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Formation and growth of the cerebral convolutions. I. Postnatal development of the median-suprasylvian gyrus and adjoining sulci in the cat*

ISIDRO FERRER, MIQUEL HERNÁNDEZ-MARTÍ†, EULALIA BERNET† AND ELENA GALOFRÉ

Unidad de Neuropatología, Departamento Anatomía Patológica, Hospital Príncipes de España, Hospitalet de Llobregat, Universidad de Barcelona and †Departamento de Anatomía Patológica, C.S. La Fe, Valencia, Spain

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INTRODUCTION

The appearance of cerebral cortical folds is the result of fortunate strategies in cortical evolution by means of which a major increase in the number and connections of nerve cells is achieved at the expense of minor increases in the whole brain volume. A number of studies have dealt with the formation of cortical convolutions and many theories have been advanced in an attempt to explain some aspects of the development of cerebral cortical folds (Bielchowsky, 1923; Schaffer, 1923; Le Gros Clark, 1945; Barron, 1950; Welker & Campos, 1963; Sanides, 1972; De Leon, 1972; Richman, Stewart, Hutchinson & Caviness, 1975; Todd, 1982; Ferrer, 1984; Prothero & Sundsten, 1984). However, few reports have described the correlation between the gross morphological modifications and histological changes during the growth of the gyrus (Smart & McSherry, 1986*a*, *b*) or have examined the consequence of cortical folding on the shape and internal organisation of nerve cells (Ferrer, Fábregues & Condom, 1987).

The purpose of the present study is to examine the gross morphological changes and modifications in the cortical thickness, as well as regional variations in the number and distribution of neurons in the median-suprasylvian gyrus and adjoining sulci of the cat's cerebral cortex in order to examine in greater detail the sequence of events that occur while cerebral convolutions form and grow.

MATERIALS AND METHODS

Animals

Cats aged 1, 5, 15, 25 days and 6 months were killed under phenobarbitone anaesthesia. The brains were perfused with saline and immediately afterwards fixed by perfusion with 1% glutaraldehyde–2·5% paraformaldehyde (v/v) in phosphate buffer. After being stored overnight at 4 °C the brains were removed from the skull and immersed in the same fixative for several weeks. Three animals were used at each age. Samples of selected cortical regions were processed for quantitative morphological studies on paraffin sections as well as for Golgi impregnations.

* Reprint requests to Dr I. Ferrer, Unidad de Neuropatología, Departamento Anatomía Patológica, Hospital Príncipes de España, 08907 Hospitalet de Llobregat, Spain.

