

A Comparison of Somatotopic Organization in Sensory Neocortex of Newborn Kittens and Adult Cats

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ABSTRACT 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 intensity 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 cortices included: (a) receptive fields of projections to SmI cortex were of fixed, local field type; (b) projections to SmII cortex responded to mechanical stimulation of the receptors; (c) ipsilateral as well as contralateral body surfaces were represented in SmII 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 Msl 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.

Differences between neurons in the neocortex of newborn kittens and adult cats have been demonstrated anatomically (Purpura, '61; Voeller, Pappas and Purpura, '63; Scheibel and Scheibel, '64), histochemically (Himwich, Pscheidt and Schweigerdt, '67) and physiologically by Purpura, Shofer and Scarff ('65). How-

ever, concomitant changes in the coding of sensory information by these neurons have not been demonstrated.

Since the work of Scherrer and Oeconomo ('54) it has been known that when an

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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, '67). These studies show that afferent connections to the neocortex of the newborn kitten are present at birth. 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, '60; Grossman, '55; Rose, Adrian and Santibanez, '57; Rose and Lindsley, '68). These studies indicate the age at which an afferent system is electrophysiologically functional from the receptor to the cortical projection area. In the above studies, however, 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.

A fundamental form of sensory coding is the phenomenon of "receptotopic" organization found throughout vertebrate sensory systems (Thompson, '67). The somatotopic organization of projections to the cerebral cortex of the cat, first described by Adrian ('40) and Marshall, Woolsey and Bard ('41), provides a well known example of this phenomenon which appears to be one neural mechanism for determining 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?

Areas of the SmI cortex of newborn kittens (≤ 24 hours post-partum) and adult cats were electrophysiologically mapped using microelectrodes. Although SmI cortex of the adult cat appears to have been

mapped previously by several investigators and summary diagrams have appeared in numerous sources (Levitt and Levitt, '68; Rose and Mountcastle, '59; Thompson, '67; Woolsey, '58), neither a detailed description of the projection pattern nor figurine maps are available in the literature. Thus it was necessary to prepare detailed maps of SmI cortex in the adult cat for comparison with neonatal preparations. Due to the extensive utilization of the cat in nervous system research, representative figurine maps from both adults and neonates have been included in this report.

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, SmII and Msl cortical fields of the newborn kitten.

MATERIALS AND METHODS

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 gm which is well within the normal range of birth weights reported by Hall and Pierce ('34).

The surgical procedures used for the two groups were quite similar. Preanesthetic injections of promazine hydrochloride (Sparine) (newborns, 0.15 mg; adults, 6 mg/kg) and atropine sulfate (newborns, 0.005 mg; adults, 0.1 mg/kg) were administered. General anesthesia was induced by an intraperitoneal injection of pentobarbital sodium (Nembutal) (newborns, 18 mg/kg; adults, 28 mg/kg); the body hair was clipped; a tracheal cannula 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 (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 intraperitoneal injections of 5% dextrose every three to four hours.

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.

Electrophysiological responses were recorded through glass insulated tungsten microelectrodes (Hubel, '57; Baldwin, Frenk and Lettvin, '65). The tungsten electrodes recorded potentials with respect to a stainless steel wire inserted through an exposed muscle of the head or neck. 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.

Mapping procedures

The mapping procedures closely resemble the "micro-electrode method of electrophysiological mapping" described by Welker and Johnson ('65) and Johnson, Welker and Pubols ('68). The microelectrode is lowered to the pial surface under visual inspection. 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 $\times 10$). The electrode was then

slowly driven through the cortex with a mechanical microdrive. Every 100–200 μ 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 wooden rod 1 to 2 mm in diameter, a glass dissecting rod less than 1 mm in diameter, small lengths of Intra-medec polyethylene tubing of various sizes, or a cat vibrissa, were used as stimulating agents to delineate each peripheral receptive field. Electrical stimulation was used to determine response latencies.

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 glabrous 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.

In order to map the cortex systematically, successive electrode punctures were made in rows with penetrations 0.5 mm or 1.0 mm apart and the rows 1–2 mm apart. The anterior-posterior and medial-lateral position 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 μ a 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.

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 methods.

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 could 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.

Response latencies

The latency of cortical responses to peripheral electrical stimulation was determined in one adult cat and several newborn kittens. The latency was measured from the shock artifact to the first unit activity. The intensity of the shock was, in all cases, suprathreshold (usually $\times 10$) and the frequency of the shocks was varied between 0.1 cps and 10 cps. These

data were also recorded on tape for subsequent verification. 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 (Eckholm, '67).

RESULTS

Response characteristics

Samples of characteristic electrophysiological responses obtained from SmI cortex in adult and newborn cats are shown in figure 1. 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. 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 1 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, '57; Brooks, Rudomin and Slayman, '61). Huttenlocher ('67) noted a similar finding in the visual cortex of young cats.

Somatotopic organization

The organization of mechanoreceptive projections to SmI cortex was similar in the adult cats and newborn kittens. 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.

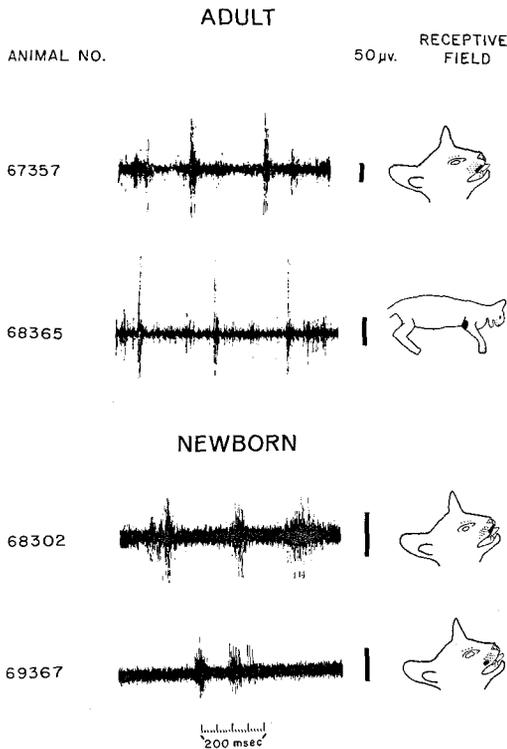


Fig. 1 Sample of unit-cluster responses recorded from SmI cortex of two adult cats (above) and two newborn kittens (below). Left to right: Animal number; sample of neural response; 50 μ V calibration; figurine showing the peripheral receptive field (blackened) effective for eliciting the activity. Bottom: 200 msec calibration with small dots at 10 msec intervals. All traces unretouched.

In this study it was found that all areas of the contralateral body surface are represented in the SmI cortex of kittens less than one day old and that these projections respond to light mechanical stimulation of the skin or hairs.

The somatotopic organization in each of these cortical regions is described in the following sections. The data shown are representative of what was found in each of the 30 preparations (table 1).

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. The surface maps

in figure 2 reflect the general organization of these projections. Further detail regarding somatotopic organization is shown in figures 8 and 9 for adult cats and figures 10 and 11 for newborn preparations.

1. 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 foot extend anteriorly up to the posterior bank of the cruciate sulcus.

2. Projections from the rump and tail are confined to the dorsomedial bank of the cruciate sulcus with those from the most distal areas of the tail lying ventral to more proximal surfaces.

3. In adult cats the organization of projections from the digits of the contralateral foot appeared quite variable. In some cases (e.g., fig. 8, puncture 10) a point-to-point correspondence with the organization of the body surface was observed which was in agreement with the diagram shown by Woolsey ('58), while other cats had projections from the digits posterior and medial to thigh and knee representations as well as near the cruciate sulcus (see fig. 2). Less variability was apparent in the newborn kitten.

4. Projections from the trunk are organized from medial to lateral on the posterior sigmoid gyrus, lying primarily between the postcruciate dimple and the bifurcation of the ansate sulcus.

