Responsiveness and Somatotopic Organization of Anterior Parietal Field 3b and Adjoining Cortex in Newborn and Infant Monkeys

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Abstract Microelectrodes were used to record from somatosensory areas 3b and adjoining areas 3a and 1 in newborn monkeys. At birth, area 3b was responsive to cutaneous stimuli and had an adult-like somatotopic organization in marmosets and one squirrel monkey, while areas 1 and 3a had only limited responsiveness. In newborn macaque monkeys, cortex was unresponsive to cutaneous stimuli; however, by 1 month, areas 3b and 1 appeared to be adult-like in responsiveness and somatotopic organization.

Key words somatosensory cortex, macaque monkeys, marmosets, squirrel monkeys

Currently, there is little information on the topographic organization of cortical sensory representations at the time of birth. Rubel (1971) demonstrated that primary somatosensory cortex (SI) of cats is roughly adult-like in somatotopic organization at birth, but the maturity of cortex at birth is not known for other representations or for other mammals. In the present study, we compare the responsiveness and somatotopic organization of the somatosensory cortex in newborn and older monkeys. Such comparisons relate to currently viable conclusions about developing sensory systems.

One common conclusion about the developing brain is that the behavioral consequences of damage to the sensory cortex vary with age, and the recovery and ability to compensate for damage are greater after lesions in newborn than adult mammals (e.g., Kennard, 1942; Benjamin and Thompson, 1959; Scharlock *et al.*, 1963; Wetzel *et al.*, 1965; Tucker *et al.*, 1968; Goldman, 1971; Murphy *et al.*, 1975; see also Meyer and Meyer, 1984, for review). In particular, lesions of subdivisions of the anterior parietal somatosensory cortex in newborn monkeys appear to produce less severe impairments in perceptual abilities than in adults (Carlson, 1984). The reasons for such age-related differences are not clear, but if sensory representations are more diffusely organized in newborns than adults, then seemingly comparable lesions may not equally deprive newborns and adults of the neural substrate for performance.

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A second general conclusion relevant to the present study is that cortical maps of receptor surfaces are not static, but are capable of some level of reorganization following the removal of inputs or alterations in the efficacy of inputs (see Kaas *et al.*, 1983, for review). Such plasticity is characteristic of both adult and developing nervous systems, but the general view is that a greater capacity for reorganization exists in newborn animals. For instance, results from a recent study in cats support the view that the magnitude of cortical reorganization is age-dependent. McKinley *et al.* (1987) used spinal cord lesions to deprive a large portion of SI of normal activation from the hindlimb. In cats lesioned 2 weeks after birth and studied 4 months later, the deprived "hindlimb" portion of SI was found to be responsive throughout to stimuli on the trunk and forelimb. When the same procedure was repeated in somewhat older cats, 6 weeks after birth, these other inputs from the trunk and forelimb failed to fully activate the "hindlimb" region of SI. Thus, a major reorganization of SI occurs after removing the source of a sensory input in 2-week-old but not 6-week-old cats. One possibility in such studies of plasticity is that the greater capacity for reorganization in young mammals (also see Kalaska and Pomeranz, 1979; Kelahan and Doetsch, 1984) is related to an immaturity in the somatotopic organization of the sensory maps.

A third basic conclusion related to the present investigation is that the organization of developing sensory maps is in part dependent on neural activity patterns (see Constantine-Paton, 1982; Stryker, 1982; Kaas, 1988). Since the prenatal and postnatal environments are quite different, it seems possible that cortical maps of skin receptors could change substantially in organization after birth as a result of major changes in the ways sensory receptors are activated. This possibility remains largely untested.

In the present study, we used microelectrode recording techniques to investigate the responsiveness and organization of area 3b and adjoining regions of somatosensory cortex in monkeys soon after birth. Because different monkey species are born at different levels of maturity, it was uncertain how results obtained from one species at birth apply to other species. Thus we considered more precocial New World marmoset monkeys and squirrel monkeys, born with enough sensorimotor development to enable them to hold onto their mothers without assistance, and more altricial Old World macaque monkeys, born with less developed sensorimotor skills and requiring some maternal assistance (Shively and Mitchell, 1986). Because somatosensory cortex of newborn macaque monkeys was unresponsive to cutaneous stimuli, we extended the study to include one macaque of 1 month of age. A brief report of some of the findings has been presented elsewhere (Krubitzer and Kaas, 1987).

METHODS

The New World monkeys in this study were infants that were neglected or rejected by mothers, and they would have died without careful handrearing. Microelectrode recordings were made from two newborn (1-day-old) marmosets (*Callithrix jacchus*), one newborn squirrel monkey (*Saimira sciureus*), two newborn macaque monkeys, and a 1-month-old macaque monkey (*Macaca fascicularis*). In all these species, the

responsiveness and organization of areas 3b and 1 had been previously studied in adult monkeys, and procedures closely followed those used for adults (Nelson et al., 1980; Sur et al., 1982; Carlson et al., 1986).

At the start of each experiment, each monkey was anesthetized with ketamine hydrochloride (20–70 mg/kg) supplemented with acepromazine maleate (4.3 mg/kg); additional injections were given as needed to maintain anesthesia (see White et al., 1982). In addition the incision line along the scalp was infused with 2% xylocaine hydrochloride as a local anesthetic. The portion of the skull over somatosensory cortex was removed, the dura was retracted, and the exposed cortex was covered with silicone fluid to prevent desiccation. A photograph was taken of the cortex, and an enlarged print was prepared so that microelectrode penetrations could be sited accurately. The animal's body temperature was maintained at 37.50°C by a thermo-statically controlled warm-water heating pad.

Recordings were obtained with low impedance (0.9–1.2 MΩ at 1,000 Hz) tung-sten microelectrodes advanced through the cortex with a stepping microdrive while the skin was stimulated by tapping and brushing. Recordings were generally obtained within the middle layers of cortex (500–1000 μm in depth) where neurons were most reliably driven by peripherial stimuli. In macaque monkeys, where the central sulcus is well developed at birth and much of area 3b is in the caudal bank of the central sulcus, electrodes were advanced down the bank of the sulcus in approximately the middle layers of the cortex and recordings were obtained at successive distances of approximately every 200 μm. After the body region activating neurons at a recording site was localized, the receptive field was carefully determined by stimulating the skin and moving body hairs with fine wires and glass probes. The receptive field was judged to be the area of skin where near threshold stimulation (moving hairs or lightly touching the skin) produced a clear neural response. Previously, we have referred to these as "minimal receptive fields," since more intense stimulation can result in larger receptive fields (e.g., Nelson et al., 1980; Sur et al., 1982; Carlson et al., 1986).

Favorable recording conditions were generally maintained for a period of 4 to 6 hr, after which the monkeys were deeply anesthetized and perfused transcardially with 0.9% saline followed by 10% formalin in saline. The brains were removed and photographed. For the marmoset brains, the cortex was peeled from the rest of the brain and flattened between glass plates placed in 10% formalin in saline. Other brains were stored in 10% formalin in saline, which was changed to a solution including 30% sucrose to aid cutting on the freezing microtome. The marmoset brains were sectioned (40 μm) parallel to the cortical surface, whereas the squirrel monkey and macaque monkey brains were sectioned (50 μm) in the parasagittal plane. Alternate sets of brain sections were stained for cell bodies with cresyl violet or for myelin with the Gallayas (1979) silver procedure.

RESULTS

In the present study, we compare the responsiveness, somatotopic organization, and architecture of area 3b and the adjoining cortex of newborn and adult marmosets, squirrel monkeys, and macaque monkeys. Further observations are included on a

1-month-old macaque monkey. The location of area 3b and the relative sizes of the brains for adult and newborn monkeys of the study are shown in Figure 1.

MARMOSETS

Recordings were obtained from two newborn marmosets. The results indicate that major features of the topographic organization of the primary field, area 3b, as well as some of the responsiveness of adjoining fields 3a and 1 are in place at the time of birth.