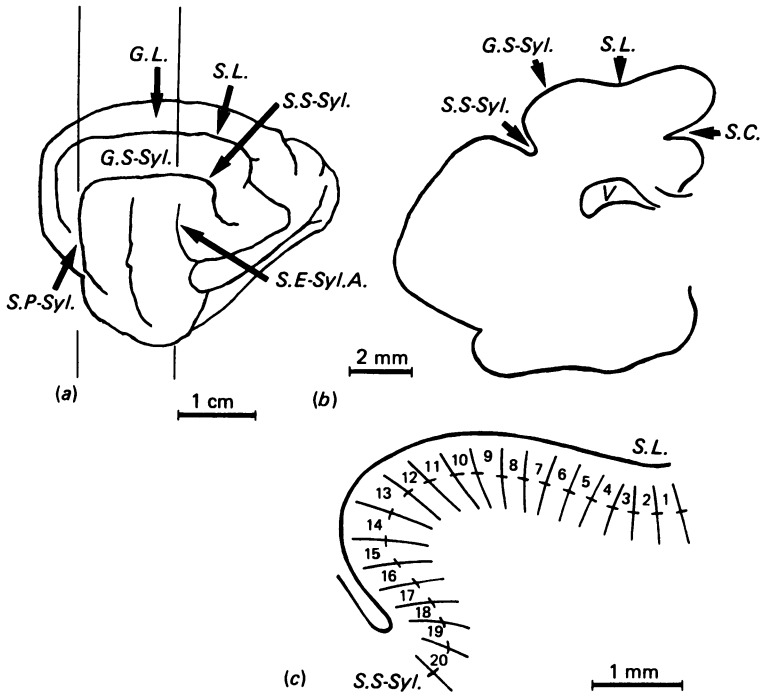

Fig. 1(*a–c*). (*a*) Lateral view of the brain in the adult cat. The vertical lines mark the limits of the cortical region, containing the S.L., G.S-Syl. and S.S-Syl., selected for quantitative morphological studies. (*b*) Coronal section of the brain in the 1 day old cat. (*c*) Division of the cerebral cortex into twenty consecutive fields, labelled 1–20, from S.L. to S.S-Syl. in the cat aged 1 day. Radial lines were traced following the curvature of the nerve cell columns. *G.L.*, gyrus lateralis; *G.S-Syl.*, median suprasylvian gyrus; *S.C.*, sulcus cinguli; *S.E-Syl.A.*, anterior ectosylvian sulcus; *S.L.*, sulcus lateralis; *S.P-Syl.*, postsylvian sulcus; *S.S-Syl.*, median suprasylvian sulcus; *V*, ventricle.

Selection of the cortical region

Morphological studies were focused on the lateral sulcus (S.L.) and the median-suprasylvian gyrus (G.S-Syl.) and sulcus (S.S-Syl.) contained between two perpendicular lines that followed, and extended from, the course of the postsylvian sulcus and the ascending branch of the anterior ectosylvian sulcus (Fig. 1 *a*, *b*).

Morphological studies on paraffin sections

The selected cortical region of the right cerebral hemisphere was embedded in paraffin, and sections 10 μm thick were cut in the coronal plane every 100 μm by means of a sliding microtome. The sections were numbered consecutively from the anterior to the posterior surfaces and were stained with cresyl violet (Nissl's stain). The three sections located halfway along the gyrus ($n/2 \pm 1$) were used for quantitative studies. A photomontage of the complete gyrus and adjacent sulci, obtained at a magnification × 63 (except for the cat aged 1 day, in which the photographs were taken at a magnification × 160), was constructed for each of the sections. Three animals were used at every age; the 45 maps (photomontages) were used for quantitative studies.

For all the photomontages a line was traced at the mid-level of the cellular cerebral cortex (layers II–VI). This line was later divided into twenty equal segments from the depth of the S.L. to the depth of the S.S-Syl. and a series of lines perpendicular to the cortical surface was subsequently drawn at these points following the curvature of the cortical nerve cell columns; these lines divided the whole of the coronal section into fields labelled 1–20 from S.L. to S.S-Syl. (Fig. 1 *c*).

The following parameters were measured at every age.

(1) Cortical thickness (in μm) including the thickness of the cellular layers (layers II–VI) along the gyrus; length of the nerve cell columns (in μm) along the gyrus; total cross sectional area (in mm^2 of the cellular cortex); areas of each one of the twenty fields (in mm^2). Because tissue shrinkage due to tissue processing was different at different postnatal ages the anterior and posterior areas of the cortical samples (sections 1 and n) were estimated before and after paraffin embedding. Measurements were made with a Morphomat 30 (Zeiss) composed of an electromagnetic panel with a pencil interfaced with a microcomputer programmed for the geometrical measurement of the digital panel signals. The crude values of the cortical thickness and cortical areas were corrected according to the percentage of tissue shrinkage at each age.

(2) Number of neurons in each one of the twenty consecutive fields and in the whole section of the gyrus. Neurons were recognised, even in the very young cats, because their nuclei were larger and less dense than those of glial cells.

