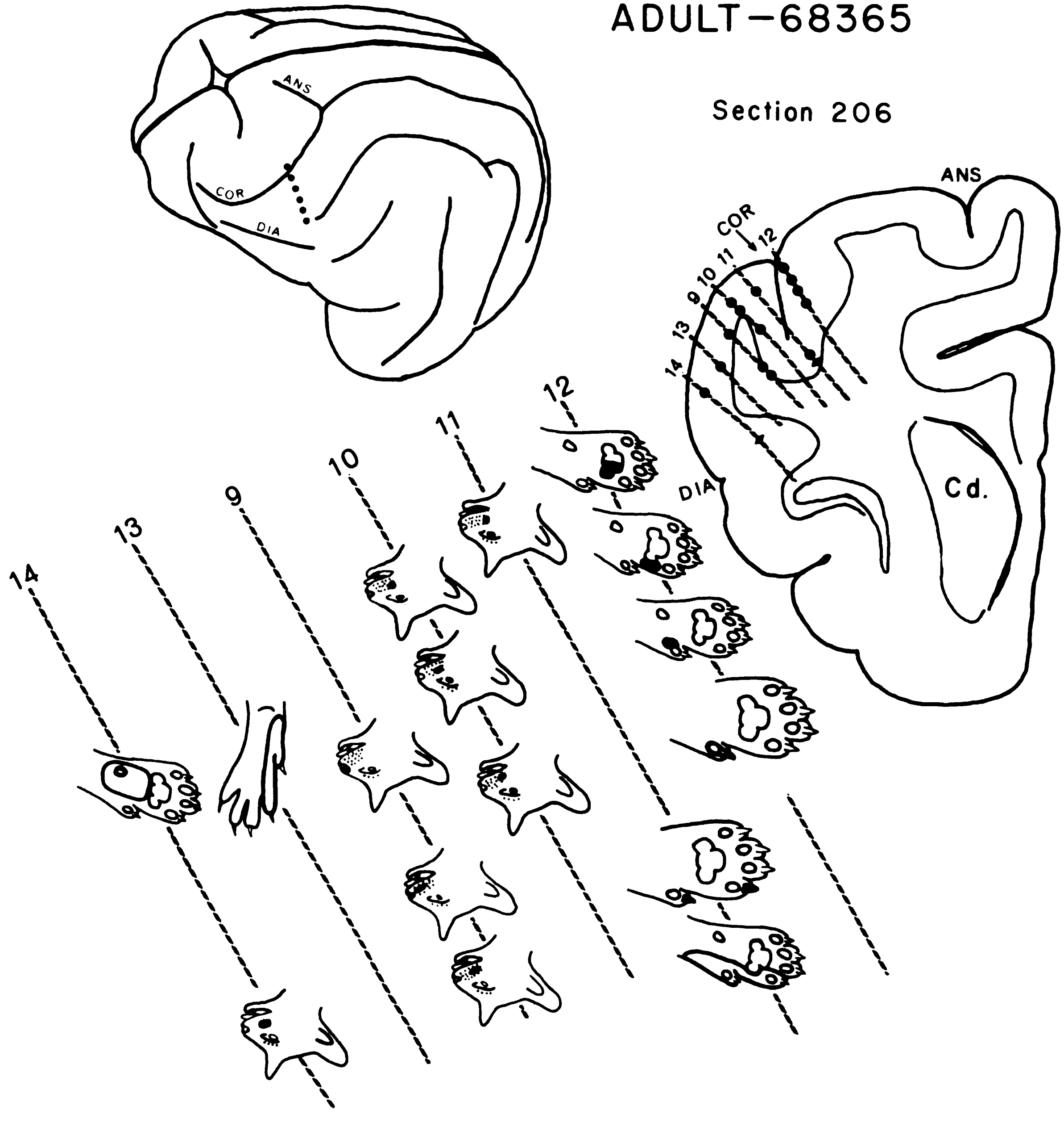

ADULT-68365
Section 206
ANS
COR
DIA
ANS
COR
12
11
10
9
13
14
DIA
Cd.
12
11
10
9
13
14

Figure 16A

Figure 16B. Photomicrograph of section adjacent to the one shown in figure 16A. Arrow points toward lesion in puncture 11. Hematoxylin stain: approximately X8.