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

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

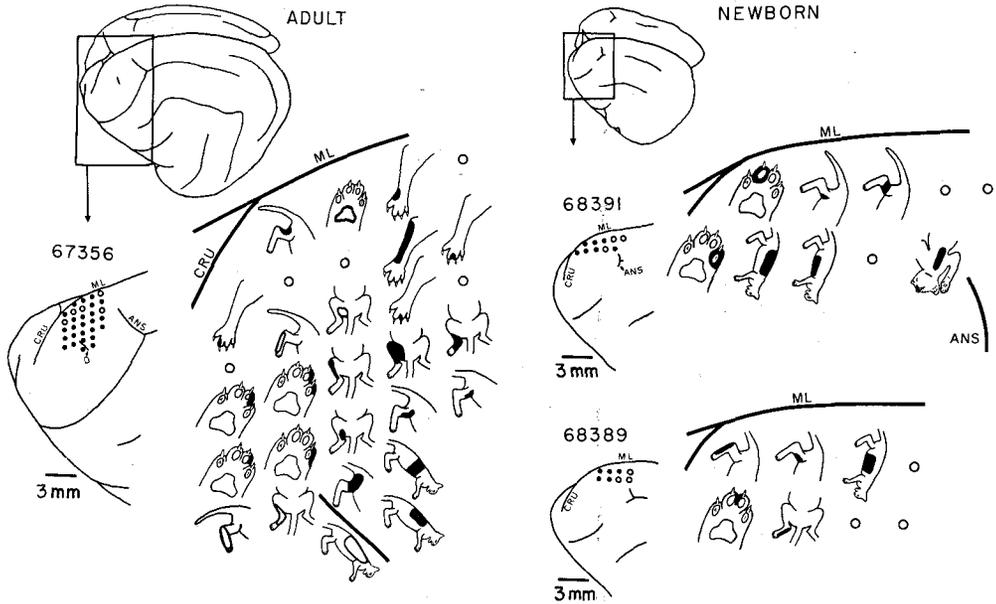


Fig. 2 Surface maps of medial aspect of posterior sigmoid gyrus. This and all succeeding surface maps are organized as follows: At the top are tracings of the left neocortex of an adult cat and newborn kitten, with the areas shown in the expanded tracings outlined. Below, the points where the electrode 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 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 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 tracings. 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, post-cruciate dimple; ML, medial longitudinal fissure.

Note that 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.

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. The surface maps in figure 3 reflect the general organization of these projections. Further detail is shown in figures 12 and 13 for adult cats and figures 14 and 15 for newborn preparations.

1. In both the newborn and adult cat, projections from the contralateral foreleg

and paw are continuous with the rostral trunk representation at the level of the bifurcation of the ansate sulcus, and extend lateroventrally toward the tip of the gyrus. Distal surfaces project to progressively more lateral areas of the cortex.

2. 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 while projections from digits 4, 3, 2

TABLE 3
Mapping experiments of forelimb
representation in Sml

Age	Preparations	Responsive punctures	Receptive fields
Newborn	11	72	102
Adult	13	134	280

and 1 are encountered progressively caudal and into the depths of the coronal sulcus (figs. 14, 15). 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 three to four per second. Responsive loci meeting all of

these criteria are defined as having "simple" receptive fields. In two newborn kittens the lateral boundary of the digit representation area was delineated. The row of electrode tracks shown in figure 14 constitutes this boundary. It should be noted that this area does not extend to the ventrolateral pole of the posterior sigmoid gyrus.

3. 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

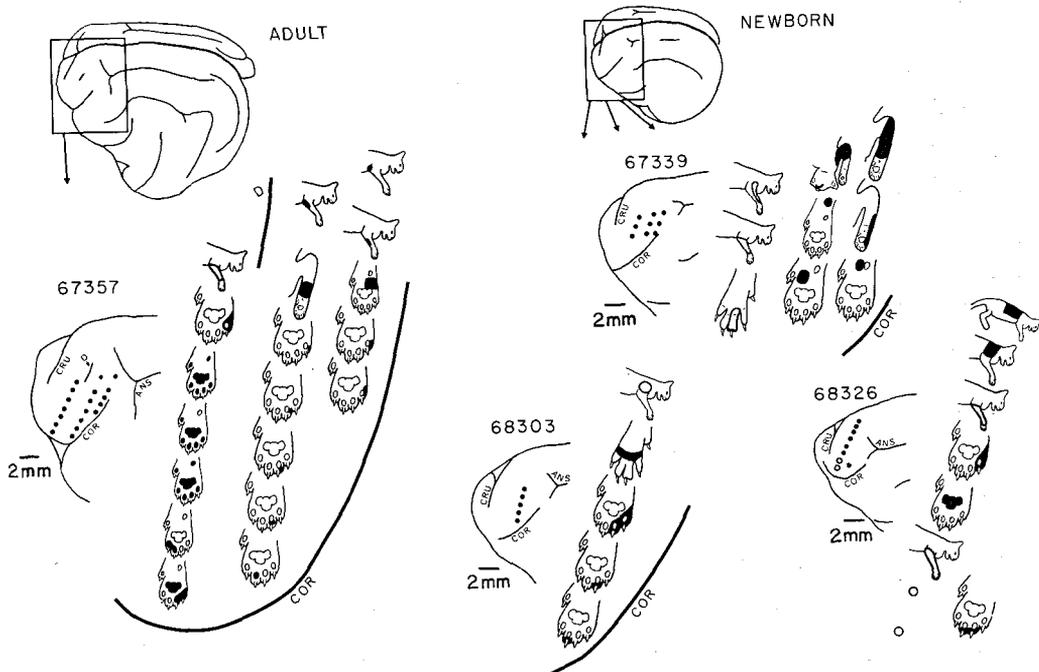


Fig. 3 Surface maps of the lateral aspect of posterior sigmoid gyrus. Note that projections from proximal portion of the foreleg are represented medial to those from more distal surfaces in both the newborn and adult cats. Receptive fields on distal surfaces are generally smaller than those on more proximal surfaces. Receptive fields requiring deep stimulation are generally found anterior to cutaneous receptive fields. Disjunctive receptive fields 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 Msl cortex rather than Sml, since it only responded to very deep stimulation and was found relatively far anterior in the posterior sigmoid gyrus. ANS, ansate sulcus; COR, coronal sulcus; CRU, cruciate sulcus; D, postcruciate dimple.

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 14 and 15.

4. 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 progressively caudal and ventral on the anterior bank of the coronal sulcus (fig. 12, penetrations 20, 26). 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 (fig. 13) and overlap with the MsI forepaw representation (Welt, Aschoff, Kaneda and Brooks, '67; Towe, Whitehorn and Nyquist, '68) causing more variability in receptive field organization. In this cortical region of the adult cats several other types of receptive fields were encountered. In many cases only deep stimulation of the contralateral arm or forepaw evoked a response. The receptive fields were often labile and quite large, covering the entire forepaw or foreleg. A further type of receptive field, designated disjunctive, was commonly found in this area of the adult cortex. Disjunctive receptive fields were 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. Figures 3 and 12 show some of the disjunctive receptive fields which were encountered and their cortical locations. 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 although the area was systematically

searched in four kittens anesthetized with barbiturate and in two unanesthetized preparations. One disjunctive receptive field was found in a 21 day-old preparation.

5. 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 (figs. 13, 17) except at its dorsomedial tip. Projections from the foreleg above the wrist were found caudal to the dorsal tip of the coronal sulcus (fig. 12).

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. The surface maps in figure 4 reflect the general organization of these projections. Further detail is shown in figures 16, 17 and 18 for adult cats and figures 19, 20, and 21 for newborn preparations.

1. 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 anteriorly in the adult cat. From figure 4 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 laterally in this area while more ventral surfaces of the body are found further medially 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.)

2. The lower lip is represented in the bank of the coronal sulcus while the upper

TABLE 4
*Mapping experiment of neck and head
representation in Sml*

Age	Preparations	Responsive punctures	Receptive fields
Newborn	9	31	60
Adult	8	45	69