The crude number of neuronal nuclear points in each field was corrected according to the formula of Abercrombie (1946):

$$P = A\frac{M}{L+M},$$

in which P is the corrected number of nuclear points per section, A is the crude count number of nuclear points seen in the section, M is the thickness of the section (10 μm in our case) and L the average length (in μm) of the nuclei. The average length of the nuclei was measured, by means of the Morphomat 30, at each age, on micrographs obtained at a magnification $\times 1000$ of tangential, serial sections of S.L., G.S-Syl. and S.S-Syl. of the left hemisphere. These values represented the average dimension of the round or oval-shaped nuclei at right angles to the plane of section on which neuronal nuclear points were counted (Abercrombie, 1946). The number of neurons in the total coronal section of the gyrus was the sum of the counts in the twenty consecutive fields of that section.

(3) Density of nerve cells in each one of the twenty fields. This was calculated by dividing the corrected number of neurons by the section area in each one of the twenty fields of the coronal section.

(4) Number of nerve cells in the total length of the gyrus. This figure was obtained at each age by multiplying the number of nerve cells in the total section of the gyrus by the total number of sections (number of mounted sections $\times$ 10).

Golgi studies

Small blocks, 3 mm thick, of the left cerebral hemisphere, containing S.L., S.S-Syl. and G.S-Syl., were processed according to the rapid Golgi method. Briefly, the blocks were postfixed in 3 % potassium bichromate–1 % osmium tetroxide (20/5 v/v) for 3–5 days; later, the samples were rapidly washed in 0·75 % silver nitrate and immersed in a fresh 0·75 % silver nitrate solution for 48 hours. Sections 100 μm thick were obtained on a sliding microtome and were mounted on glass slides.

RESULTS

General morphological findings

In the cat aged 1 day the S.S-Syl. was almost fully developed but the S.L. was only suggested by a discrete depression of the cortical surface; this latter sulcus was, however, easily identifiable in the 5 days old cat and it was almost fully formed in the

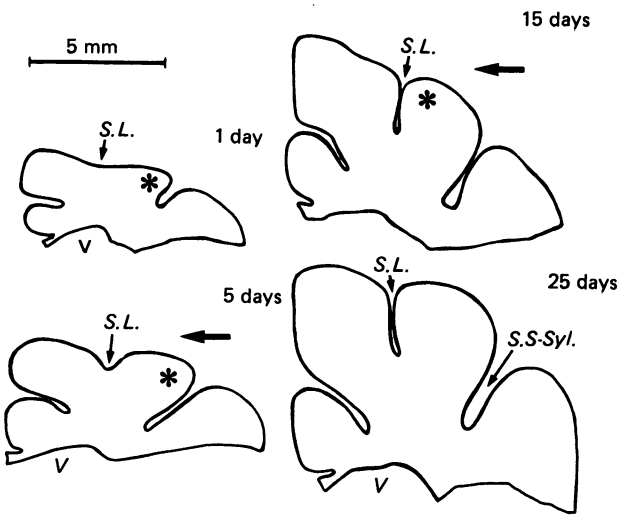

Fig. 2. Camera lucida drawings of coronal sections of the brain of cats at different postnatal ages. *S.L.*, sulcus lateralis; *S.S-Syl.*, median suprasylvian sulcus; *V*, ventricle. The prominence of the gyral ridge is labelled with an asterisk; the large arrows indicate the displacement of the gyral ridge towards the midline that occurs during the formation and growth of the S.L.