Our understanding of the location, extent, and somatotopic organization of area 3b in normal adult marmosets is based on the study of Carlson *et al.* (1986) on the closely related tamarins, as well as several recent studies on marmosets (Huerta *et al.*, 1986; Krubitzer and Kaas, 1986; Wall *et al.*, 1986). Results from these studies indicate that neurons within 3b are responsive to light tactile stimulation of the contralateral body surface. As in other primates, the general progression of body part representation is from hindfoot to face and mouth in mediolateral cortical se-
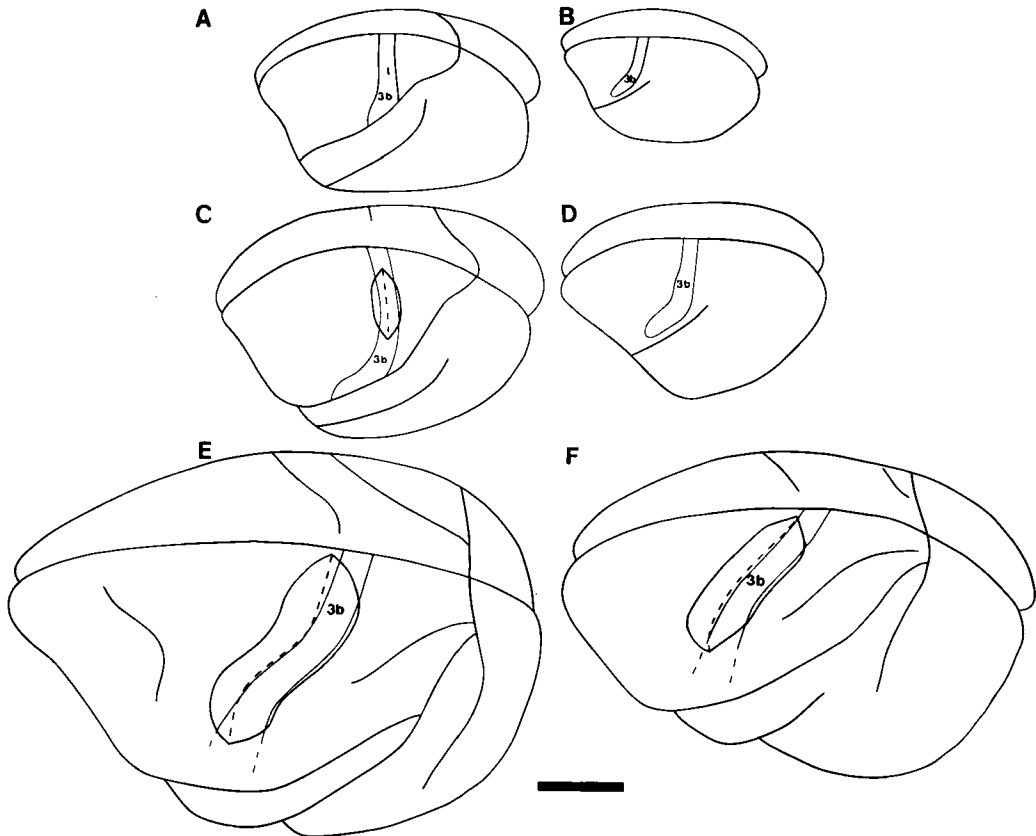

FIGURE 1. Dorsolateral view of the brains of adult (left) and newborn (right) (A, B) marmosets, (C, D) squirrel monkeys, and (E, F) macaque monkeys indicating the locations of area 3b of somatosensory cortex. The central sulcus has been opened for macaque and squirrel monkeys, and a dashed line indicates the bottom of the sulcus. Calibration bar: 10 mm.

quence. Although there is variation from case to case in the amount of cortical territory devoted to given skin surfaces, and in the relative location of some skin surfaces, especially dorsal hand surfaces, the overall somatotopy of 3b is highly consistent from animal to animal. Recording sites in area 3b result in orderly progressions of receptive fields, and the receptive fields are of the order of size shown in Figure 2. Receptive fields on the glabrous hand, which activates a large proportion of area 3b, are small and often restricted to a portion of a single digit or a part of the palm, whereas receptive fields on the trunk, which is sparsely represented in the cortex, typically include a significant portion of the trunk.

In newborn marmosets, the location and shape of area 3b were similar to that of adults (Fig. 1B). Neurons in 3b responded crisply to light tactile stimulation and the moving of hairs. Whereas the small body parts in newborn marmosets made it difficult to delimit receptive fields precisely on glaborous skin surfaces, the receptive fields obtained from brushing hairs on the hairy skin could be delimited with assurance. Typical receptive fields occupied about the same proportions of skin surfaces as in adults (cf. Figs. 2 and 3). Of course, since the newborn marmoset is much smaller than the adult, the receptive fields were absolutely much smaller than in the adult. As in adults, receptive fields on the forepaw digits of the newborns were largely on a single digit. Typically, the major response was evoked by stimulating the claw of a single digit, whereas a weak response or no response was obtained by stimulating adjoining digits. Strong responses from two digits were uncommon.

Recordings were obtained from a mediolateral sector of area 3b of newborn marmosets that extended from the trunk representation to that of the upper lip representation. Comparisons of the results from infants (Fig. 3) with those from adults (Fig. 2) reveal many somatotopic similarities. The most medial recordings in the newborn marmoset 86-46 were from the part of area 3b devoted to the trunk. Recording sites near the rostral border of area 3b (Fig. 3, upper) had receptive fields on the back that extended to the body midline, whereas more caudal recording sites related to receptive fields on the lateral and ventral trunk. These observations suggest that, as in 3b in the normal adult marmoset, the back is represented rostral to the belly. In the cortex immediately lateral to the trunk representation, recording sites were found related to the forelimb and neck. Parts of the forelimb and neck are commonly found represented between the trunk and hand in normal adults. More laterally in 3b, a large block of cortex represents the hand in both adult and newborn marmosets. In adults, the most lateral part of area 3b is devoted to parts of the face and oral cavity. Recordings in the newborn marmoset indicated that the lateral portion of 3b was roughly normal in somatotopy at the time of birth. The receptive field progression in lower Figure 3, when compared with the progression in lower Figure 2, shows that in both newborns and adults, receptive fields progress from lower rostral face to upper caudal face in rostrocaudal recording sequences.

There was a suggestion of some differences in the somatotopic pattern of newborn compared to adults. Generally in primates the glabrous digits 1–5 are represented in a lateromedial sequence with distal digits rostral to proximal digits, and glabrous pads occupying caudal and medial positions. Hairy surfaces of the hand tend to be found in islands of tissue largely caudal, medial, and lateral to the representations of the glabrous digits. This general pattern is evident in adult marmosets
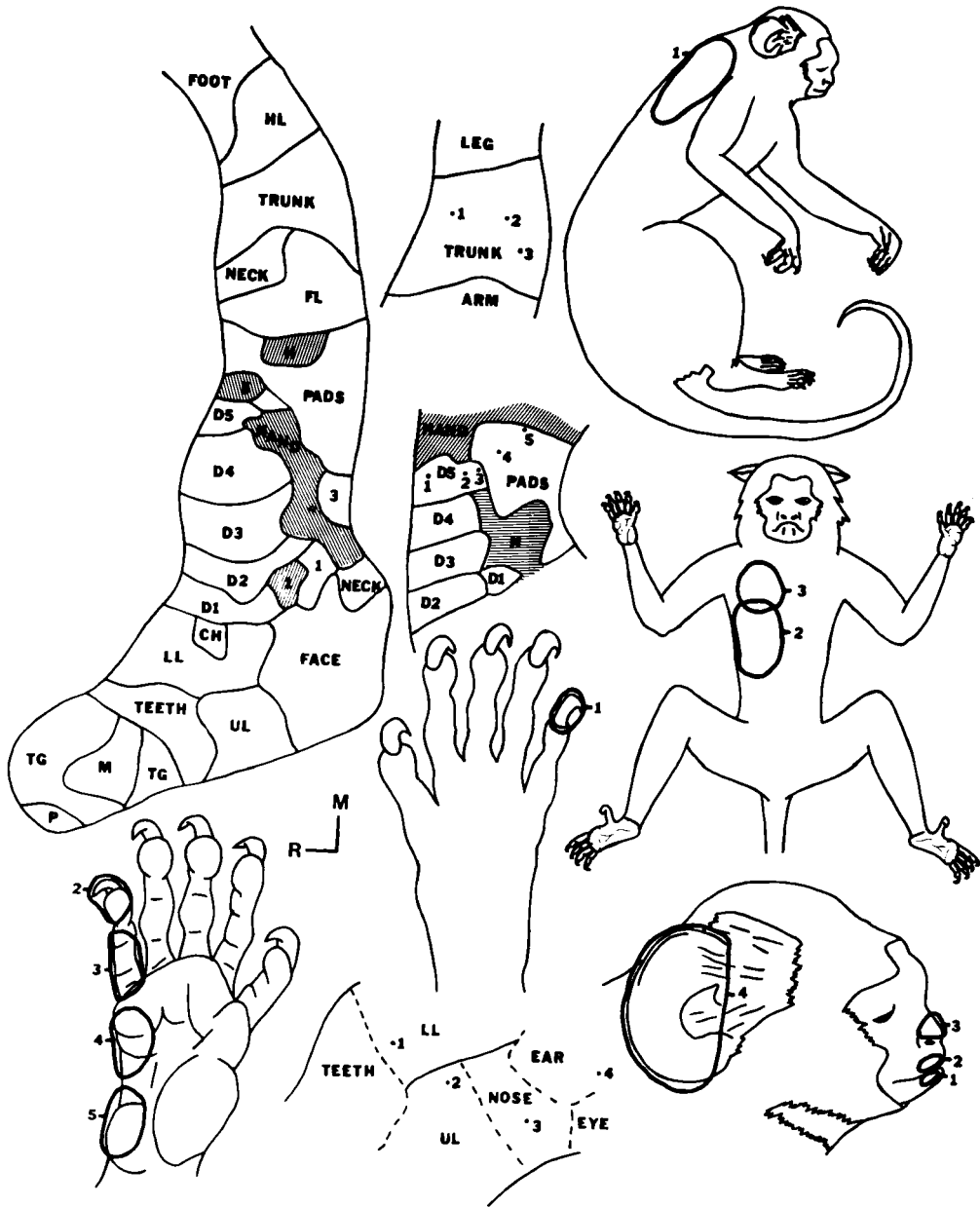
FIGURE 2. The somatotopic organization of area 3b in an adult tamarin (*Sagiunus*) and representative receptive fields. Redrawn and modified from Carlson *et al.* (1986). Area 3b is outlined in the upper left (see Fig. 1 for location in parietal cortex). Thin lines divide locations where recording sites were activated by the designated body parts. Representations of dorsal hairy surfaces of the hand are shaded. Digits of the hand are numbered from thumb (D1) to little finger (D5). Portions of maps from other tamarins are in the upper middle, center, and lower center. Numbered dots correspond to electrode penetrations and recording sites. The receptive fields for the numbered recording sites are likewise numbered on the outlines of body surfaces. HL = hindlimb; FL = forelimb; H = hand; LL = lower lip; UL = upper lip; M = mouth; TG = tongue; P = palate.