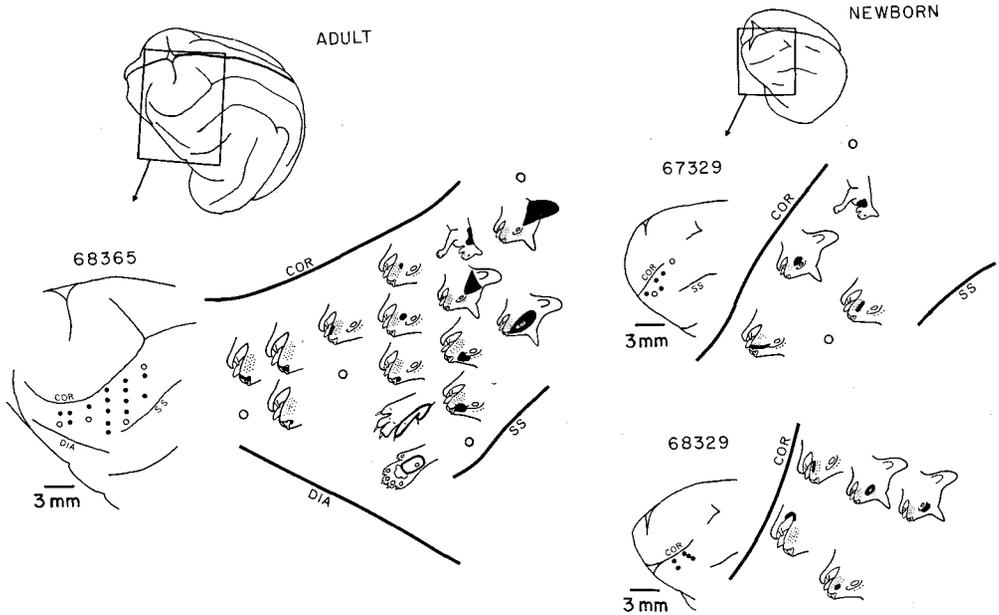


Fig. 4 Surface maps of coronal gyrus. Note that anterior surfaces of the face are represented rostral and ventral of the more posterior surfaces. Dorsal surfaces of the head project to more ventrolateral cortical loci than ventral surfaces. Projections from the forepaw, found near the suprasylvian sulcus in the adult are in SmII cortex. COR, coronal sulcus; DIA, diagonal sulcus; SS, suprasylvian sulcus.

lip is represented progressively toward the exposed surface of the gyrus (figs. 18, 19, 20, 21).

3. Projections from progressively more ipsilateral portions of the face are found as the electrode tip is moved progressively further anterior. The tip of the nose, inside the mouth and non-hairy surfaces of the lips are bilaterally represented (figs. 13, 18, 21).

Other aspects of sensory-motor cortical organization

Organization of SmII. In three barbiturate-anesthetized kittens, mechanoreceptive projections were found in the cortical area just caudal and ventral to the anterior suprasylvian sulcus (SmII of Woolsey, '58). The surface map from one such experiment is shown in figure 5. Although there are not enough data to show the detailed organization in this area, several features of these projections may be indicated. Projections to SmII from all major body surfaces appear to be electrophysiologically functional by 24 hours

after birth in the kitten and these projections respond to physiological stimulation of the receptors. 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 SmII were larger than those found in SmI, a relationship also reported in the adult cat (Carreras and Anderson, '63).

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 6 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. 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.

Columnar-organization in SmI cortex. The columnar organization of cell bodies

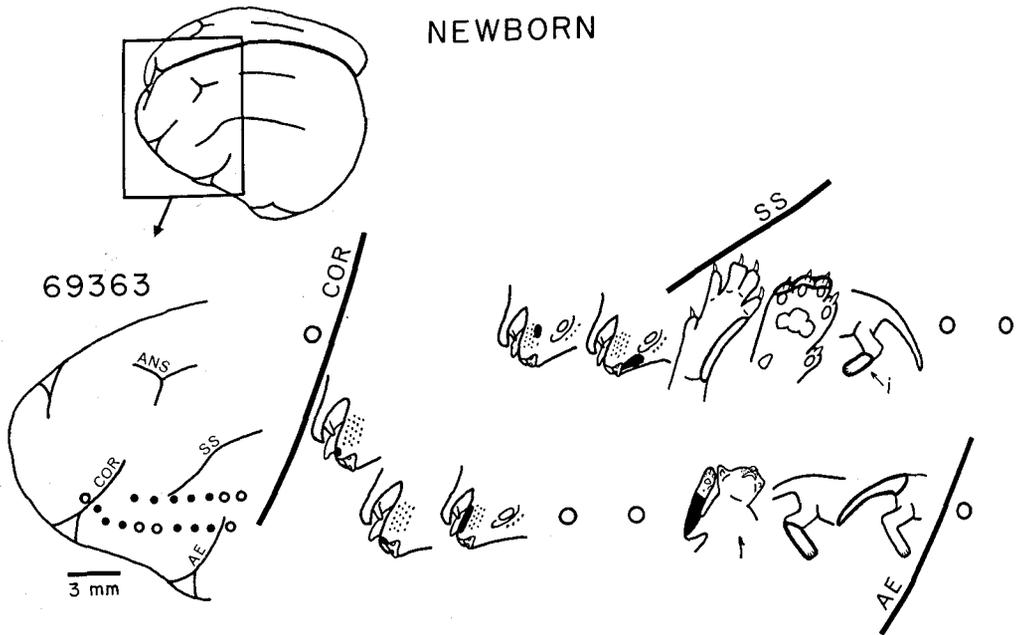


Fig. 5 Surface map from the coronal and anterior ectosylvian gyri of a newborn cat. Note that projections to SmII cortex are responsive to mechanical stimulation and lie in the anterior ectosylvian gyrus. Projections to SmII cortex come from both the ipsilateral (i) and contralateral body surfaces. Projections to SmII 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 of more posterior surfaces, and that dorsal surfaces of the head are represented caudal to the projections from more ventral portions. AE, anterior ectosylvian sulcus; ANS, ansate sulcus; COR, coronal sulcus; SS, suprasylvian sulcus.

in the primary sensory-motor cortex is vividly apparent in Nissl-stained sections of the newborn cortex (fig. 7). 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 ('57) 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

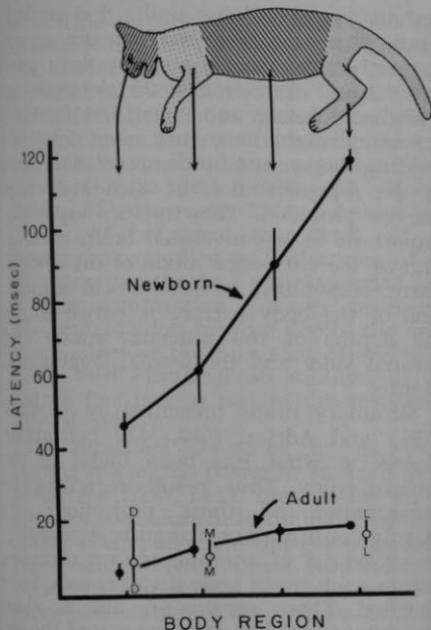


Fig. 6 Latencies from electrical stimulation of the body regions to evoked unit activity in the SmI cortex of newborn and adult cats. The shaded regions on the body figurine (top) designate the general body part in which stimulation yielded the latencies shown below. Solid points and bars indicate the 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 ('66); M-M from Mountcastle, Davies and Berman ('57); L-L from Levitt and Levitt ('68). Darian-Smith et al. ('66) included latencies to SII cortex as well as SmI.

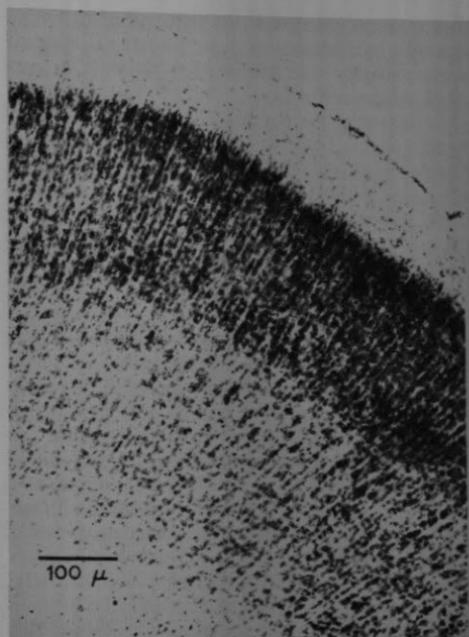


Fig. 7 Photomicrograph of thionin-stained section through the posterior sigmoid gyrus near the coronal sulcus of a newborn kitten. Notice the radial columns of densely packed cells.

Observations on postcruciate MsI cortex in newborn kittens. Numerous investigators (see Welt et al., '67) have studied the response properties of neurons in the postcruciate motosensory area (MsI) of the cat brain. This area lies rostral to the postcruciate dimple and is bounded laterally by the coronal sulcus. Hassler and Muhs-Clement ('64) classified this area praecentralis 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 observations of this area in the newborn kitten. Responses elicited from this area in the newborn kitten had the following characteristics.

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 figs. 2, 3).

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. ('67) 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 SMI cortex of the unanesthetized newborn kitten, are similar to what has been found in the barbiturate-anesthetized adult cat's SMI cortex (Welt, personal communication).

DISCUSSION

These results provide answers to the questions originally 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.