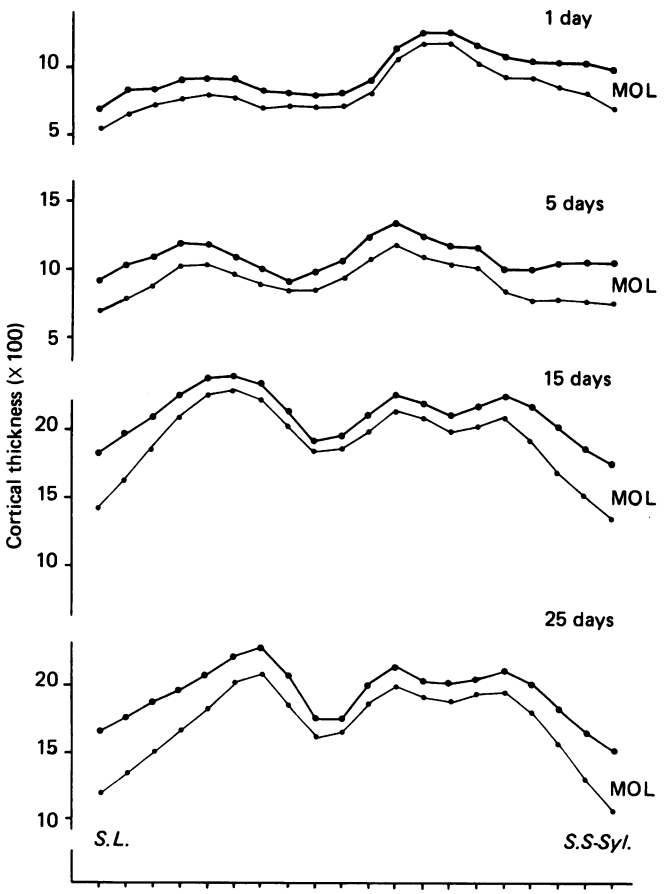

Fig. 3. Thickness (in μm) of the cerebral cortex and molecular layer (MOL) from *S.L.* to *S.S-Syl.* at different postnatal ages.

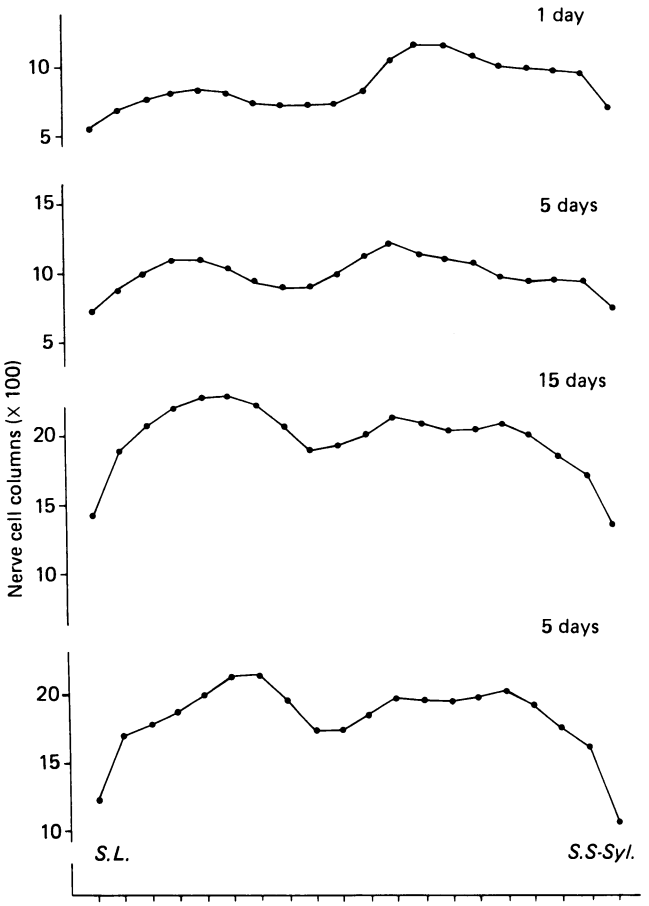

Fig. 4. Length of nerve cell columns (in μm) from *S.L.* to *S.S-Syl.* at different postnatal ages.

cat at 15 days. During the first two weeks of postnatal life the growth of the G.S-Syl. was characterised by two distinctive gross morphological features: one of them was the larger increase in the distance from the ventricle to the crown of the gyrus when compared with the distance from the ventricle to the pial surface of the adjacent sulci; the other was the progressive displacement of the gyral ridge from the almost fully formed S.S-Syl. towards the developing S.L. (Fig. 2). It is suggested from these observations that the sulci remain as relatively fixed zones throughout the process of cortical folding and that the growth of the G.S-Syl. occurs following a lateral to medial volumetric gradient.