Figure 16B

Figure 17. **Organization of projections from mouth and face - Adult**

Receptive fields found in a row of electrode penetrations through the coronal gyrus 5 mm anterior to those in the previous figure (16) are shown. Top left: Tracing of left neocortex showing points at which electrode entered the cortex. Right: Tracing of coronal section showing electrode tracks and the approximate depths of responsive points (dots and solid diamonds). The diamonds mark points at which small "marking" lesions were made. The peripheral receptive fields are shown below the brain tracing. The order of figurines corresponds to the order of responsive points in the section tracing. Blackened areas depict receptive fields in which cutaneous stimulation evoked a neural response while heavily outlined area (puncture 31) indicates where pressure stimulation of deeper tissues was necessary. ANS = ansate sulcus; COR = coronal sulcus; DIA = diagonal sulcus; ML = medial longitudinal fissure; RF = rhinal fissure. Punctures 31 and 32 were made at 1 mm apart.

Note: At this level projections from inside the mouth and anterior portions of the face are found. The lower jaw representation "spills over" onto the medial bank of the coronal sulcus (puncture 33). In puncture 16, as the electrode was advanced through the cortex, receptive fields moved progressively further ipsilateral. A lesion made at the site of the last responsive point indicates that the face representation is bounded by the diagonal sulcus ventrolaterally.