FIGURE 3. The somatotopic organization of area 3b and adjacent cortex of a 1-day-old marmoset, and representative receptive fields. The summary was based on receptive fields for recording sites marked by dots. Area 3b was identified histologically (see Fig. 1 for the location of area 3b). W = wrist; N = neck; P = pads. Other conventions as in Figure 2.

(Fig. 2), but it was not fully apparent in the newborn marmoset (Fig. 3). In the newborn, the mediolateral segregation of strips of cortex successively devoted to digits 5–1 was only weakly apparent, and a portion of rostral 3b was activated by glabrous pads.

Conclusions based on recordings from case 86-46 (Fig. 3) were supported by results from another newborn marmoset (case 86-43; Fig. 4). Most of area 3b was found to be responsive to cutaneous stimuli. The hindlimb, trunk, forelimb, hand, and face were found in a mediolateral sequence across cortex, and the glabrous digits were rostral to the pads and hairy hand.

Attempts were also made to record caudal to area 3b in area 1 and rostral to area 3b in area 3a of newborn marmosets. In anesthetized adult marmosets, area 1 is inconsistently responsive to cutaneous stimuli. Recording sites with cutaneous receptive fields can be obtained in some experiments, but it is more common not to find recording sites within area 1 with clearly defined receptive fields (Carlson et al., 1986). Area 3a is largely unresponsive to light touch, although occasionally neurons are found in 3a that are activated by light touch or taps on the hand and digits, especially the claws (Carlson et al., 1986). In the newborn marmoset, neurons at only a few locations immediately rostral and caudal to 3b were activated by cutaneous stimuli (Figs. 3, 4). Caudal to area 3b in area 1, responses were obtained to light touch of digit 2, the palm, the wrist, and the forelimb; the somatotopic pattern revealed by these recordings at least roughly corresponds to that seen in adult marmosets. Rostral locations in area 3a were activated by light touch on the hand,
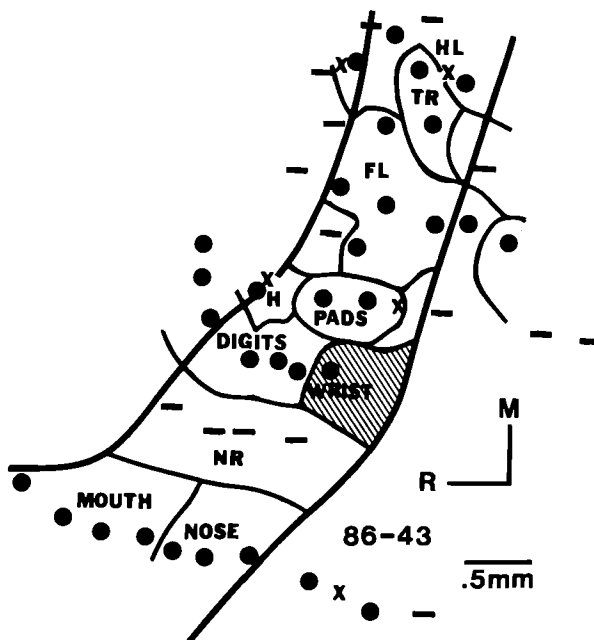

FIGURE 4. The somatotopic organization of area 3b in a 1-day-old marmoset (86-43). As in the previous figure, an adult-like pattern is apparent. Both mediolateral and rostrocaudal sequences of recording sites reveal a mature pattern. A large × marks lesions at physiological boundaries, and a minus (−) marks penetrations where neurons were unresponsive to cutaneous stimulation. Abrreviations as in previous figure.

forearm, or back of digit 1 in a somatotopic pattern that approximates that found in area 3a in adults.

Cortical architecture was examined in three newborn and six adult marmosets. In the two experimental cases, the cortex was removed, flattened, and cut parallel to the surface. In such preparations from adult monkeys, area 3b is densely myelinated in sections through the middle to deep layers of cortex, whereas more rostral fields 3a and motor cortex and caudal fields 1 and 2 are less densely myelinated (Fig. 5A). In newborn marmosets, the responsive zone associated with a somatotopic pattern characteristic of area 3b also is more densely myelinated than surrounding cortex. For example, in the case illustrated in Figure 5B, a mediolateral band of more densely myelinated cortex is apparent, and marked lesions indicate that the zone of cortex that was responsive to cutaneous stimuli is within this myelinated band. However, the myelination is clustered in many small patches and is much less uniformly distributed than in adult marmosets.

In one newborn marmoset, the cortex was cut parasagittally and stained for Nissl substance (Fig. 5D). Similar preparations in the adult (Fig. 5C; also see Carlson et al., 1986) demonstrate architectonic features typical of area 3b in other primates (e.g., Nelson et al., 1980; Sur et al., 1982). Thus layer IV is densely packed with cells and darkly staining, layer V is sparsely packed with cells and lightly staining, and layer VI is somewhat densely populated and darkly staining (Fig. 5C). Although 3b in the 1-day-old infant has basically similar features (Fig. 5D), the laminar boundaries of cortical layers are less sharp and neurons are more densely packed.

SQUIRREL MONKEYS

Recordings from area 3b and adjoining fields 3a and 1 in one newborn squirrel monkey revealed that area 3b in the newborn closely resembles the adult in responsiveness to cutaneous stimuli and somatotopic organization, whereas the responsiveness of area 1 to cutaneous stimuli is greatly reduced in the newborn.

The location of 3b in adult squirrel monkeys is illustrated in Figure 1C, and a summary of the somatotopic organization of 3b, based on Sur et al. (1982), is shown in Figure 6. Further details of the somatotopic organization and responsiveness of anterior parietal cortex in adult squirrel monkeys are included in the reports of Sur et al. (1982), Cusick et al. (1985) and Merzenich et al. (1987). The somatotopic organization of 3b in squirrel monkeys is basically like that described for other primates, with a progression of representation of body parts from foot to mouth in a medial to lateral sequence in cortex. Neurons throughout area 3b are highly responsive to cutaneous stimulation. Typical receptive field sizes and configurations are illustrated in Figure 6. As for other primates, neurons in the hand representation have small cutaneous receptive fields (RF 1, Fig. 6 bottom), whereas neurons in the trunk representation are activated by cutaneous inputs from relatively large areas on the trunk (RF, E, Fig. 6 middle).