Cortical thickness and length of cortical nerve cell columns

As might be expected, an increase in cortical thickness was observed during development; however, this increase was not homogenous along the cortical ribbon nor was it similar at different postnatal ages. As a rule the gyral region was thicker than the sulcal regions at every age but there also was a greater increment of this parameter in the gyrus than in the sulci throughout development.

In addition, in the cat aged 1 day, the gyral region adjacent to the S.S-Syl. was thicker than the gyral region adjacent to the S.L., but in the following days a progressive increase in the thickness of the latter gyral region was observed; in the cat

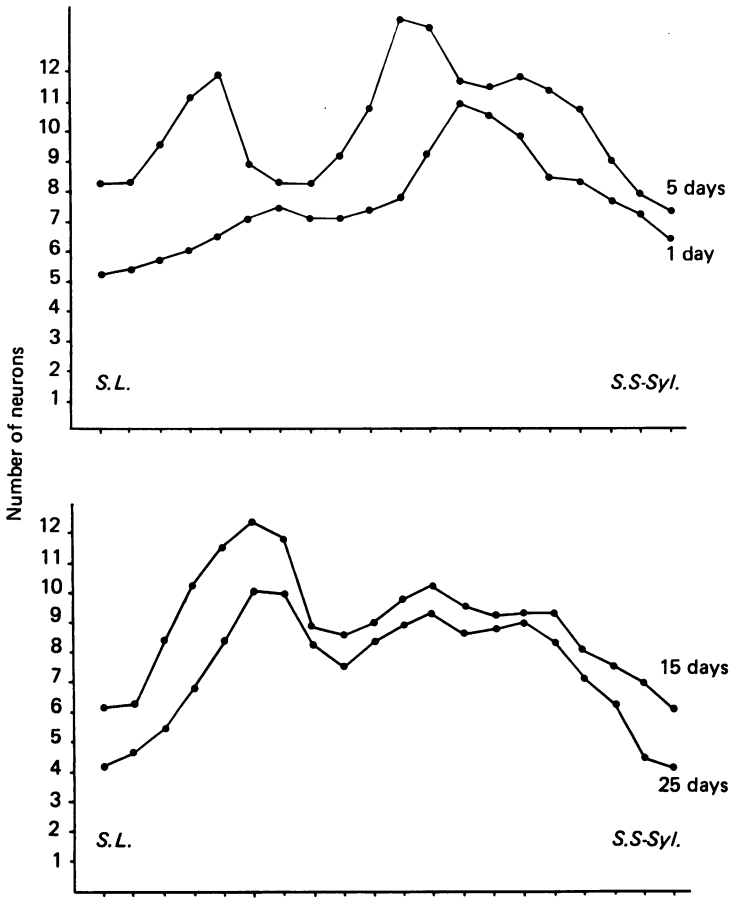

Fig. 5. Average number of nerve cells in coronal sections of the cerebral cortex from *S.L.* to *S.S-Syl.* at different postnatal ages.

25 days old the upper lateral edges of the gyral crown had a similar cortical thickness (Fig. 3).

The thickness of the molecular layer differed regionally and it also changed during development; the molecular layer was thinner in the gyrus than in the sulci and this difference increased as the formation of the gyrus progressed.

The length of nerve cell columns also decreased towards the sulcal zones, but this reduction was smaller than that of the thickness of the cellular cerebral cortex (layers II–VI) because nerve cell columns progressively curved following the concavity of the infolding (Fig. 4).

Number of nerve cells per section

In the cat aged 1 day a greater number of nerve cells was observed in the gyral region next to the S.S-Syl.; however, in the cat aged 5 days there was a progressive increase in the number of neurons in the gyral region adjacent to the developing S.L.; in cats aged 15 and 25 days the greatest number of neurons was found in the gyral region adjacent to the S.L. while the number of neurons decreased in the region adjacent to the S.S-Syl. In addition, a progressive reduction in the number of neurons was observed in the sulci when compared with the gyrus throughout development (Fig. 5).