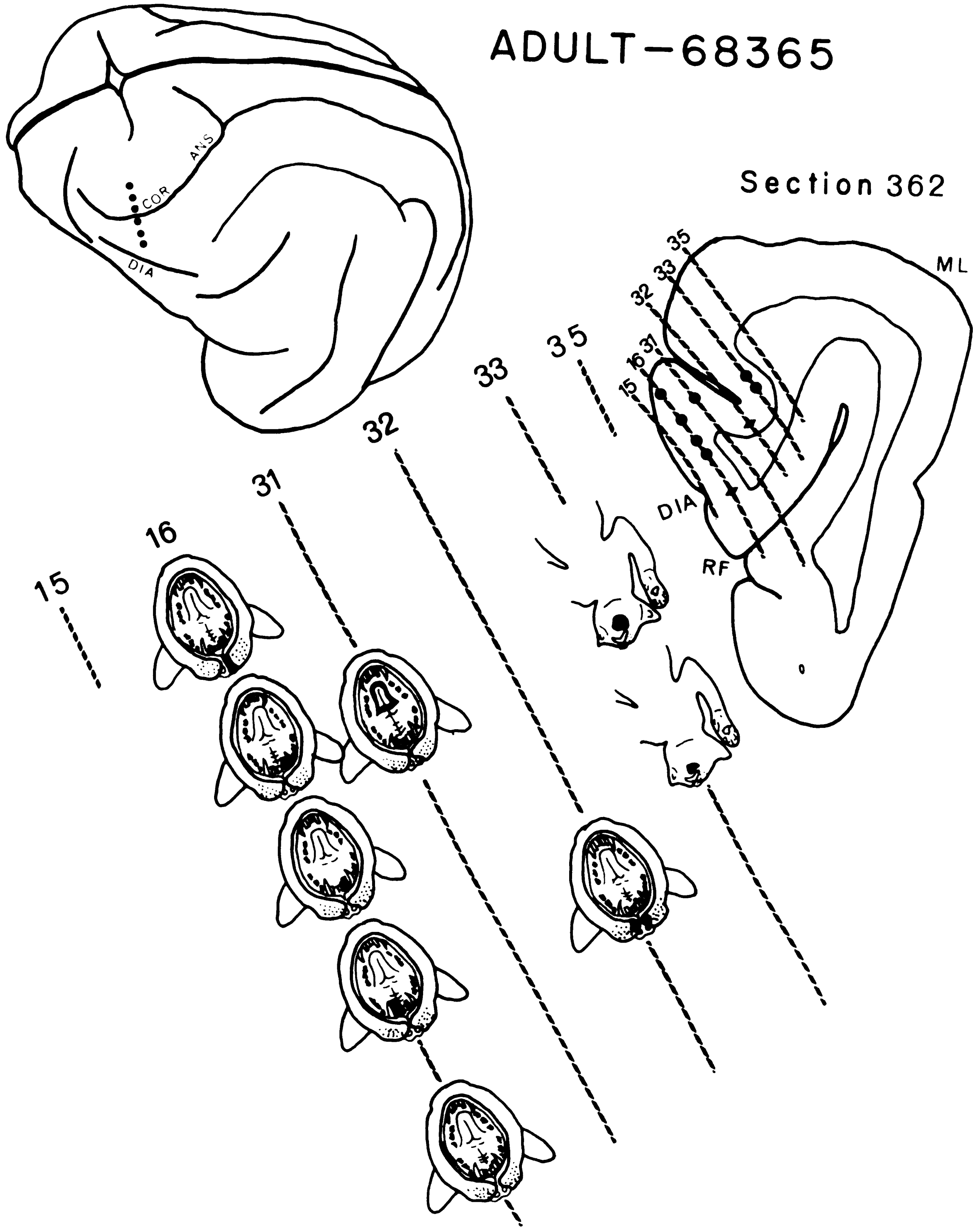

ADULT-68365
Section 362
ANS
COR
DIA
ML
35
33
32
31
16
15
DIA
RF
35
33
32
31
16
15

Figure 17

Figure 18. Organization of projections from head and neck - Newborn

Receptive fields found in one row of electrode penetrations down the caudal bank of the coronal sulcus of a newborn kitten are shown. Top left: Tracing of left neocortex from this preparation showing the points at which the electrode entered the cortex (dots). Dotted line shows the angle at which the section was cut. Section at right was cut through the caudal bank of the coronal sulcus which is reflected by the widened cellular area in the vicinity of the electrode tracks. The approximate depths at which peripheral stimulation evoked a neural response are shown along each electrode track. The peripheral receptive fields evoking a response within each electrode penetration are shown below. The order of figurines corresponds to the order of responsive points in the section tracing. Blackened areas of the figurines depict receptive fields in which cutaneous stimulation evoked the response. COR = coronal sulcus; ML = medial longitudinal fissure. Punctures were spaced a 1 mm intervals.

Note: Projections from the neck are medial of those from the lips. Mandibular portions of the head are found deeper in the sulcus than maxillary portions (punctures 2, 3 and 4). Projections from the forepaw (puncture 2) were found in the fundus of the coronal sulcus, but not more dorsally in the caudal bank.