In the newborn squirrel monkey, area 3b had about the same relative size and location (Fig. 1D) as in the adult (Fig. 1C). Microelectrode recordings were obtained from a large sector of area 3b extending from near the medial wall to near the lateral
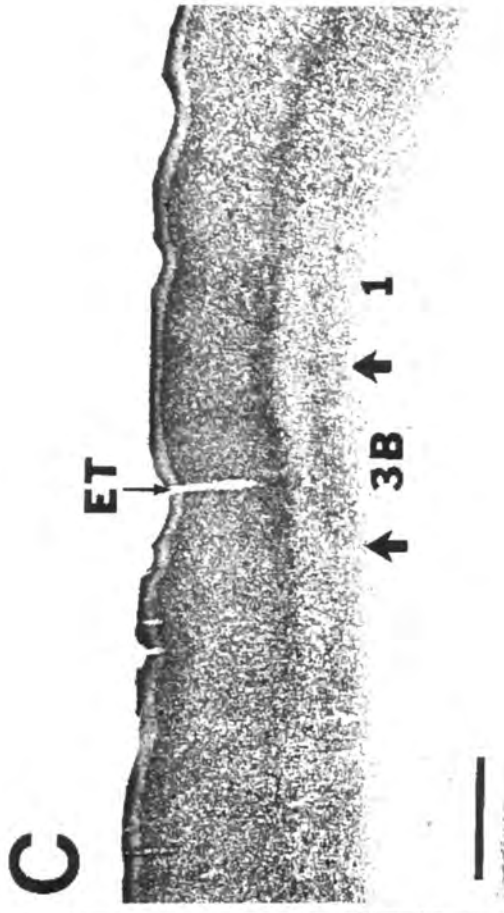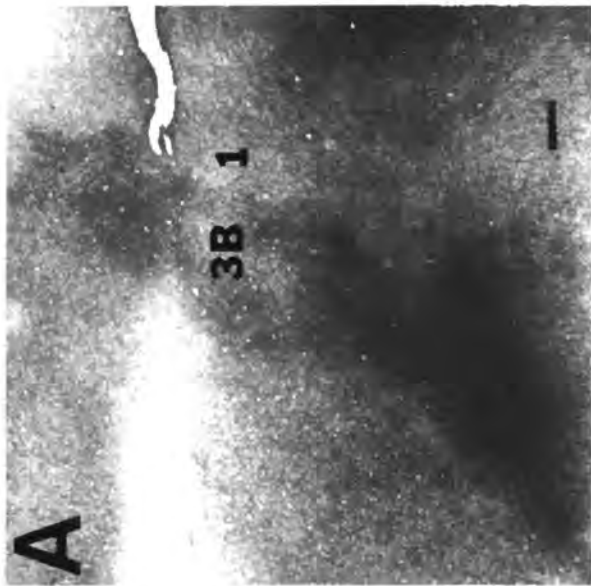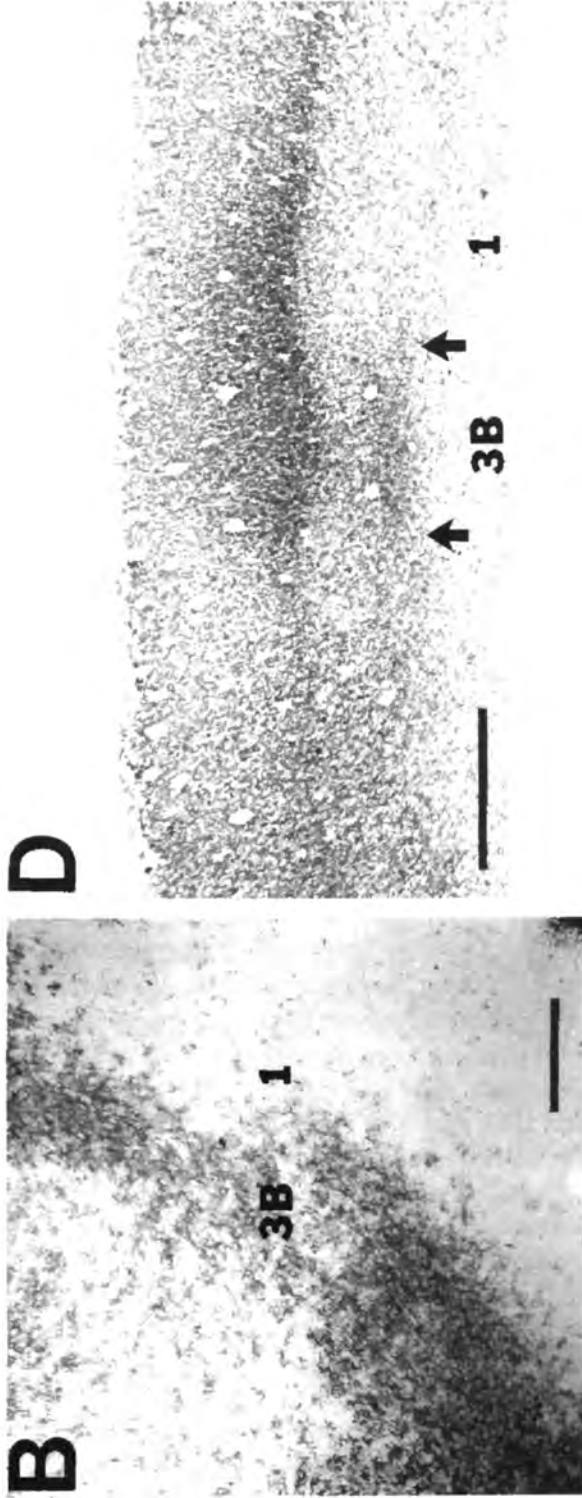
FIGURE 5. Lightfield photomicrographs of brain sections through area 3b in adult and newborn marmosets. (A) Myelin stain preparation of a 40-μm section cut parallel to the surface of artificially flattened cortex in the region of area 3b of an adult. Area 3b is apparent as a darkly stained region (cf. Fig. 1). (B) Similar preparation from a 1-day-old marmoset. Area 3b is more densely stained than surrounding cortex, but less densely stained and more unevenly stained than in the adult. (C) Area 3b in a 50-μm parasagittal brain section stained for Nissl substance from an adult. Arrows indicate architectonic boundaries. An electrode track (ET) within 3b is also apparent. (D) Area 3b in a similar parasagittal section cut from the brain of a newborn. Thick arrows mark architectonic boundaries. Calibration bar: 1 mm.
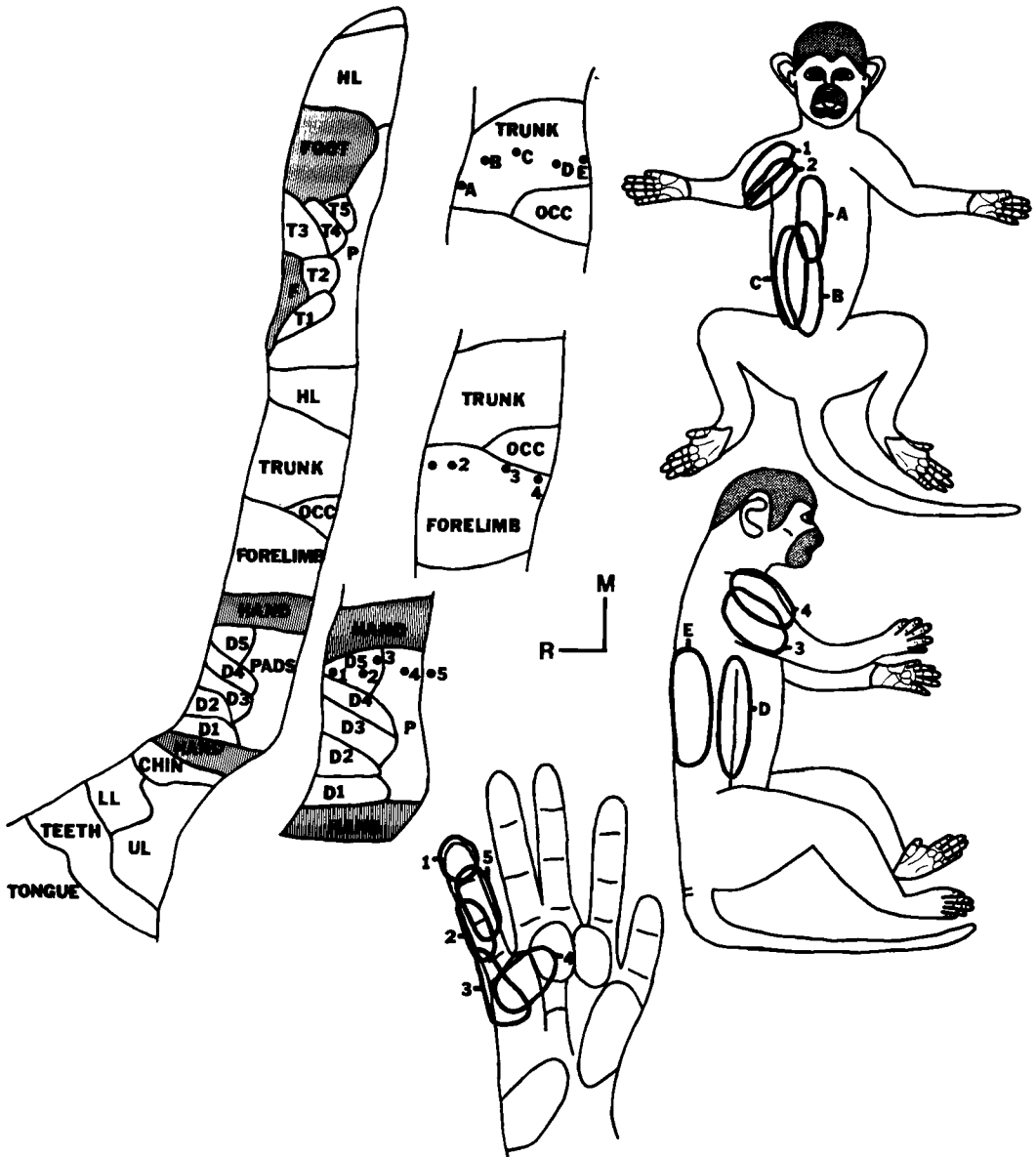
FIGURE 6. The somatotopic organization of area 3b and representative receptive fields for an adult squirrel monkey. The summary and receptive fields have been redrawn and modified from Sur *et al.* (1982). Conventions as in previous figures.

fissure. Most of the explored portion was responsive to moving hairs and lightly touching the skin. However, several small regions (see Fig. 7 upper left) within 3b were unresponsive to cutaneous stimuli. The existence of several unresponsive regions in area 3b is not characteristic of adults, although small unresponsive zones occasionally occur in adults as a result of local disruption of blood flow or other trauma. Since no trauma or interruption of blood flow was evident in the infant

cortex, the unresponsive zones in 3b of the newborn squirrel monkey may reflect the immaturity of the cortex.

Receptive fields for recording sites in area 3b of the newborn squirrel monkey were approximately adult-like in proportion relative to body size. Thus for both adults and the newborn, receptive fields on the glabrous hand were typically confined to a part of a digit or one or two pads, whereas receptive fields on the upper arm and trunk included much of the arm or trunk (Figs. 6, 7).

The somatotopic pattern of activation in area 3b of the newborn squirrel monkey resembles the adult pattern. In both, the digits of the foot (T5–T1), the hindlimb, trunk, forelimb, and digits of the hand (D5–D1) are represented in a mediolateral sequence in cortex. In adult squirrel monkeys, the ventral trunk is represented at the rostral border of area 3b (Fig. 6 upper right), and the same arrangement was revealed in the newborn squirrel monkey (Fig. 7 right). In the cortex devoted to the hand in adults, rostrocaudal rows of recording sites displayed distal to proximal progressions of receptive fields on the glabrous digits, with a reversal of the receptive field progression as the row of recording sites extends into area 1 (see lower Fig. 6). Similarly in the newborn squirrel monkey, distal digits, proximal digits, and palmer pads activated successively more caudal sites in area 3b. Scattered patches of the hand region of area 3b were devoted to the dorsal hairy hand in the newborn monkey (Fig. 7). Whereas this patchlike distribution differs from the more continuous representation of the dorsal hand skin in some adult squirrel monkeys (Fig. 6), such a mixture of locations related to the dorsal and to the ventral hand is well within the range of variability found within normal adults (Merzenich *et al.*, 1987). Results from the newborn squirrel monkey also differed from those in adults in that no neurons were activated in the lateral part of area 3b that represents the face.