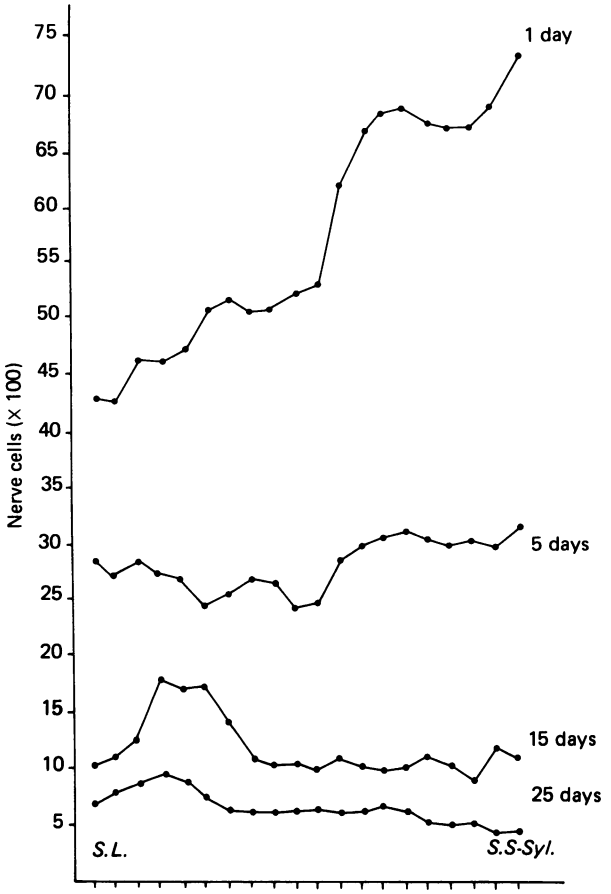

Fig. 6. Average density of nerve cells in coronal sections of the cerebral cortex from *S.L.* to *S.S-Syl.* at different postnatal ages.

Table 1. *Average number of nerve cells in the total length of the gyrus at the different postnatal ages. The percentage of cumulative neuron loss is considered after the maximal number of nerve cells is attained at Day* 15

Postnatal age	No. of nerve cells	Cumulative neuron loss (%)
Day 1	2643200	—
Day 5	3779784	—
Day 15	4327200	—
Day 25	3847140	16
Six months	3418488	21

Intracortical regional differences in the neuronal density during development

As a result of the maturation of neurons, probably together with an increase in the number of glial cells (Hillebrand, 1966), there was a decrease in the neuron density throughout development.

In the 1 day old cat nerve cells were more densely packed in the gyral region adjacent to the S.S-Syl. (and in the S.S-Syl. itself) than in the gyral region adjacent to the developing S.L.; an increase in the clustering of nerve cells in this latter region was