NEWBORN—68300

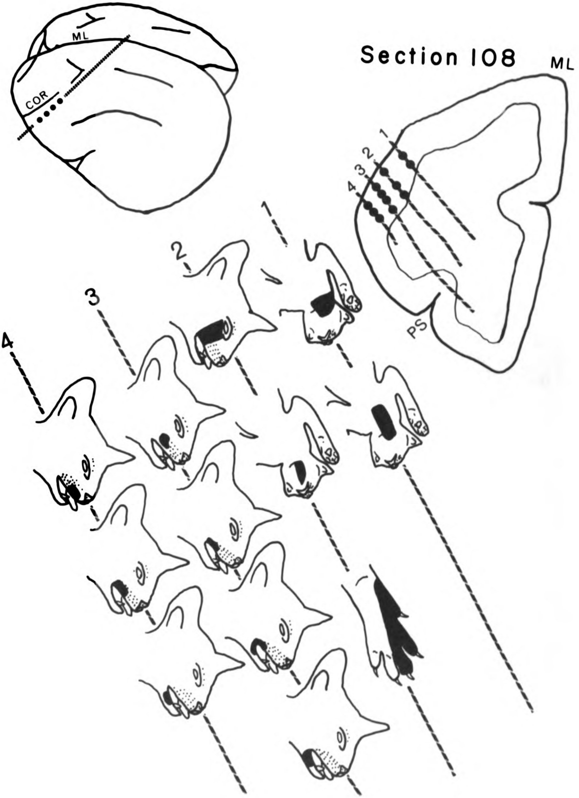


Figure 18

Figure 19. Organization of projections from face - Newborn

Receptive fields found in one row of electrode penetrations through the coronal sulcus of a newborn kitten are shown. Top left: Tracing of left neocortex from this preparation showing points at which the electrode entered the cortex. Top middle: Schematic view of brain cut transversely throught the posterior sigmoid gyrus. Dotted line shows approximate angle at which parasagittal section was cut. Top right: Tracing of a parasagittal section through the numbered electrode tracks showing their course through the cortex and the approximate depths at which peripheral stimulation evoked a neural response (dots). The peripheral receptive fields evoking a response within each electrode penetration are shown below. The order of the figurines corresponds to the order of responsive points in the section tracing. Blackened areas of the figurines depict receptive fields in which cutaneous stimulation evoked a response. AE = anterior ectosylvian sulcus; COR = coronal sulcus; CRU = cruciate sulcus; RF = rhinal fissure; SS = suprasylvian sulcus. Punctures were made at 1 mm intervals.