In the adult squirrel monkey, area 1 is almost as responsive to tactile stimulation as 3b. Area 1 contains a parallel, roughly mirror image replication of the cutaneous representation in 3b. As in other primates, area 3a is largely devoted to inputs related to muscle spindles, but some recording sites are often adequately activated by cutaneous inputs as well. In the newborn squirrel monkey, only a small portion of area 1 was activated by cutaneous inputs, and this portion of area 1 was along the border of area 3b. Neurons in this responsive region of area 1 were activated by light touch on the pads of the hand, and receptive field sizes were similar to those of area 3b. Since the recordings were along the margin of area 3b, they may actually reflect activity in area 3b rather than area 1. Cortex medial, lateral, and caudal to this responsive portion of area 1 was unresponsive to cutaneous stimuli. In area 3a, neurons were activated at only a few recording sites along the 3b border, and strong taps on the skin were required to drive these cortical neurons.

At the end of the recording session, marker lesions were placed at boundaries of the representation judged to be within area 3b. When lesions were matched with architectonic distinctions, the results showed that the representation (Fig. 7) was coextensive with a distinct architectonic field with the identifying features of area 3b (Fig. 8A, B). Nevertheless, this area 3b in the newborn squirrel monkey was immature in appearance. In particular, cells were more densely packed and layers were more poorly differentiated than in the adult.
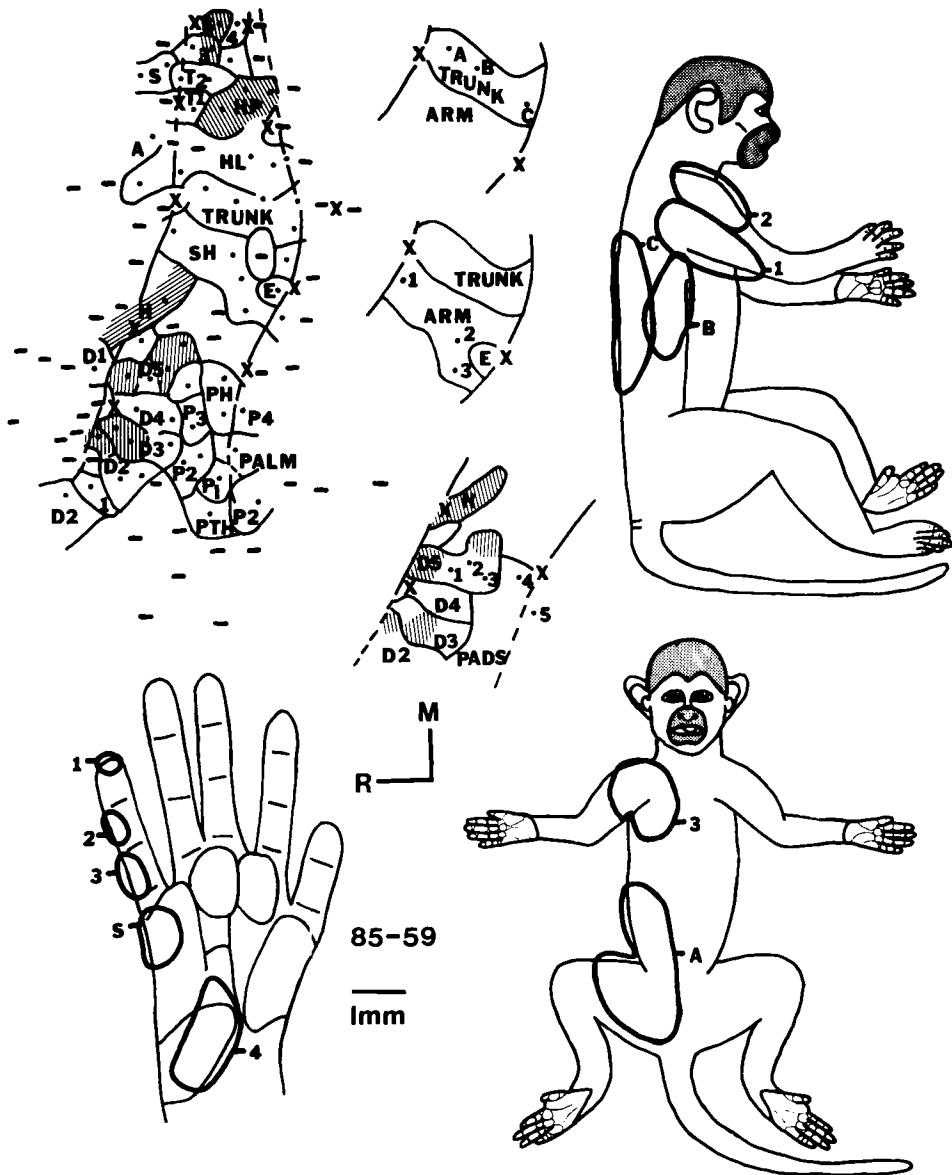
FIGURE 7. The somatotopic organization of area 3b and representative receptive fields for a 1-day-old squirrel monkey. Most features of the respresentation in area 3b were similar to the adult (Fig. 6). Area 3b boundaries were determined architectonically. Some cortex immediately rostral (area 3a) and caudal (area 1) to area 3b were responsive to cutaneous stimuli. Dots mark electrode penetrations in responsive cortex, and an × marks penetrations with marker lesions. Penetrations in unresponsive cortex are marked with a minus (−). Other conventions as in previous figures.
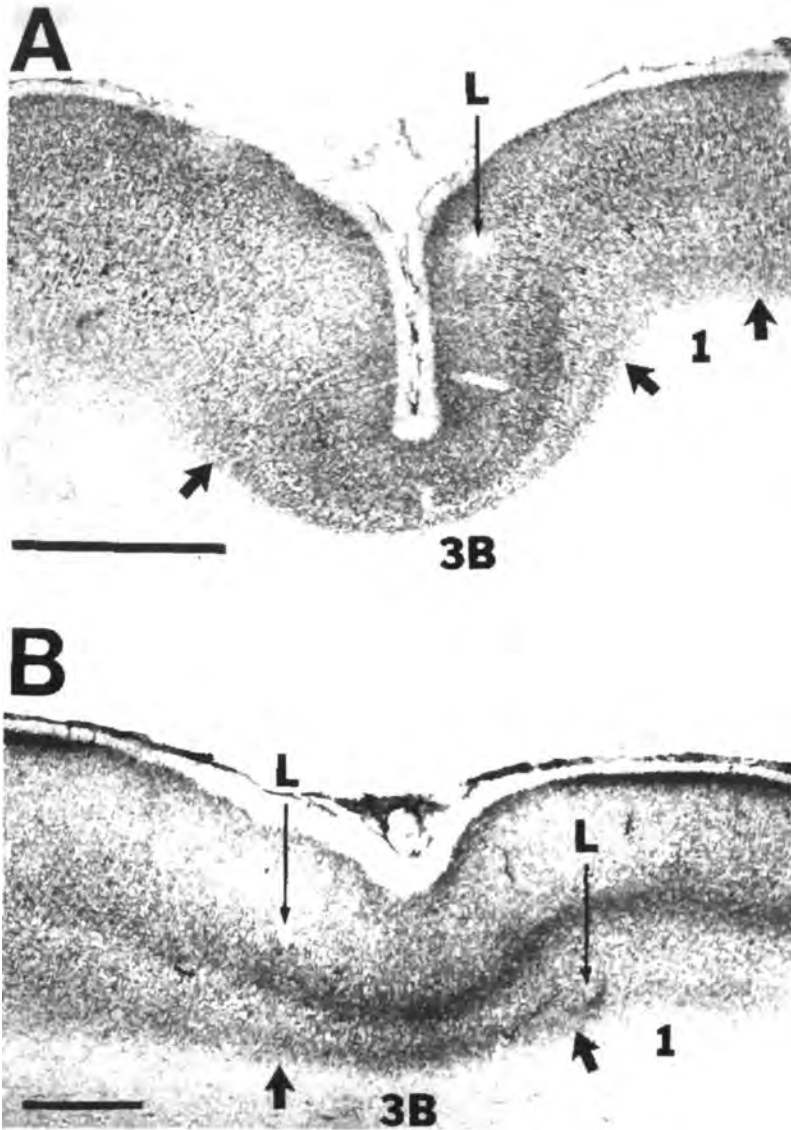
FIGURE 8. The cytoarchitecture of area 3b in adult (A) and newborn (B) squirrel monkeys. The lightfield photomicrographs are of parasagittal Nissl preparations sectioned at 50 μm. Microlesions (L) were used to mark physiological boundaries and relate microelectrode maps to cortical architecture. Calibration bar: 1 mm.

MACAQUE MONKEYS

Observations were obtained from two newborn (1-day-old) macaque monkeys and one macaque monkey of 1 month of age. In anesthetized newborn macaque monkeys, areas 3b and 1 were unresponsive to cutaneous stimuli, but responsiveness to cutaneous stimuli and adult-like somatotopic organization appeared by at least 1 month of age.