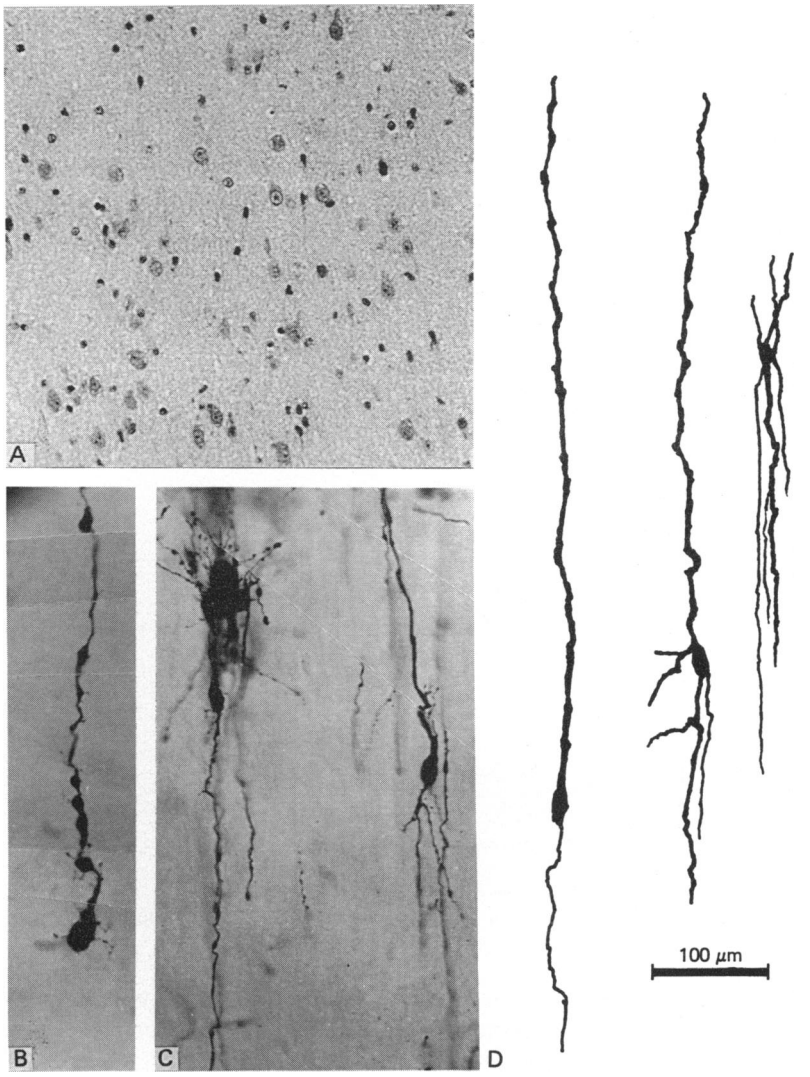

Fig. 7(A–D). Migrating neuroblasts in the telencephalic white matter of cats aged 5 days (A, B, C) and 15 days (D). (A) Nissl's stain, ×63; (B) and (C) Rapid Golgi method, ×160; (D) Camera lucida drawing of Golgi-impregnated migrating nerve cells.

found in the cat aged 5 days, and neurons were more densely packed in the gyral region adjacent to the S.L. than in the gyral region adjacent to the S.S-Syl. in cats aged 15 and 25 days (Fig. 6).

Number of neurons in the total length of the gyrus

As shown in Table 1, an average increase of 40% in the number of neurons was encountered between Day 1 and Day 15, but an average decrease of 16% was found between Day 15 and Day 25; later, an additional decrease of about 5% was observed in the cat aged six months. A lack of available data between the two latter ages has made it impossible to determine the exact timing of this last reduction in the number of nerve cells.

Migration of neuroblasts during postnatal cortical histogenesis

A number of immature neurons was found to be present in the white matter of the telencephalon during the first two weeks of postnatal life in the cat. Small numbers of migrating neuroblasts were also observed in the white matter of the 25 days old cat, but not in the cat aged six months.

When impregnated according to the rapid Golgi method, migrating neuroblasts showed a bipolar appearance with a proximal, delicate neurite directed towards the deep white matter, and a distal, varicose apical dendrite that was directed towards the cortical surface (Fig. 7). In some instances, small numbers of inverted pyramidal neurons were also encountered in the white matter.

DISCUSSION

An increase in the number of neurons is found in the cortical region between the S.L. and the S.S-Syl. during the first two weeks of postnatal life in the cat. Since H^3-thymidine labelling studies in the cerebral cortex of the cat have demonstrated that cortical neurogenesis occurs between embryonic Day 31 (E31) and embryonic Day 57 (E57) (Luskin & Shatz, 1985) the recruitment of cortical neurons in postnatal development may be explained by the arrival of migrating neuroblasts generated during prenatal stages. Although there is no available data for the cat's cerebral cortex, the rate of migration of neuroblasts from the ventricular zone to their definitive placement in the cortical plate may be inferred from observations in other species (Fujita, Shimada & Nakamura, 1966; Hicks & D'Amato, 1968; La Vail & Cowan, 1971; Rakic, 1974). Based on these studies it may be postulated that the bulk of neurons generated between E50 and E57 in the cat reach their definitive cortical position in the upper cortical layers between postnatal Days 3 and 15 approximately, thus accounting for the increase in the number of neurons in the early stages of postnatal cortical histogenesis. This increase is supplemented by the presence of large numbers of migrating neuroblasts as revealed with the Golgi method in the telencephalic white matter of very young cats.