Note: Mandibular portions of the face are represented anterior of the maxillary surfaces. The response to forepaw stimulation (puncture 11) was found in the SII cortical area. The SmI forepaw representation does not appear to extend this far lateral on the posterior sigmoid gyrus since punctures 13 and 14 were unresponsive.

NEWBORN-68302

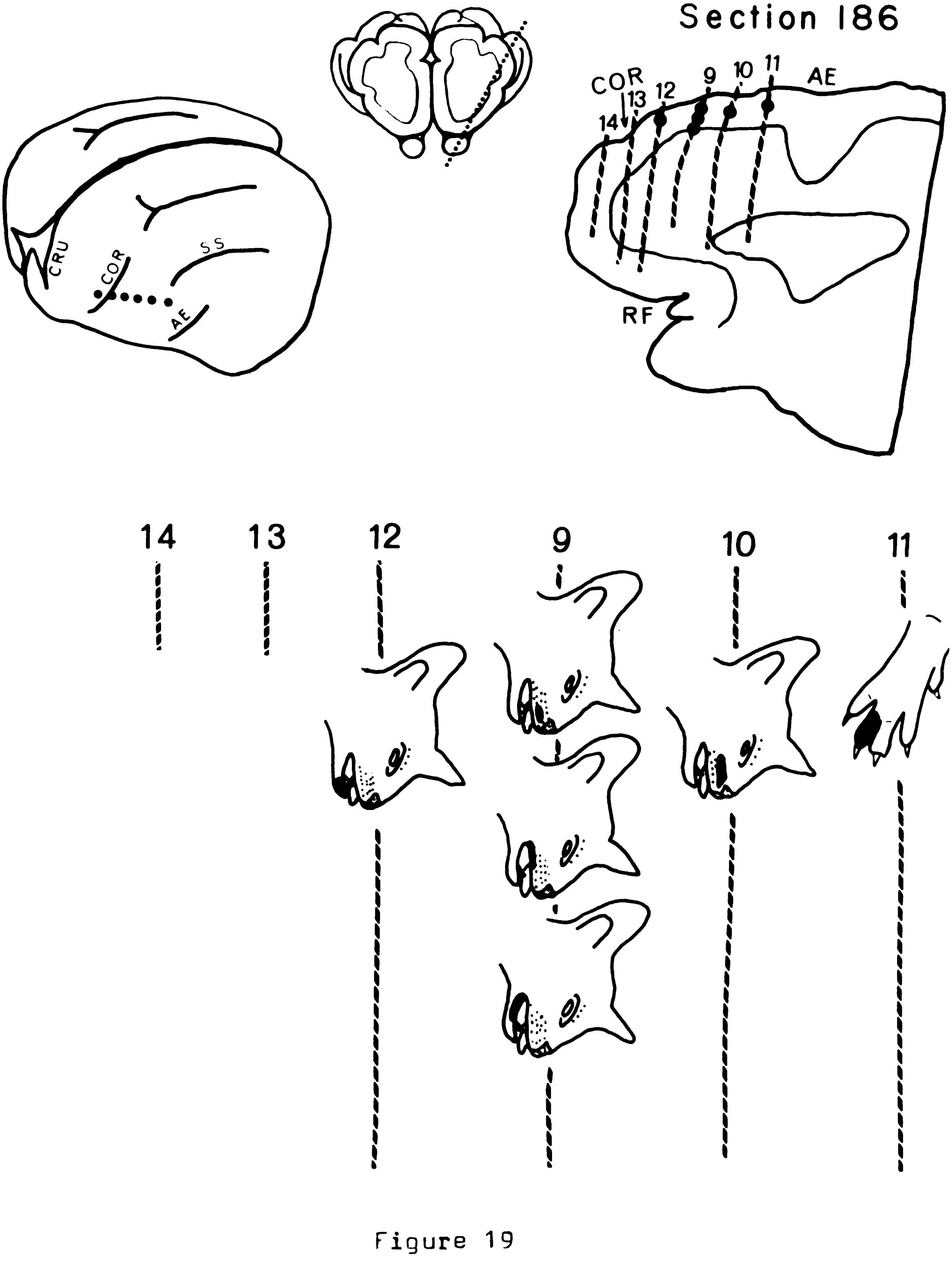


Figure 19

Figure 20. Organization of projections from face - Newborn

Receptive fields found in a row of electrode penetrations through the coronal gyrus 1 mm lateral to those in the previous figure (19) are shown. Top left: Tracing of left neocortex showing points at which the electrode entered the cortex. Top middle: Schematic view of brain cut transversely through the posterior sigmoid gyrus. Dotted line shows approximate angle at which parasagittal section was cut. Top right: Tracing of parasagittal section through the numbered electrode tracks showing the approximate depths of responsive points (dots). The peripheral receptive fields are shown below with the order of figurines corresponding to the order of responsive points in the section tracing. Blackened areas correspond to "cutaneous receptive fields". AE = anterior ectosylvian sulcus; COR = coronal sulcus; SS = suprasylvian sulcus. Punctures were made at 1 mm intervals.

Note: Projections seen in these punctures are from the most anterior portions of the face and inside the mouth. Comparing receptive fields in this figure with those in the previous figure indicates that projections from anterior portions of the face are found lateral to those from more posterior surfaces. This figure also indicates that mandibular surfaces are found rostral to maxillary surfaces. Puncture 2 shows that as the electrode is advanced through the rostral tip of the coronal gyrus, receptive fields become progressively more ipsilateral.