Previous studies allow comparisons of results from infants with those from adults. In the adult macaque, area 3b is largely on the posterior bank of the central sulcus (Fig. 1E). Neurons in 3b are responsive to light tactile stimulation of the contralateral body surface, and there is considerable consistency in reported results (see Pons *et al.*, 1987). The summary of 3b organization in adults in Figure 9 is based on the detailed description of Nelson *et al.*, (1980). As in other primates, a topographic pattern from hindlimb to face is found in a mediolateral sequence in 3b. Receptive field size varies with small receptive fields on the distal digit tips (Fig. 9) and large receptive fields on the trunk. The somatotopic organization of area 3b in macaque monkeys has been described by a number of investigators (e.g., Whitsel *et al.*, 1971; Paul *et al.*, 1972; Nelson *et al.*, 1980; McKenna *et al.*, 1982; Iwamura *et al.*, 1983). As for other primates relatively large regions of cortex are devoted to the hand and foot, with relatively smaller regions representing the trunk and proximal limbs.

In both of the newborn macaques, cortex along the caudal bank of the central fissure and on the dorsolateral surface of the postcentral gyrus was extensively explored for several hours. In the two cases, roughly 200 recording sites were examined. Neurons did not respond to light tactile stimulation in either case, although strong taps over a general body region could sometimes elicit a response. The recording sites included parts of area 3b or area 1 that would normally represent the face, hand, forelimb, trunk, and hindlimb. The weak responses to strong taps that were obtained revealed a gross mediolateral somatotopic pattern that proceeded from hindlimb, to hand, to face. Subsequent examination of the brain sections from these cases demonstrated that many recording sites were in or near layer IV of area 3b and area 1 (Fig. 10). Such sites would be highly responsive to cutaneous stimuli in adult monkeys.

Recordings from a 1-month-old infant macaque produced quite different results. The responsiveness and somatotopic organization of area 3b, area 1, and even part of area 2 appeared to be largely adult-like in the 1-month-old macaque. Although our sampling of somatosensory cortex in the month-old macaque monkey was limited, the results were highly consistent (Fig. 11). Most electrode penetrations were placed in a mediolateral strip of area 1 on the postcentral gyrus. In penetrations near the central sulcus, the electrode was advanced into the depths of the sulcus so that recordings were obtained from area 3b on the caudal bank of the fissure, as well as from area 1. As in adults, neurons in both area 1 and area 3b responded to light tactile stimulation of the contralateral body surface. Receptive fields were proportionally the size of those in adults (Fig. 11). The progression of recording sites from medial to lateral in 3b in the infant revealed a somatotopic sequence from hindlimb to face. In the most medial recording sites in 3b, neurons were activated by light touch on the hindlimb. This cortex corresponds to the region where the hindlimb is represented in area 3b of adult macaques. A more lateral row of recording sites had receptive fields on the trunk. Thus, as in adults, the trunk is represented lateral to the hindlimb. Neurons in successively more lateral sequences of recording sites were activated by cutaneous inputs from first the forelimb, then the dorsal hand, next digits 5 through 1, and finally the face. This topographic pattern matches that found in the adult. In
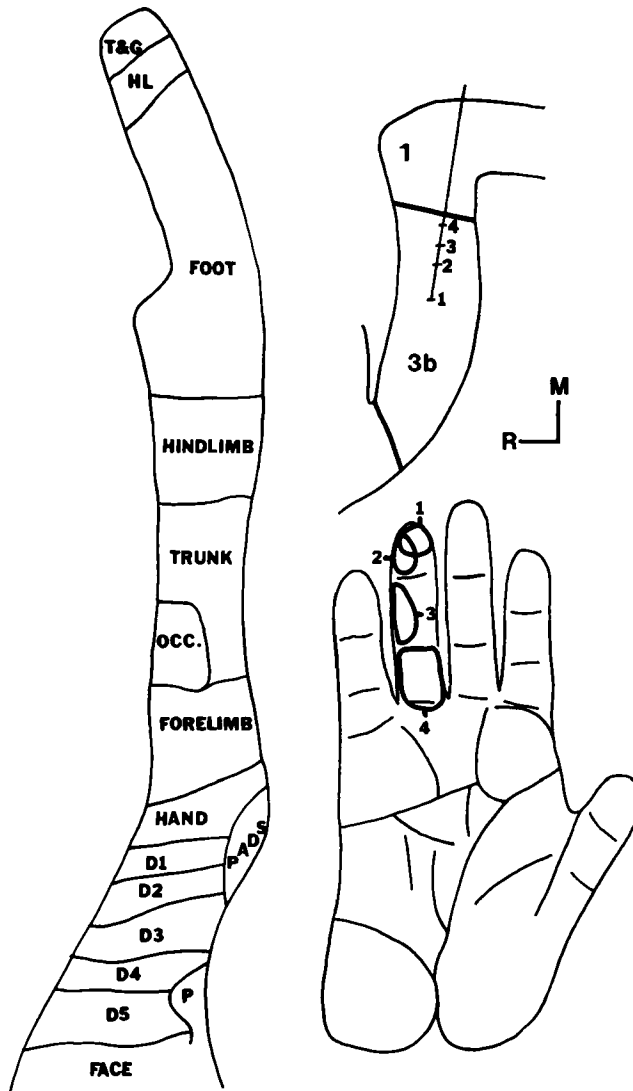
FIGURE 9. The somatotopic organization of area 3b in an adult macaque monkey and representative receptive fields. The map of area 3b (right) has been redrawn and modified from Nelson *et al.* (1980). (See Fig. 1 for the location of area 3b.) The receptive field sequence on the glabrous hand corresponds to the recording site sequence indicated on part of a parasagittal brain section showing the caudal bank of the central sulcus in the region of the hand representation. Lines mark the deep border of area 3b with area 3a and the superficial border of area 3b with area 1. Deeper recording sites than 1–4 correspond to small receptive field on the digit tip and around the nail bed. See Pons *et al.* (1987) for more extensive data from the area 3b hand representation of adults. P = pads; HL = hindlimb; T & G = tail and genitalia.
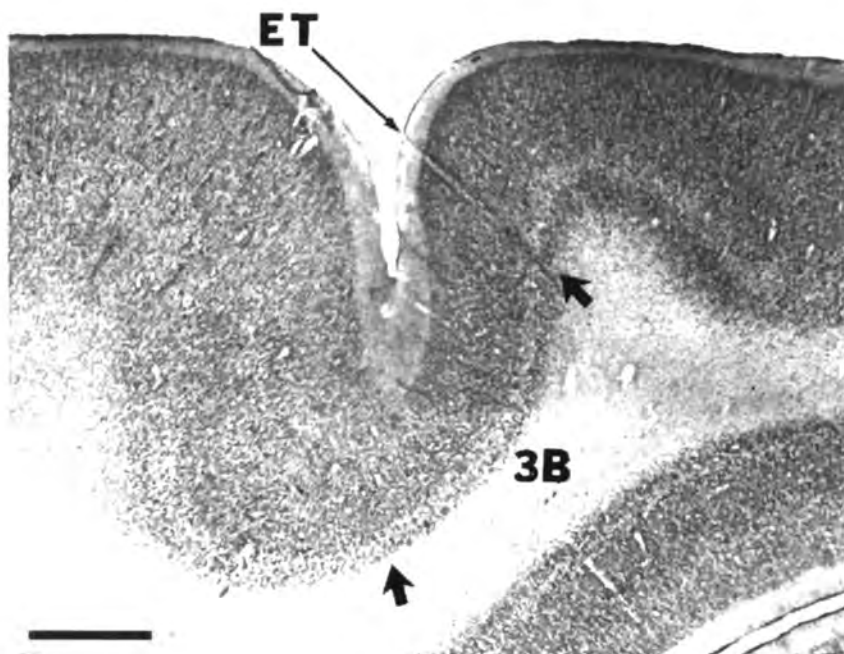
FIGURE 10. A lightfield photomicrograph revealing the immature appearance of areas 3b and 1 in a 1-day-old macaque monkey. ET marks an electrode track that traveled through layer IV in this animal. Abbreviations as in previous figure.

adults, most of the hand region of area 3b is activated by the distal phalanges of the digits, whereas the proximal digits and the pads activated cortex near the area 3b/1 border. A typical receptive field sequence demonstrating this relationship in the adult is shown in Figure 9. Receptive fields 1–4 progress from the digit tip to the proximal phalange as recording sites progress from the middle of area 3b to the area 3b/1 border (deeper parts of area 3b are devoted to the tip of the digit). Similar data are shown for the month-old macaque, where receptive fields progress from digit tip (the finger changes from D5 to D4 due to electrode angle) to the palm, and then back to the digit tip for recording sites in area 1 (Fig. 11).

In adult macaques, area 1 has a parallel somatotopic organization that roughly mirrors that of area 3b. Like 3b, neurons in area 1 are driven by light tactile stimulation. Although incompletely mapped in the 1-month-old infant, neurons in area 1 were highly responsive to tactile stimulation. The recordings that were made in area 1 revealed topography from hindlimb to face with a mediolateral sequence in cortex that is similar to that found in adults.