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, '40, '41; Amassian, '51; Celesia, '63; Cohen, Landgren, Strom and Zotterman, '57; Livingston and Phillips, '57; Marshall, Woolsey and Bard, '41; Patton and Amassian, '52; Woolsey, '47, '58). 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, Johnson and Pubols, '64) 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.

Summary maps presented by Woolsey ('58) and Adrian ('40, '41) 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 ('66). These authors, however, did not attempt to explore the banks of the coronal sulcus. 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 criterion 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 glabrous 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, '64; Mountcastle, '57). However, Morse, Adkins and Towe ('65) reported that 82% of the neurons they studied in SmI cortex of the chloralose-anesthetized cat responded only to skin deformation (deeper pressure). The contradiction may be due to the anesthetic effect or the fact that Morse et al. ('65) used electrical stimulation of the central foot pad to isolate the responsive cortical units.

Mountcastle ('57) 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 similar relationship was found in the present study for both newborn and the adult cats.

Columnar organization. Mountcastle ('57) 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., '66; Brooks et al., '64), SmII (Carreras and Anderson, '63), motor-sensory (Welt et al., '67) and visual (Hubel and Wiesel, '65). 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.

In Nissl-stained sections of SmI cortex of the adult cat, the columnar organization of cells has been noted by Hassler and Muhs-Clement ('64). This cytoarchitectural characteristic, although apparent

in the adult, is more striking in the newborn cat, as in the newborn rat (Caley and Maxwell, '68).

Receptive field organization. All of the receptive fields found in the post-dimple 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. ('67). 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 ('57) and Brooks and Levitt ('64).

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, '57; Welker, Johnson and Pubols, '64; Rose and Mountcastle, '59). 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, '57; Rose and Mountcastle, '59; Welker et al., '64) the size of the receptive fields was inversely related to their distality.

Differences between the adult cat and newborn kitten in the organization of sensory-motor cortical areas

Latency. 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 ('54), Rose and Lindsley ('68) and Marty ('67) respectively. Studies by Ekholm ('67) and Purpura et al. ('65) 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 sensory-motor cortices appear to be mainly in the realm of complexity. These differences are manifested 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. In the adult cat, however, discontinuities in the somatotopic organization were encountered. An example is shown in figure 9A, 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 ('57) never found ipsilateral projections to SmI cortex in his extensive analysis of neurons in this area, and Woolsey ('58) reports that aside from the perioral regions, only the contralateral body surface is represented in SmI cortex. However, Nakahama ('58) 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 ('59) reported that a few units in the postcentral gyrus of the monkey (*Macaque*) responded to ipsilateral stimulation.

In the newborn cat, aside from 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 have been termed disjunctive receptive fields in the lateral sigmoid gyrus of the adult cat and their apparent absence in newborn kittens. Welt et al. ('67) found single neurons with similar receptive fields in MSl 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. ('68) also showed 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 ('65) did not find disjunctive receptive fields of this type in the dorsal roots of raccoons, coatimundis or cats.

The boundaries of SmI cortex were also 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 (fig. 3, 67339), while it appeared to gradually merge with MSl cortex in the adult cat. The overlap between SmI and MSl cortex in the adult is confirmed by Towe et al. ('68) and Brooks et al. ('64).

The most striking example of the difference in complexity lies in a comparison between receptive fields found in MSl cortex of the unanesthetized or chloralose-anesthetized adult cat and observations on this area in the newborn kitten. A wide variety of receptive field 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., '64; Morse et al., '65; Towe, Patton and Kennedy, '64; Towe et al., '68; Welt et al., '67). 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 five or ten seconds. The qualities described above for the unanesthetized newborn kitten are quite similar to what is commonly found in Msl cortex of barbiturate-anesthetized adult cats (Welt, personal communication; Rubel, unpublished observations). Thus it appears that the same sources of input to Msl cortex which are rendered quiescent by barbiturate anesthesia in the adult cat, have not yet become electrophysiologically functional in the newborn kitten.

Physiological significance of sulci

Welker and Seidenstein ('59), 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 ('63) 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 subdivisions" and that "the cortex of the gyral crowns is functionally more active than that of the (sulcal) fundi" (p. 493). 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" (p. 494). Conversely, Hand and Morrison ('69), studying axonal degeneration following small electrolytic lesions in the forepaw representation of the ventrobasal complex (VB) of cats, 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.

Results of the present study support both of the reports mentioned above. In support of Welker and Seidenstein ('59), these data 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 thalamocortical radiations from the VB face representation as they course antero-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 crowns. 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.

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 ('63) 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 similar to those found in the adult cortex. Both simple and complex fields were reported, cells had defi-

nite receptive field orientations, and were aligned in columns with cells of a given column having similar 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. In direct contrast to these findings is the report by Pujol and Marty ('68). 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 ('42) indicated that the cortex is organized in a cochleotopic manner with the basilar portion represented rostrally on the cortex and the apex represented caudally. 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 (Marty, '67; Pujol and Marty, '70). Only future experiments using microelectrode methods and local stimulation of the cochlea will answer this question.

It appears that the primary somatic sensory cortex is formed during ontogeny as a point-to-point reflection of the distribution of mechanosensitive receptors in the animal's body. This organization may be brought about by the sorting of thalamocortical radiations into a precise somatotopic organization as they approach the cortex, which would create the appearance of cell columns as fibers penetrate the cortical grey matter. As the axons grow up the columns, they may send collaterals to cells at several levels, thus accounting for the electrophysiologically defined columnar organization (Mountcastle, '57). It is at approximately this point of development that the kitten is born. The cortex is composed

of densely packed columns of cells, noticeably barren with respect to dendritic and axonal processes (Purpura, '61), 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 intra-cortical 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 ('68) who find a dense network of interconnections within each functional subdivision 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 (Mountcastle et al., '57; Woolsey, '58) that barbiturates severely depress the spontaneous firing of SmI cortical neurons, and change the receptive field properties of neurons in MsI and SmII (Carreras and Anderson, '62; Welt et al., '67). Other authors including Yamamoto and Schaeppi ('61) have suggested that barbiturates are most effective in blocking polysynaptic neuronal systems especially in the cortex and brain stem. These suggestions, along with the observation that there is little or no spontaneous activity in the cortex of unanesthetized newborn cats (Huttenlocher, '67; and this study) and the observations noted on MsI cortex of newborns, lead to the conclusion that these intracortical connections may not be developed in the newborn.

The main purpose of the present 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 newborn kitten's SmI cortex are capable of making discriminations regarding the exact locus of delicate mechanical stimulation. 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, since the results also suggest many ways in which the adult cortex processes somatic sensory information that the newborn kitten is not capable of performing. Of particular interest for future research efforts on the developing somatic sensory and motor cortex would be studies of afferent inhibition (Mountcastle, '57), receptive field intensity coding, frequency coding (Mountcastle et al., '57), and receptive field types in Msl cortex.

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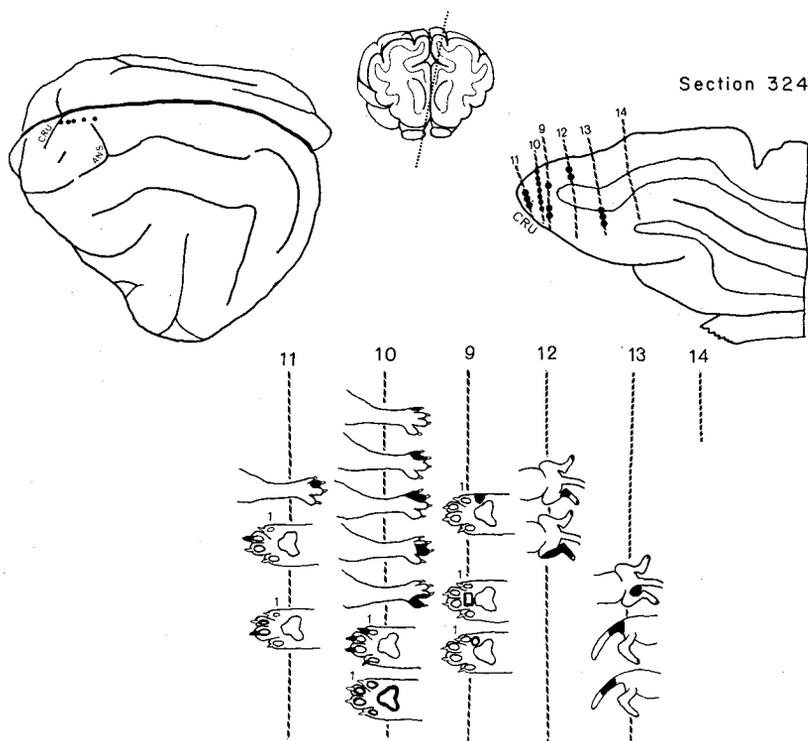
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ADULT-67351



EXPLANATION OF FIGURE

8 This and all succeeding section maps are organized as follows: Top left, tracing of left neocortex showing points where the electrode entered the cortex. Top middle (where included), 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 field evoking a response within each electrode penetration is 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 figurines of the foot, digit 1 is at the top and digit 4 at the bottom.