NEWBORN–68302

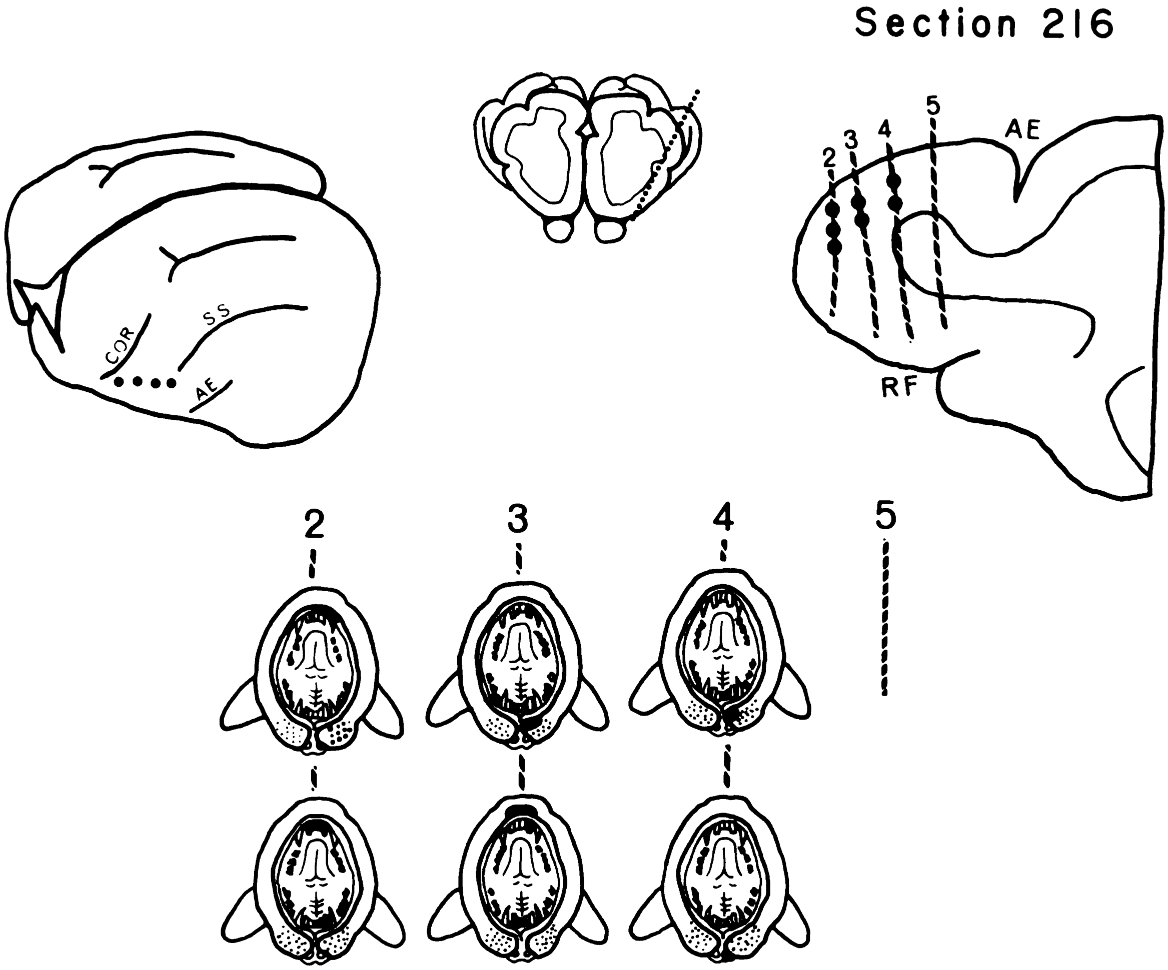


Figure 20

Figure 21. Latencies from electrical stimulation of the body regions to evoked unit activity in the SmI cortex of newborn and adult cats.

The shaded regions on the body figurine (top) designate the general body part in which stimulation yielded the latencies shown below. Solid points and bars indicate respectively the mean latency and ranges found in this study. Open points and bars indicate means and ranges found in other studies on the adult cat using similar procedures. D-D from Darian-Smith, Isbister, Mok and Yokota (1966); M-M from Mountcastle, Davies and Berman (1957); L-L from Levitt and Levitt (1968). Darian-Smith et al. (1966) included latencies to SII cortex as well as SmI.