In the 1-month-old macaque infant, marker lesions placed at physiological boundaries were identified in brain sections stained for Nissl substance. Thus recording sites could be related to architectonic areas 3b and 1. In adults, 3b is characterized by a darkly staining layer IV that is densely populated with granule cells.
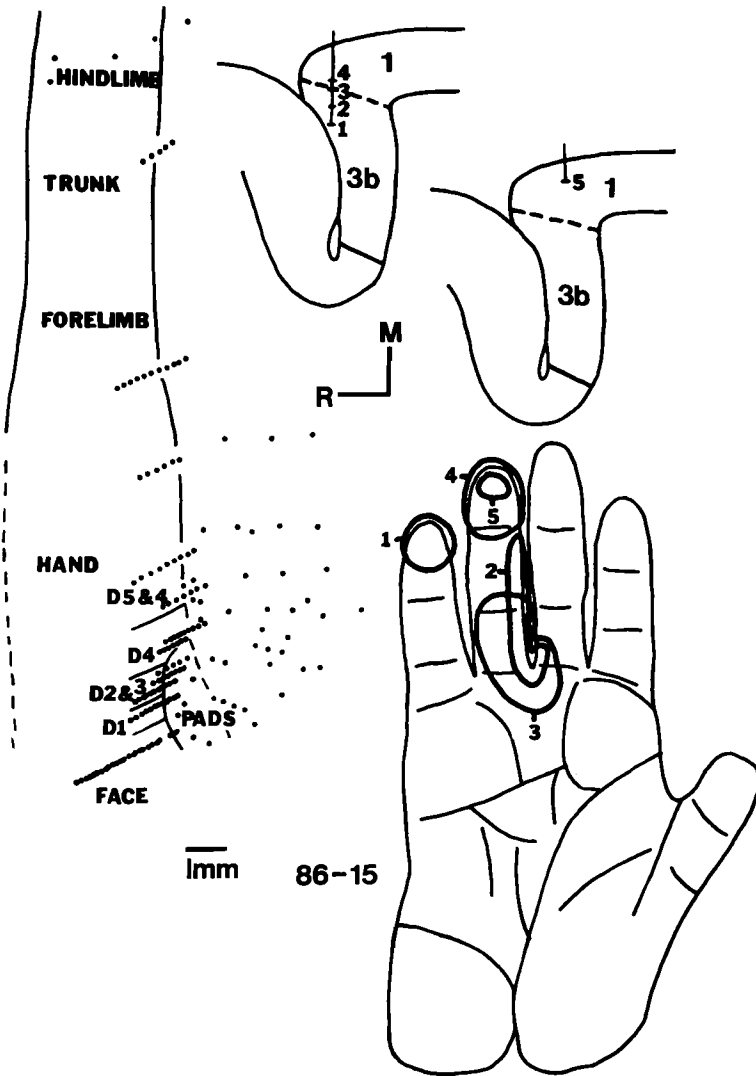
FIGURE 11. The somatotopic organization of area 3b of a 1-month-old infant macaque monkey, and representative receptive fields from areas 3b and 1. On the left, a surface view of area 3b unfolded from the central sulcus (see Fig. 1). Solid lines mark architectonic boundaries, and dashed lines indicate regions where the precise location of the borders were less certain. Recording sites spaced along electrode penetrations are projected to the surface (dots). Although the mapping was incomplete, a hindlimb to face progression from medial to lateral in area 3b was evident, and digits (D1–D5) and pads of the hand were found in expected locations. Receptive fields on the hand correspond to recording sites along electrode penetrations indicated on two drawings of parasagittal brain sections on the upper right.
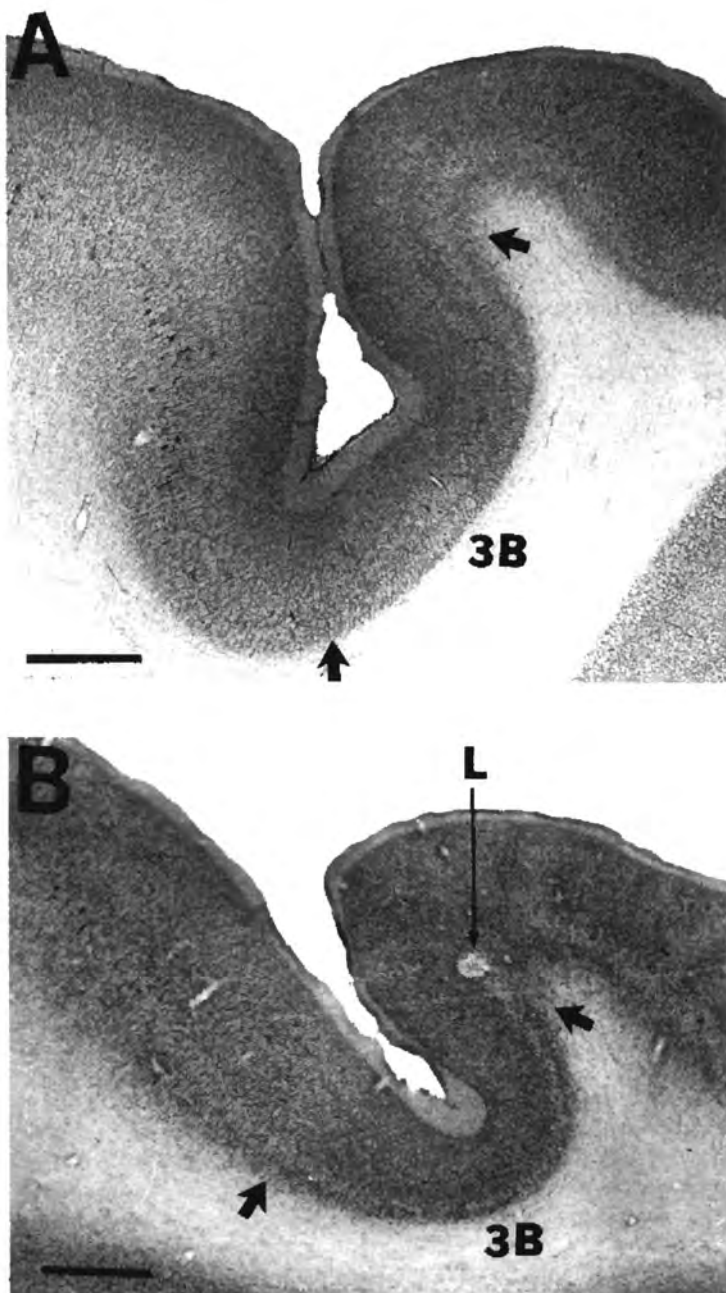
FIGURE 12. Lightfield photomicrographs of parasagittally sectioned somatosensory cortex that has been stained for Nissl substance in the adult (A) and 1-month-old infant (B). The laminar distinctions of 3b in the 1-month-old infant are less clear than those in the adult. Abbreviations as in previous figures. Calibration bar: 1 mm.

Layer VI is also darkly stained and packed with neurons, whereas layer V appears lighter and is less densely packed with cells (Fig. 12A). Although the appearance of 3b in the 1-month-old macaque is much like that described for the adult (Fig. 12B), overall cell packing is much denser and laminar differences in cell density are less pronounced.

DISCUSSION

The present study is the first attempt to determine the responsiveness and somatotopic organization of somatosensory cortex in newborn monkeys. Microelectrode recordings were made in architectonically identified subdivisions of somatosensory cortex of three species of infant monkeys. The results indicate that normal maps of much of the skin can be revealed in area 3b of marmoset and squirrel monkeys immediately after birth and by at least 1 month of age in macaque monkeys. Neurons in these maps are responsive to light tactile stimuli and the movement of hairs, and receptive fields are proportionately the same size as in adults. The results suggest that (1) adult-like somatosensory cortical representations can develop without the benefit of refinements based on postnatal sensory experience, (2) area 3b is at a more mature stage of development in newborn marmoset and squirrel monkeys than in newborn macaque monkeys, (3) responsiveness in higher order fields such as area 1 may mature later than responsiveness in primary fields such as area 3b, and (4) the apparant capacity of infants to more fully compensate for deafferentation and lesions than adults is not based on immature equipotentiality in the somatotopic organization of primary somatosensory cortex. These and other issues are discussed below.

RESPONSIVENESS OF AREAS 3b AND 1 TO SOMATOSENSORY STIMULI IN INFANT MONKEYS

Neurons in area 3b of newborn marmoset and squirrel monkeys were found to be responsive to light tactile stimulation of the glabrous skin and the movement of hairs on the hairy skin. In addition, receptive fields occupied about the same proportions of skin as in adult monkeys. These observations correspond to those made by Rubel (1971) for neurons in SI of cats (evidence is presented elsewhere that area 3b of monkeys is the homologue of SI as generally described in other mammals; see Kaas, 1983), and they are consistent with the general observation that receptive field properties in sensory cortex of newborn mammals can have many adult-like features (e.g., Hubel and Wiesel, 1963; Armstrong, 1975; Kennedy *et al.*, 1983). Of course, this does not mean receptive field properties are fully developed in these neurons at birth. We noted a general lack of spontaneous activity in the recorded neurons, and they often appeared to respond less vigorously than those in adults. In addition, neurons were sometimes difficult to drive at isolated sites or over parts of the field.

Other investigators (e.g., Hubel and Wiesel, 1963; Rubel, 1971; Kennedy *et al.*, 1983; Albus and Wolf, 1984; Braastad and Heggelund, 1985) have noted similar differences in the responsiveness of neurons in infant mammals, as well as the failure

of immature neurons to demonstrate other adult-like response properties (such as binocular activation, or direction selectively for neurons in visual cortex). Undoubtedly, detailed comparisons of neuron response properties in adult and infant monkeys would reveal many age-related differences (see Ferrington and Rowe, 1985, on the maturation of tactile signaling capacities of neurons in the somatosensory systems of cats). Yet, it is clear that many adult-like receptive field properties, including those related to receptive field size, can be present at the time of birth.