Shown here are receptive fields found in one row of electrode penetrations near the medial edge of the posterior sigmoid gyrus of an adult cat. Note that 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. 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.

PLATE 2

EXPLANATION OF FIGURES

- 9A Receptive fields found in one row of penetrations in the medial bank of the posterior sigmoid gyrus of an adult cat. Note that rump, tail and trunk representations are located posterior and ventral to projections from the distal portions of the leg. Distal positions 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. Solid diamonds are at responsive points where marking lesions were made. ANS, ansate sulcus; COR, coronal sulcus; CRU, cruciate sulcus. Punctures 14-19 were made at 1.0 mm intervals.
- 9B Photomicrograph of section traced in figure 9A. Shows parts of electrode tracks 14-19 (arrows). Thionin stain.

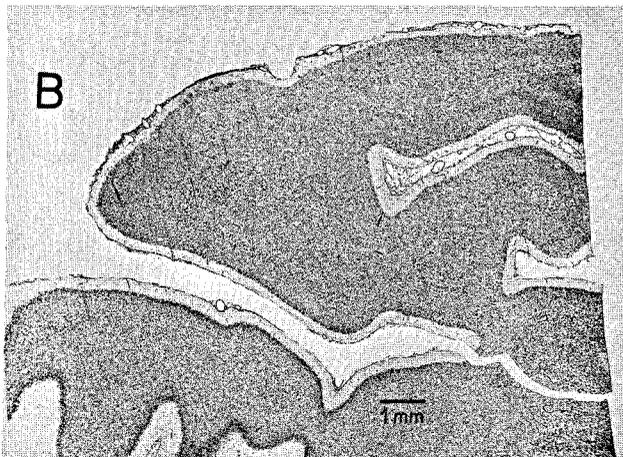
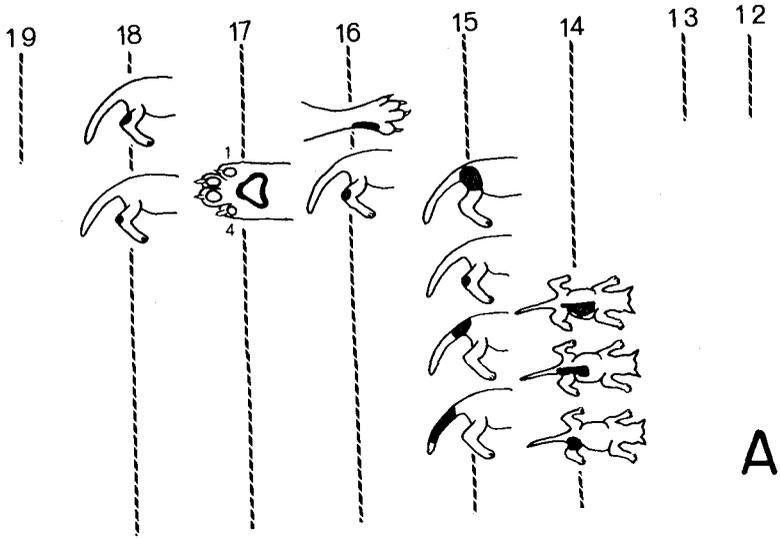
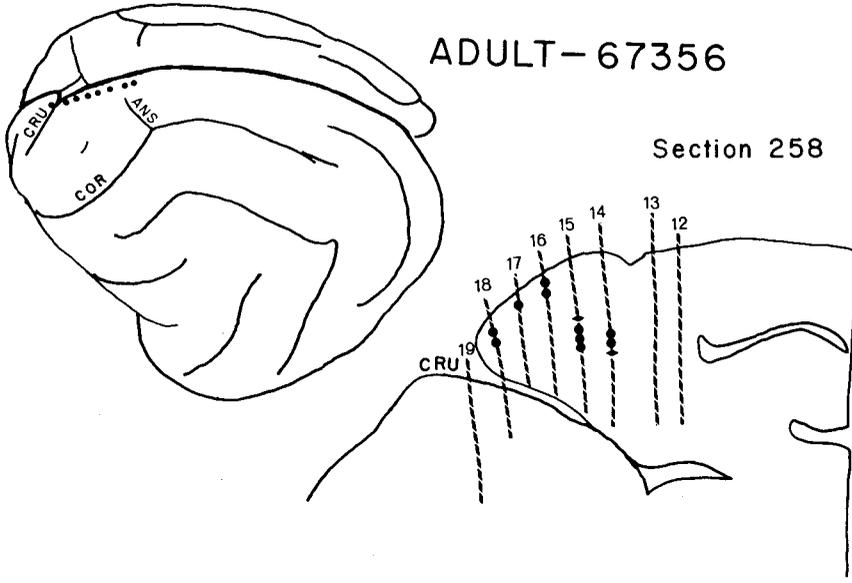
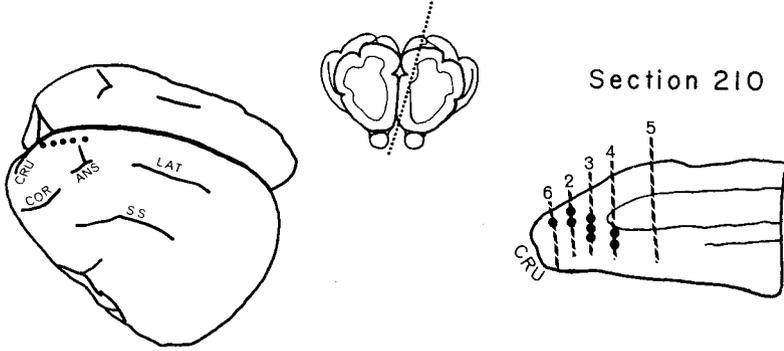


PLATE 3

EXPLANATION OF FIGURES

- 10 Receptive fields found in one row of electrode penetrations near the medial edge of the posterior sigmoid gyrus of a newborn kitten. Note that 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. ANS, ansate sulcus; COR, coronal sulcus; CRU, cruciate sulcus; LAT, lateral sulcus; SS, suprasylvian sulcus. Punctures 6, 2, 3, and 4 were made at 1 mm intervals.
- 11 Receptive fields found in rows of electrode tracks near the medial edge of the posterior sigmoid gyrus in two newborn kittens. Note that as in the adult, the rump, tail and trunk representations are located posterior to projections from the foot. 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. 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.

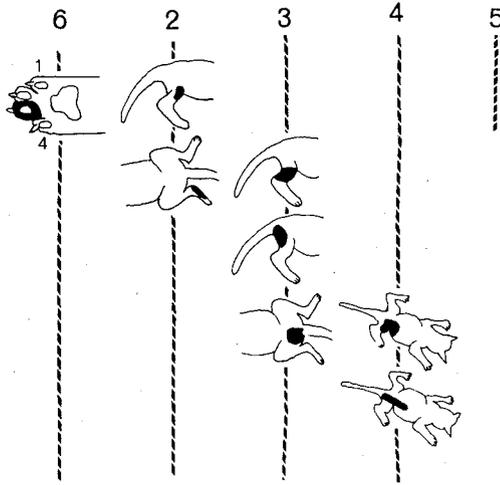
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10

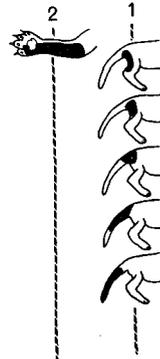
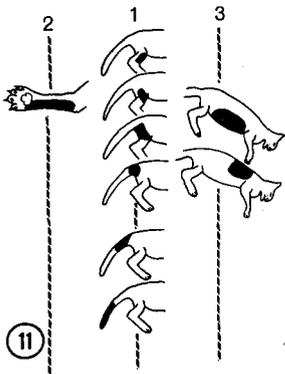
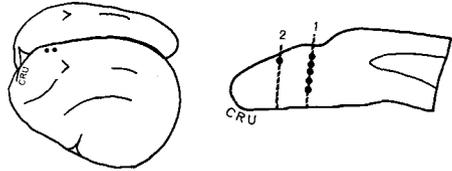
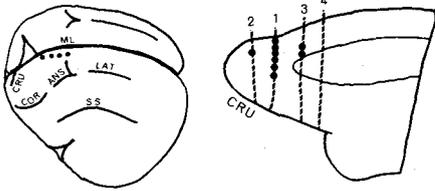
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Section 150