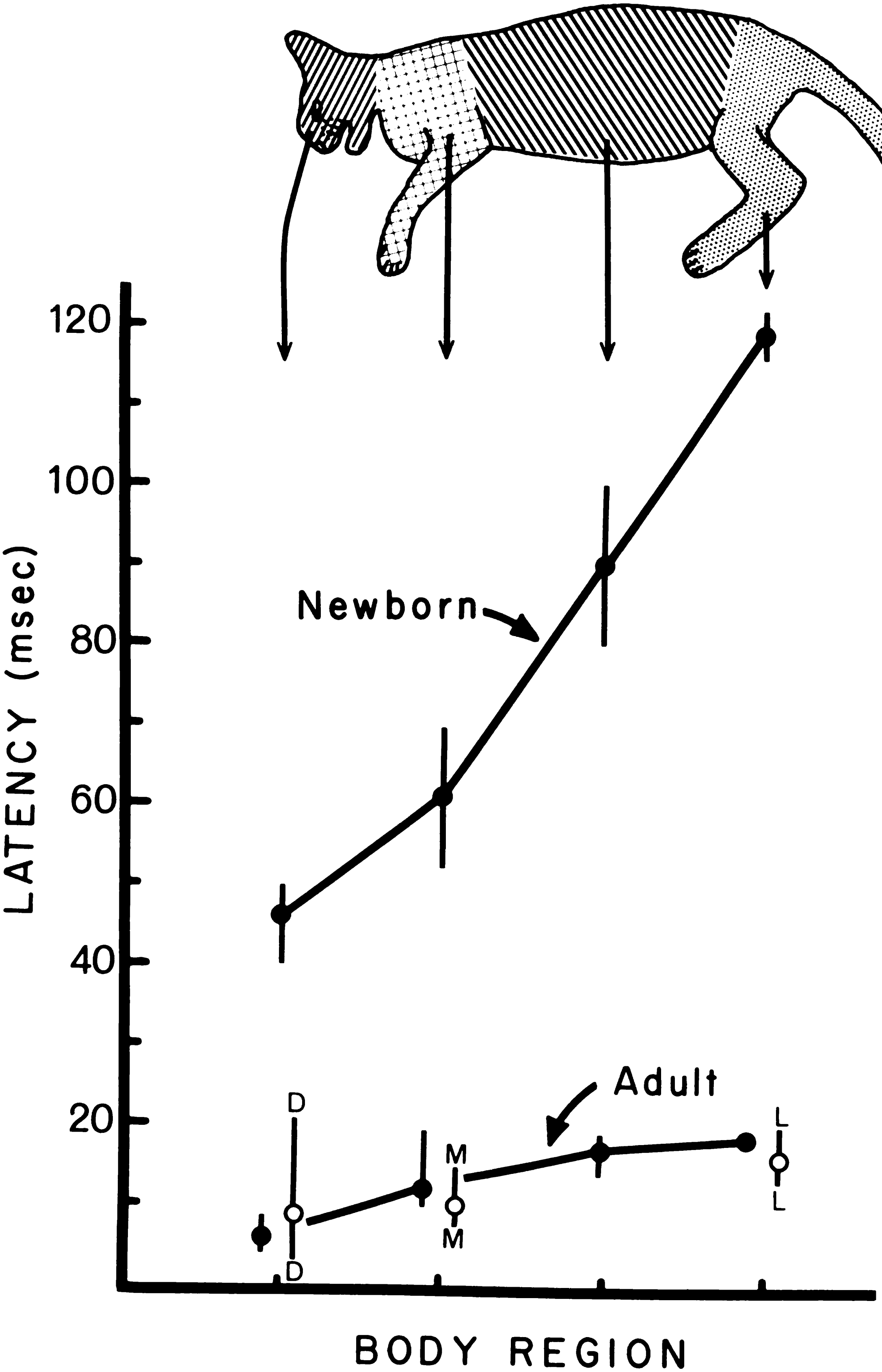

120
100
80
60
40
20
LATENCY (msec)
Newborn
Adult
D
D
M
M
L
L
BODY REGION

Figure 21

Figure 22. Surface map from the coronal and anterior ectosylvian gyri of a newborn cat.

Top: Tracing of the left neocortex from this preparation with the area shown in the expanded tracing (below) outlined. Below: The points where the electrode entered the cortex are represented by open and closed circles on the expanded tracing. Closed circles indicate that a response to peripheral stimulation was found within 1.0 mm of the surface. Open circles indicate no responsive points within the penetration. All of these points were histologically verified. The peripheral receptive fields and their organization are shown at the right. Only the first receptive field encountered in each penetration is shown. Blackened areas on the figurines indicate that cutaneous stimulation evoked the neural response while heavily outlined receptive fields indicate that a deeper pressure stimulus was necessary. Open circles on the figurine map correspond to the open circles on the brain tracing. The approximate position of sulci is indicated by the heavy lines on the figurine map. AE = anterior ectosylvian sulcus; ANS = ansate sulcus; COR = coronal sulcus; SS = suprasylvian sulcus.

Note: Projections to SII cortex are responsive to mechanical stimulation and lie in the anterior ectosylvian gyrus. Projections to SII cortex come from both the ipsilateral (i) and contralateral body surfaces. Projections to SII respond predominantly to "deep" stimulation, and tend to have larger receptive fields than those found in SmI cortex. On the coronal gyrus, projections from the face indicate that anterior portions of the head are represented lateroventral in the cortex than more posterior surfaces, and that dorsal surfaces of the head are represented caudal to the projections from more ventral portions.