Since neurons in area 3b of squirrel monkeys and marmosets have proportionately normal receptive field sizes at birth, the connectional framework from the peripheral receptor array to cortical neurons must be in place at birth. Furthermore, since receptive field size in part depends on cortical inhibitory mechanisms (see Alloway and Burton, 1986; Dykes et al., 1984), GABA-ergic cortical neurons may be functional as well.

In newborn macaque monkeys, neurons in area 3b and in area 1 failed to respond to cutaneous stimuli. Neurons at only a few sites were activated in area 1 of newborn marmosets, and only a few area 1 sites along the area 3b/1 border were activated in a newborn squirrel monkey. It seems unlikely that the neurons in unresponsive regions of cortex were nonfunctional, although this remains a possibility. In rats, neurons in SI do not yet have synaptic contacts with thalamocortical afferents at birth (Wise and Jones, 1978), and these connections (Killackey and Belford, 1979) and neuronal responsiveness (Armstrong-James, 1975; Verley and Axelrod, 1975) take several postnatal days to develop. However, the development of the neocortex is much more advanced at birth in monkeys than in rats, and even the late-maturing callosal connections have acquired an adult-like pattern of origins and terminations by the time of birth in macaque monkeys (Killackey and Chalupa, 1986). Thus cortical neurons in monkeys may well be functional in alert newborn monkeys, and the lack of responsiveness of area 1 neurons in newborn marmosets and squirrel monkeys, and area 3b and area 1 neurons in newborn macaque monkeys may relate to the depressive effects of anesthetics or perhaps other factors of the recording condition. Anesthetics are known to especially block polysynaptic pathways in adult mammals (see Rubel, 1971), and immature systems with less secure synaptic connections may be more susceptible to disruption.

Whereas a lack of responsiveness in the anesthetized preparation does not necessarily indicate that the cortical areas are nonfunctional in the alert animal, differences in responsiveness of cortical neurons across fields in the same animal and across species suggest differences in the developmental time-course across fields and across species. One observation is that area 1 was less responsive at birth than area 3b in marmosets and squirrel monkeys. In part, this difference may reflect the greater susceptibility of higher order fields to disruption by anesthetics. Although both area 3b and 1 receive afferents from the ventroposterior nucleus of the thalamus, area 1 appears to be a higher order cortical field that is largely processing information from area 3b (see Kaas and Pons, 1988, for review). Even in adult marmosets, area 1 can be unresponsive to cutaneous stimulation under anesthetic conditions that allow area 3b to be quite responsive (Carlson et al., 1986), suggesting that a relay from area 3b to area 1 is disrupted by the anesthetics. The difference in responsiveness of areas 3b and 1 in newborn monkeys may also be related to mat-

uration differences in cortical fields. The results of early studies of myelination patterns suggest that higher-order fields mature later than primary fields (e.g., Flechsig, 1920). Thus area 1 may have fewer functional synapses or more disruptable synapses at birth than area 3b. However, there is evidence that different cortical areas develop mature densities of synapses at the same time (Rakic *et al.*, 1986).

A second relevant observation is that areas 3b and 1 were not responsive to cutaneous stimuli in newborn macaque monkeys, but these fields were responsive 1 month later. This result suggests that area 3b and perhaps other cortical fields are less mature at birth in Old World than in New World monkeys. This possibility is supported by differences in the sensorimotor development of New World and Old World monkeys at birth (see Shively and Mitchell, 1986). Newborn marmosets receive little help from their mother after birth, and the infant must cling to the mother and climb to nipples unaided. Similarly, unless the infant is weak, newborn squirrel monkeys cling to their mothers and move about on her back without assistance. In contrast, newborn macaque monkeys require support and assistance from their mother.

REPRESENTATION OF SKIN RECEPTORS IN AREAS 3b AND 1 OF INFANT MONKEYS

The results indicate that basically adult-like somatotopic maps appear very early in areas 3b and 1 of monkeys. These maps can be revealed at birth in area 3b of marmosets and squirrel monkeys, and by the age of 1 month in macaque monkeys. The somatotopic patterns are largely within the considerable range of normal variation observed in adult monkeys (Merzenich *et al.*, 1987). In the only other mapping study of somatosensory cortex in newborn mammals, Rubel (1971) observed a basically adult-like pattern of somatotopic organization in SI of newborn cats. Other studies have demonstrated that neurons in sensory cortex of other newborn mammals can be responsive and have appropriate receptive field locations (e.g., Kennedy *et al.*, 1983). Thus adult-like sensory maps may be in place at birth for at least some cortical fields in a number of mammalian species.

Recently, considerable evidence has accumulated to support the view that neural activity patterns are important in the development and maintenance of sensory maps (see Constantine-Paton, 1982; Kaas *et al.*, 1983; Jenkins and Merzenich, 1987; Merzenich *et al.*, 1987; Kaas, 1988). A currently popular view is that crude topographic features of cortical maps can develop without instruction from the receptor sheet, but refinement of the map and much of the individual variability in the map depends on synaptic selection based on correlated activity originating in peripheral stimulation sequences (see Kaas, 1988). The present results, together with those of Rubel (1971), indicate that the basic somatotopic patterns of normal cortical maps can develop without the benefit of postnatal stimulation (for further discussion, see Young and Rubel, 1986). Of course, prenatal stimulation patterns may be important, and postnatal stimulation patterns may add refinements that were not detected in the present study. Some differences in infant and adult maps were apparent in area 3b of marmosets, suggesting that postnatal refinements of maps do occur. Postnatal stimulation patterns may also relate to the development of individual differences in the organization of somatosensory cortex (Merzenich *et al.*, 1987). Finally, we know

little about the development of maps in higher-order sensory fields, but there is evidence that higher-order visual areas in cortex more extensively compensate for primary visual cortex lesions in infant than adult cats (Spear *et al.*, 1980; Tong *et al.*, 1984).

HISTOLOGICAL APPEARANCE OF AREAS 3b AND 1 AT BIRTH

Photomicrographs in the present report demonstrate that area 3b can be delimited in newborn monkeys by characteristics that identify the field in adult monkeys. At earlier prenatal periods, the somatosensory fields are much more uniform in appearance and area 3b may not be distinct (Killackey and Chalupa, 1986). Striate cortex is also easy to identify in these newborn monkeys (unpublished observations, Lund *et al.*, 1977; O'Kusky and Colonnier, 1982), and other fields are apparent as well. Thus studies depending on the architectonic identification of area 3b are possible from the time of birth. However, it is also obvious that area 3b and other fields are immature in appearance at birth. Cortex is thinner, neurons are more densely packed, layers are less differentiated, and myelination patterns are less distinct. The changes that subsequently occur include enlargement of neurons and dendritic processes (Lund *et al.*, 1977). However, thalamic afferents are undoubtedly in place before birth (Rakic, 1981), and the immature neurons have some adult-like response properties at or shortly after birth (see Results).

CONSEQUENCES OF DEAFFERENTATION AND LESIONS OF SOMATOSENSORY CORTEX IN INFANTS AND ADULTS

Newborn and young mammals appear to be more capable of recovery from damage to somatosensory cortex than adults. The experiments of Carlson (1984) indicate that lesions of the hand region of area 3b in newborn macaque monkeys fail to produce the impairments in the ability to make tactile discriminations that follow such lesions in adults, and depriving large portions of SI of normal sensory activation with spinal cord lesions in young kittens is followed by a recovery of responsiveness in the deprived cortex that does not occur after such lesions later in development (McKinley *et al.*, 1987). The results of the present experiments suggest that the apparently different consequences of lesions and deafferentations in infant and adult mammals are not related to differences in the basic organization of SI or area 3b at the time of damage. The somatotopic maps in area 3b of monkeys (present study) and SI of cats (Rubel, 1971) have adult-like organization at or soon after birth. The adult-like structure of these somatosensory representations suggests, but does not demonstrate, that the major activating connections of the primary representations are adult-like at or soon after birth, and that the greater recovery after infant lesions is not a consequence of the persistence of developmentally exuberant inputs. In newborn cats (Innocenti *et al.*, 1980) and rats (Olavarria and Van Sluyters, 1985), the late-maturing callosal connections remain exuberant until after birth for at least visual areas of cortex, but even the callosal pattern of connections matures before birth in macaque monkeys (Killackey and Chalupa, 1986).

One explanation for differences in the effects of lesions in infants and adults is that the lesions or the behaviors are not really equivalent (see Goldman, 1974; Meyer

and Meyer, 1984). Thus, given the difficulty of matching lesions in infants and adults, the lesions could spare parts of critical structures in infants. Whereas it is difficult to experimentally approach these problems, the responsiveness of somatosensory cortex in infant monkeys means that lesions could be evaluated for equivalency with greater accuracy. Carlson (1984) placed lesions in cortex according to the expected position of the hand representation. The present results indicate that it is possible to map the relevant region of cortex with microelectrodes in both infant and adult monkeys and remove equivalent portions of the maps.

Developmental studies of the effects of nerve section, repair, and regeneration on somatosensory cortex in marmosets have not revealed major differences between maps of area 3b in adults with section and repair of the median nerve as infants or adults (Wall et al., 1986). In both types of preparation, the portion of cortex related to the median nerve was reactivated in a somatotopically disorganized manner. This result is consistent with the observation that the somatotopic organization of area 3b is adult-like at birth and the supposition that an adult-like pattern of thalamocortical inputs is in place. The nerve section and repair experiments provided no evidence for the possibility that postnatally overabundant connections are shaped and preserved by peripheral stimulation patterns in order to correct the effects of disorganized peripheral nerve regeneration.

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