Section 144



11

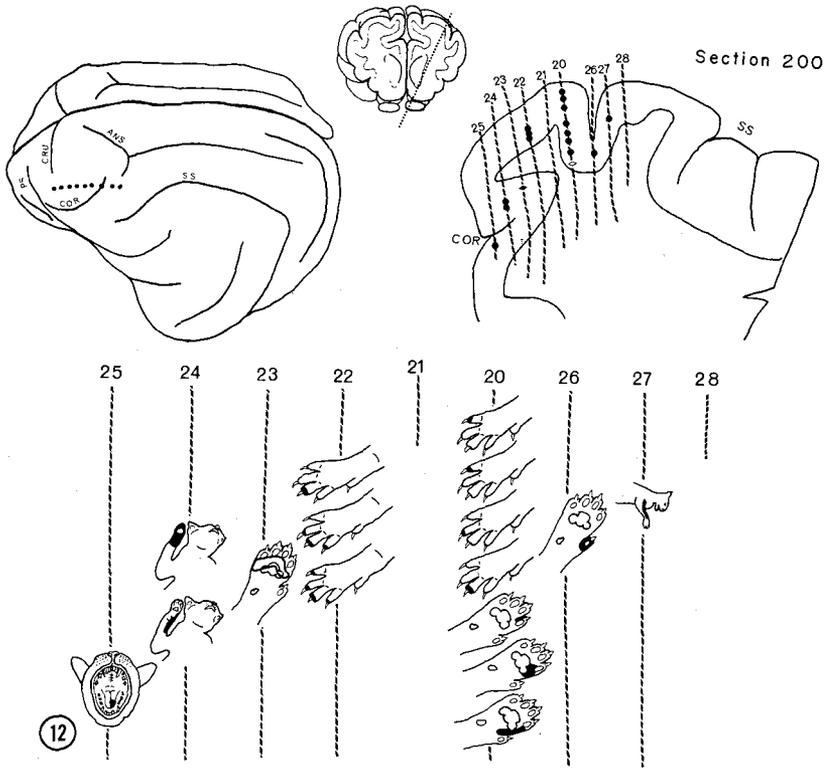
PLATE 4

EXPLANATION OF FIGURES

- 12 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. Solid and open diamonds are respectively responsive and unresponsive points where small marking lesions were made. Note that 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 Msl 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. ANS, ansate sulcus; COR, coronal sulcus; CRU, cruciate sulcus; PS, presylvian sulcus; SS, suprasylvian sulcus. Punctures 20-24 were made at 1 mm intervals.

- 13 Receptive fields found in one row of electrode penetrations through the forepaw digit representation on the lateral tip of the posterior sigmoid gyrus of an adult cat. Open diamond is at unresponsive point where marking lesion was made. Note that projections from digits 3 and 4 extend to the lateral tip of the gyrus. Projections from the fourth digit (puncture 32) were found anterior to those from digit 3 (punctures 29, 30, 31). Whenever the electrode enters 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). COR, coronal sulcus; CRU, cruciate sulcus; PS, presylvian sulcus; SS, suprasylvian sulcus. Punctures 29-32 were made at 1 mm intervals.

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ADULT-68347

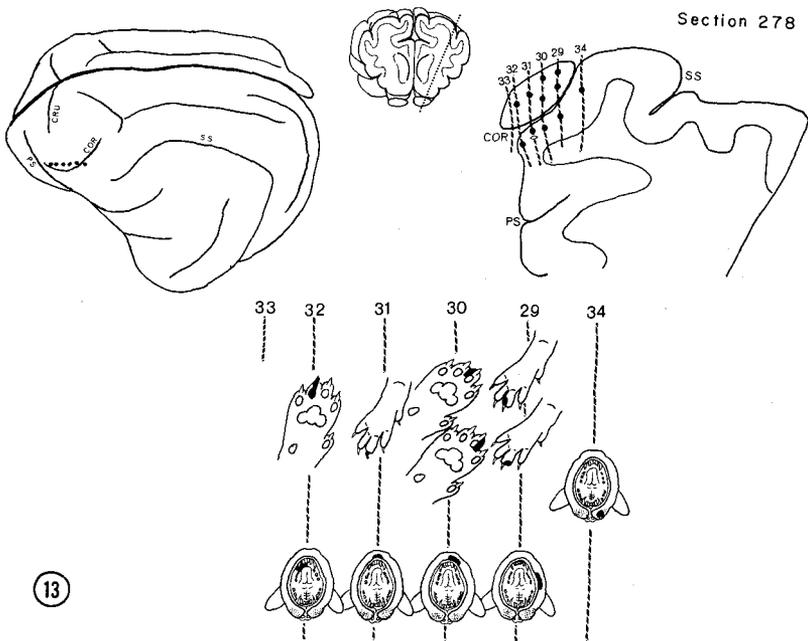


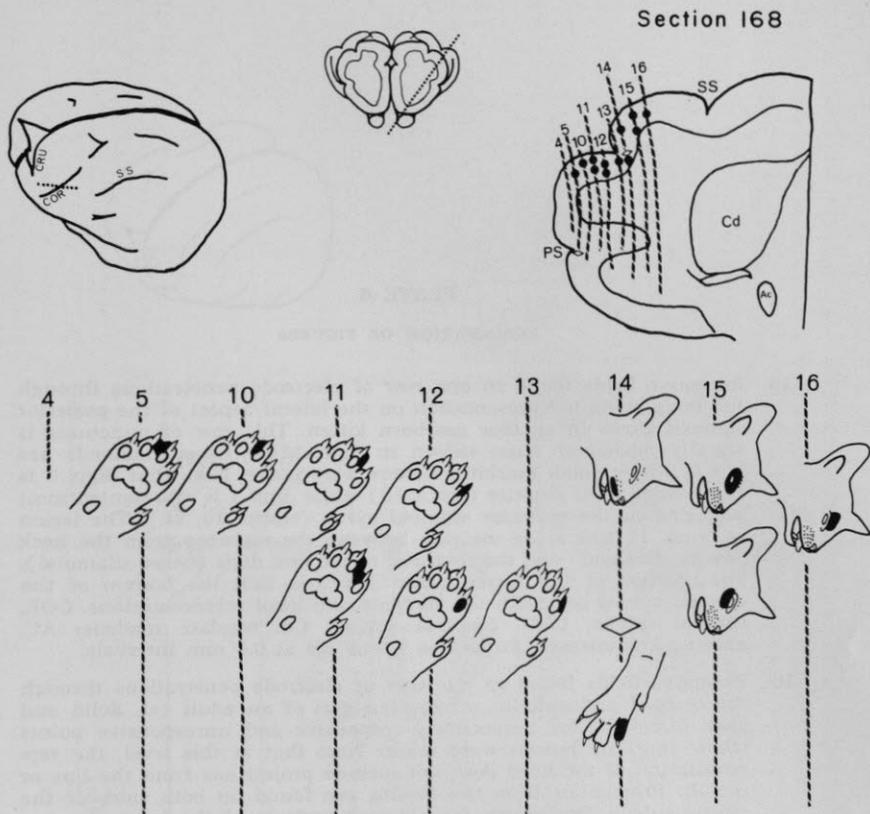
PLATE 5

EXPLANATION OF FIGURES

- 14A Receptive fields found in one row of electrode penetration through the forepaw digit representation in the lateral aspect of the posterior sigmoid gyrus of newborn kitten. Note that as the electrode is moved from anterior to posterior on the posterior sigmoid gyrus (tracks 5, 10, 11, 12, 13, 14), receptive fields progressively near 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 the dorsal surfaces of the head are represented posterior to ventral surfaces. 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.
- 14B Thionin-stained section shown in figure 14A. Parts of electrode tracks 5 and 10-15 can be seen.