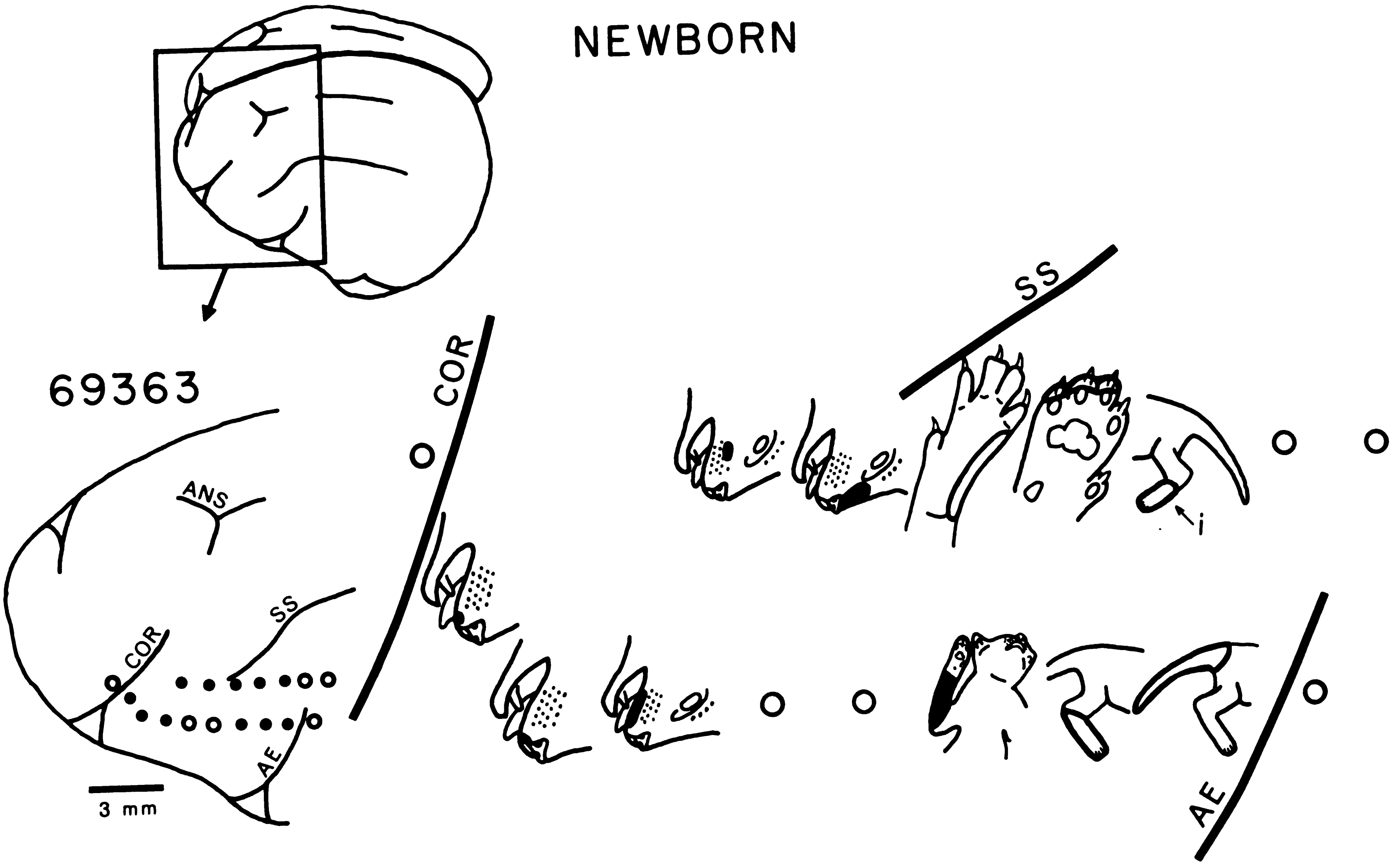


Figure 22

Figure 23. Photomicrograph of thionin-stained section through the posterior sigmoid gyrus near the coronal sulcus of a newborn kitten. Notice the radial columns of densely packed cells. Approximately X 155.

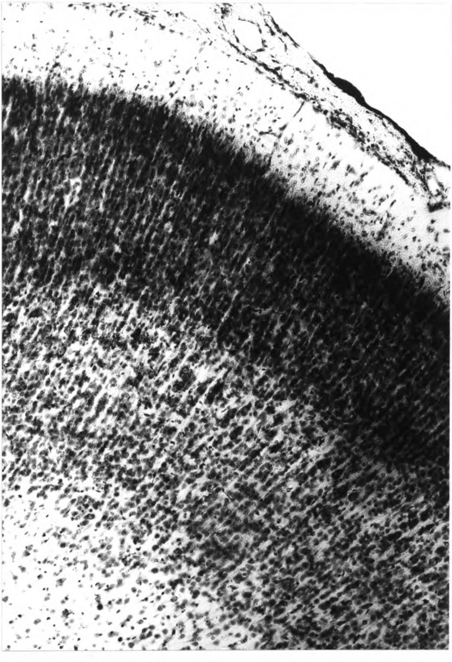


Figure 23