NEWBORN-68329

A



B

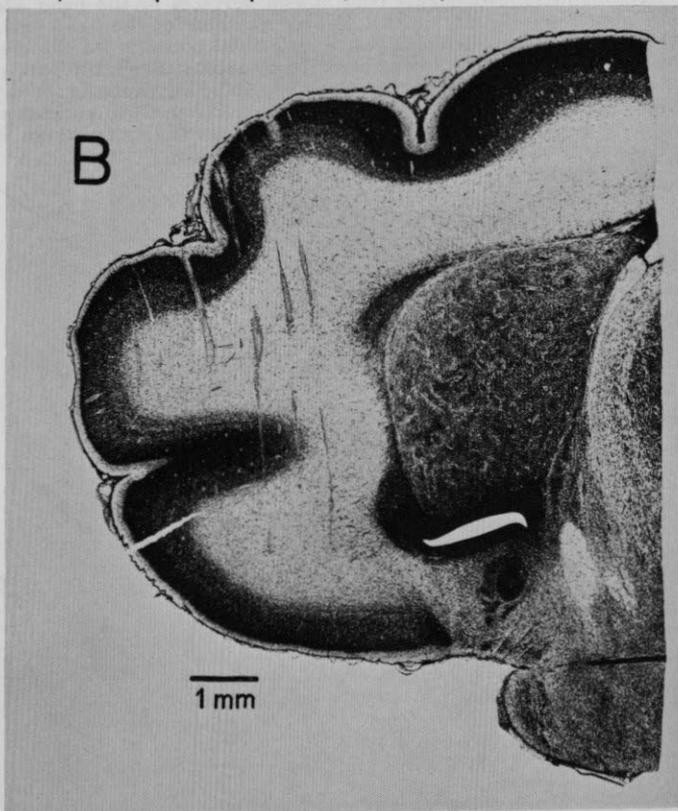
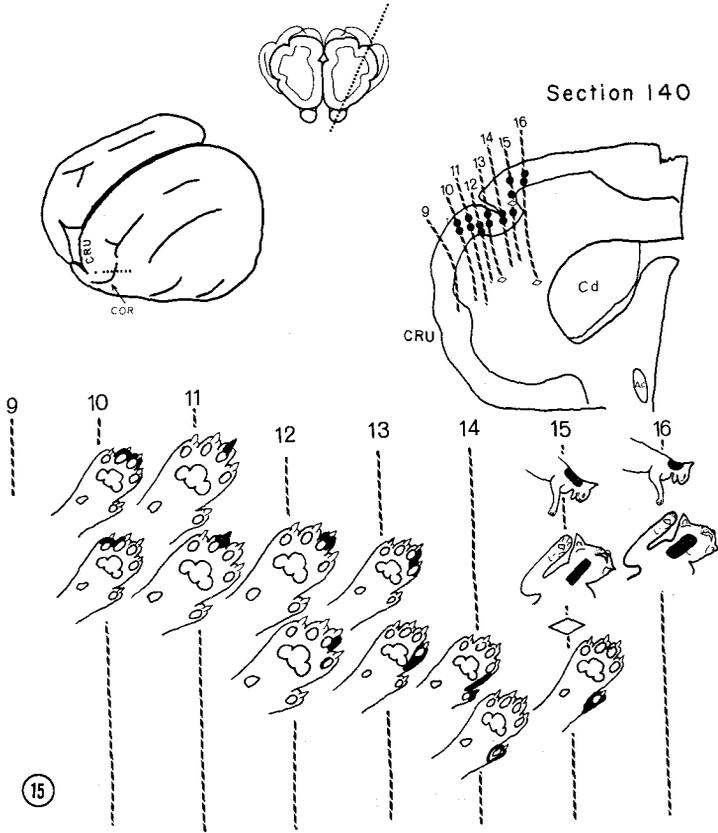


PLATE 6

EXPLANATION OF FIGURES

- 15 Receptive fields found in one row of electrode penetrations through the forepaw digit representation on the lateral aspect of the posterior sigmoid gyrus in another newborn kitten. This row of punctures is slightly medial of those shown in figure 14A. Open diamonds are points where small marking lesions were made. Note that digit 5 is represented most anterior (track 10) while digit 1 is represented most posterior on the posterior sigmoid gyrus (tracks 14, 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 sulcus separates the forepaw and head representations. COR, coronal sulcus; CRU, cruciate sulcus; Cd, caudate nucleus; AC, anterior commissure. Punctures 10-16 are at 0.5 mm intervals.
- 16 Receptive fields found in one row of electrode penetrations through the coronal and anterior ectosylvian gyri of an adult cat. Solid and open diamonds are respectively responsive and unresponsive points where marking lesions were made. Note that 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, SmII forepaw projections are encountered (punctures 23, 25). 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.

NEWBORN-68326



ADULT-68365

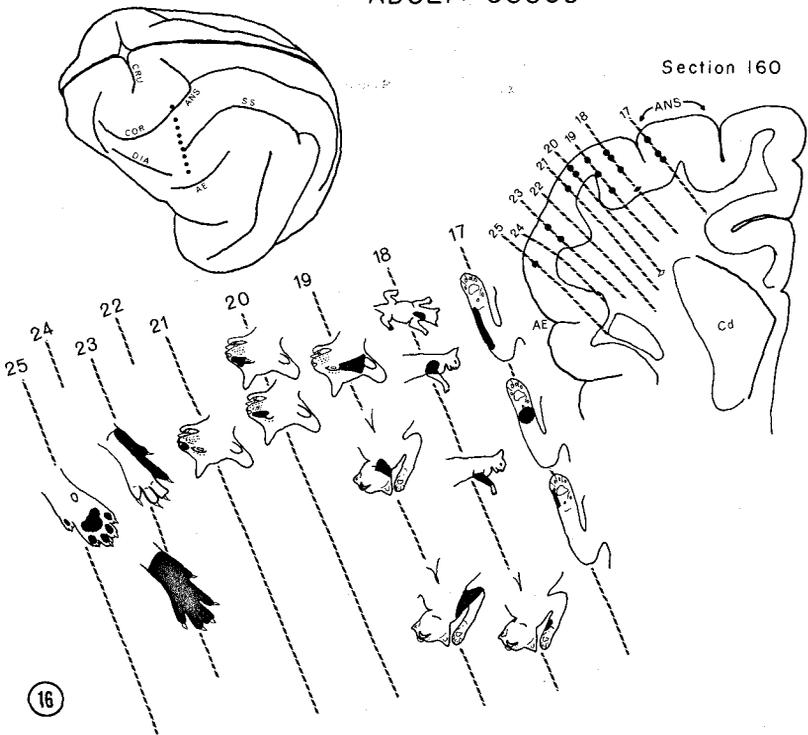


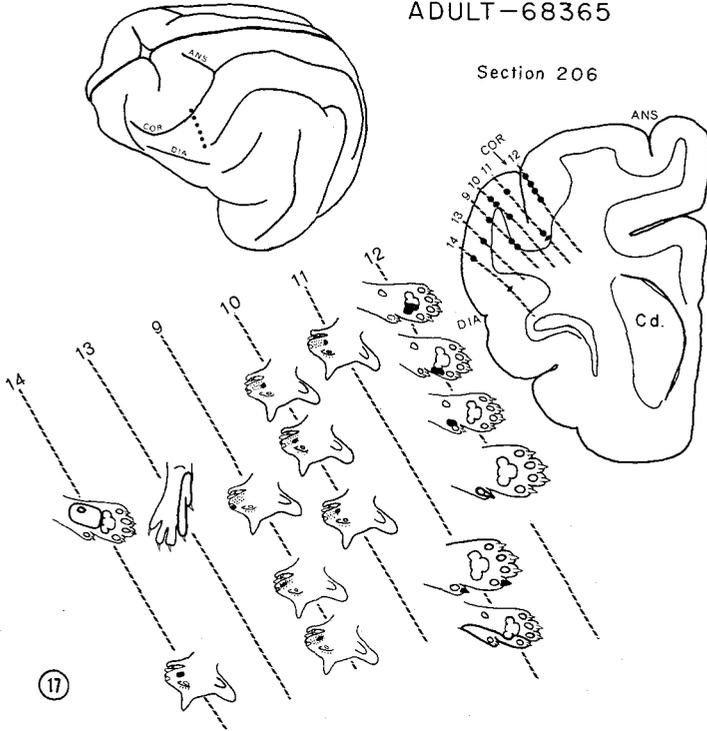
PLATE 7

EXPLANATION OF FIGURES

- 17 Receptive fields found in a row of electrode penetrations through the coronal gyrus 2 mm anterior to those in the previous figure. Solid diamonds indicate responsive points where marking lesions were made. Note that 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. SmII forepaw projections are found near the suprasylvian sulcus (punctures 13, 14). 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.
- 18 Receptive fields found in a row of electrode penetrations through the coronal gyrus 5 mm anterior to those in the previous figure. Solid diamonds indicate responsive points at which small marking lesions were made. Note that 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. ANS, ansate sulcus; COR, coronal sulcus; DIA, diagonal sulcus; ML, medial longitudinal fissure; RF, rhinal fissure. Punctures 31 and 32 were made 1 mm apart.

ADULT-68365

Section 206



ADULT-68365

Section 362

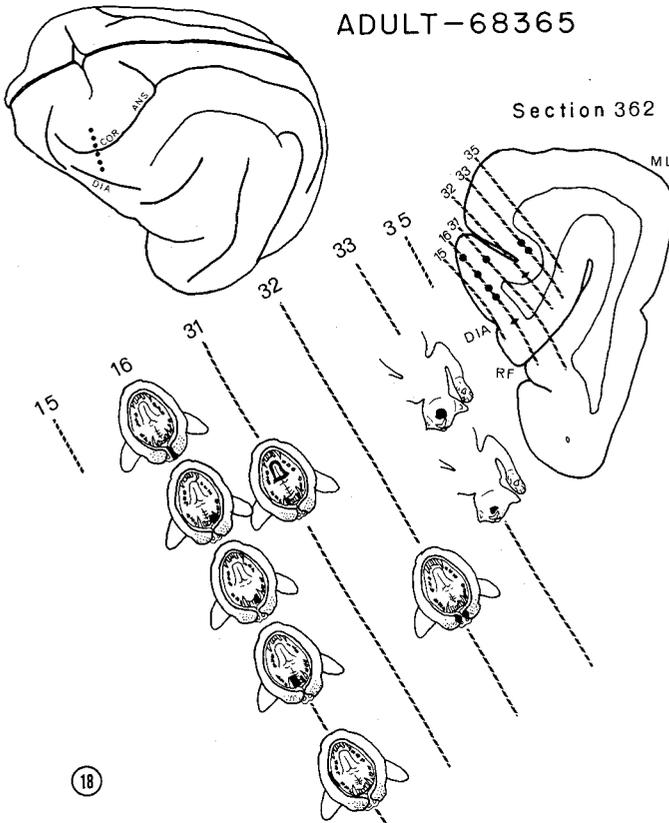
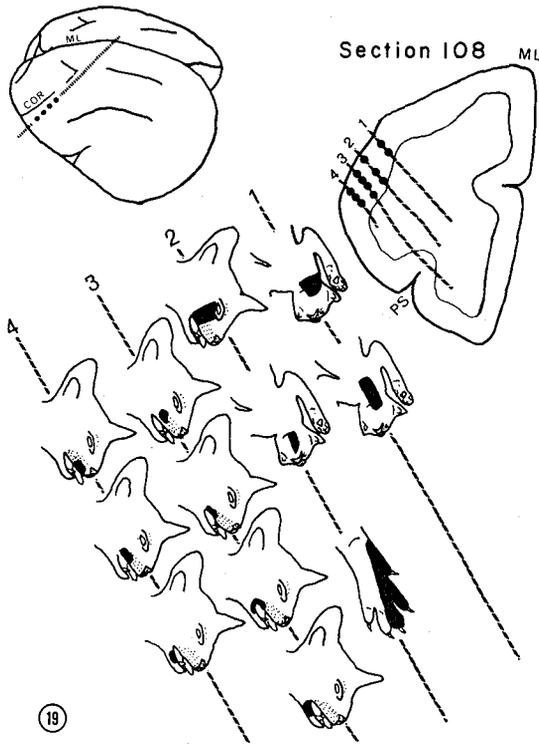


PLATE 8

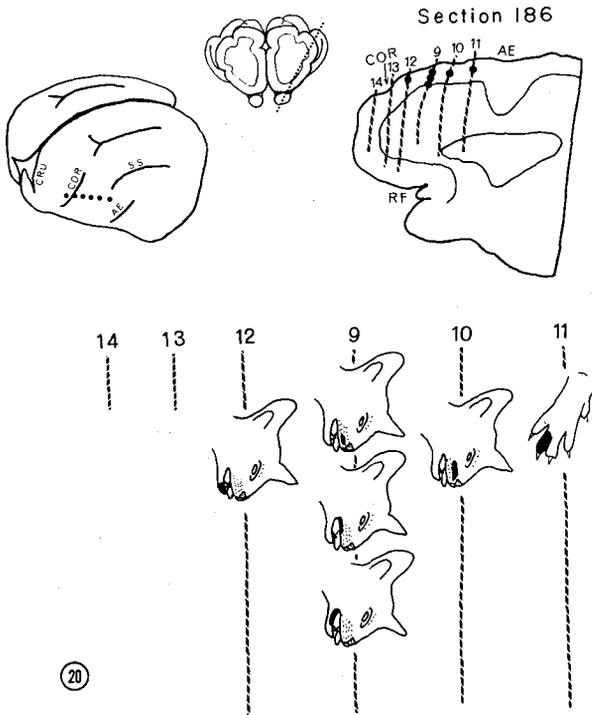
EXPLANATION OF FIGURES

- 19 Receptive fields found in one row of electrode penetrations down the caudal bank of the coronal sulcus of a newborn kitten. Note that 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, 4). Projections from the forepaw (puncture 2) were found in the fundus of the coronal gyrus, but not more dorsally in the caudal bank. Dotted line on brain tracing indicates angle at which section was cut. COR, coronal sulcus; ML, medial longitudinal fissure. PS, presylvian sulcus. Punctures were spaced at 1 mm intervals.
- 20 Receptive fields found in one row of electrode penetrations through the coronal sulcus of a newborn kitten. Note that mandibular portions of the face are represented anterior of the maxillary surfaces. The response to forepaw stimulation (puncture 11) was found in the SmII 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. AE, anterior ectosylvian sulcus; COR, coronal sulcus; CRU, cruciate sulcus; RF, rhinal fissure; SS, suprasylvian sulcus. Punctures were made at 1 mm intervals.

NEWBORN-68300

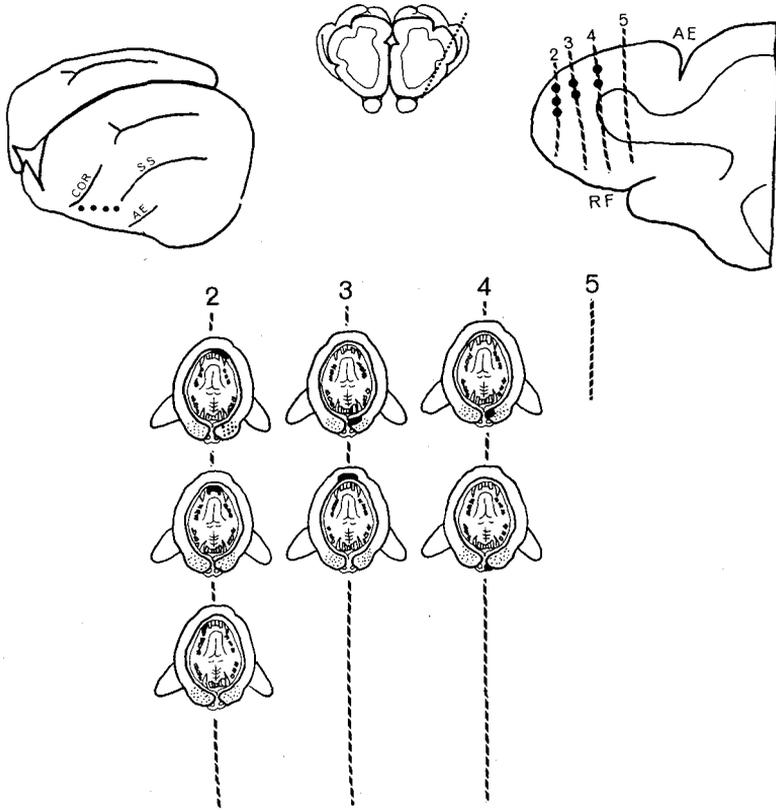


NEWBORN-68302



NEWBORN-68302

Section 216



EXPLANATION OF FIGURE

- 21 Receptive fields found in a row of electrode penetration through the coronal gyrus 1 mm lateral to those in the previous figure. Note that projections seen in these punctures, from the most 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. AE, anterior ectosylvian sulcus; COR, coronal sulcus; RF, rhinal fissure; SS, suprasylvian sulcus. Punctures were made at 1 mm intervals.