A progressive decrease in the number of cortical neurons is observed from Day 15 to Day 25; later on, an additional loss is observed in the six months old cat, but the lack of intermediate samples does not permit us to know exactly when this latter decrease takes place. If the growth in width of the vertical gyri between the postsylvian sulcus and the anterior ectosylvian sulcus occurs at a different rate from the longitudinal growth of the suprasylvian gyrus, the estimates of total neuronal number in the gyrus will be affected, and this could be an explanation for the fluctuation in total neuron number. However, the relationship between the total length of the G.S-Syl. and the length of the region of this gyrus between the postsylvian sulcus and the ascending branch of the anterior ectosylvian sulcus remains constant throughout development; hence, the fluctuation in total neuron number may actually represent a progressive decrease in the number of cortical neurons. Nerve cell loss, although to a greater degree than that recorded for the cat, has also been reported in the cerebral cortex of the developing hamster (Finlay & Slattery, 1983) and mouse (Heumann & Leuba, 1983), the olfactory cortex of the rat (Friedman & Price, 1986) and the cerebral hemispheres of developing chick embryos (Hyndman & Zamenhof, 1978). Similarly, transitory populations of neurons have recently been observed to occur in the temporal (Valverde & Facal-Valverde, 1987) and in the visual cortex (Wahle & Meyer,

1987) of the kitten. These data suggest that nerve cell loss occurs in the cerebral cortex of mammals (and, probably, in homologous structures in birds) as is known to occur in other structures of the developing nervous system (see Kallen, 1965; Cowan, 1973; Oppenheim, 1981, 1985, for review).

The complete development of the G.S-Syl. and the formation of the S.L. seems to be produced as a consequence of the imbalance between the increase in volume of the gyral region and that of the relatively fixed sulcal zones. In the postnatal cat this is manifested by the progressive enlargement of the gyral region adjacent to the developing sulcus (S.L.), an enlargement greater than that of the region adjacent to the almost fully formed S.S-Syl., while both limiting sulci (S.L. and S.S-Syl.) retain a relative constant distance from the ventricular wall throughout the process of cortical folding. Such a characteristic gross developmental pattern is associated with a regional increase in the cortical thickness that is supported by a corresponding regional increase in the number of nerve cells in the region adjacent to the developing sulcus.

Although a cumulative arrival of migrating neuroblasts may account, in part, for the number of neurons in the cortical region adjacent to the developing sulcus, a lateral intracortical displacement of immature neurons may occur as well. This displacement is suggested because, from Day 1 to Day 25, the density of neurons increases along the gyral region adjacent to the S.S-Syl. Hence, since true migration of neurons on the tangential plane is not possible because of the radial orientation of nerve cells, an alternative explanation could be that immature neurons are continually displaced in the lateral plane towards the developing sulcus as neurons located near the S.S-Syl. become less densely packed.

Similar conclusions, as regards the interpretation of the sulcal regions as relatively fixed zones as well as the tangential spreading of the more mature tissue at the gyral crown, while at the site of the future sulci growth is retarded, have been anticipated by Smart & McSherry (1986*a*, *b*) in the cerebral cortex of the ferret.

An intralaminar displacement of nerve cells also occurs during the process of cortical folding; nerve cell columns converge towards the hilum in the gyral region, but these columns progressively curve following the concavity of the infolding in the sulcal zones. As a result, although the length of nerve cell columns tends to be preserved to some extent, the cerebral cortex is progressively thinner in the sulci than in the gyri and the molecular layer is progressively thicker in the former than in the latter. Finally, neurons of layer VI are tangentially orientated in the sulci, whereas similar neurons preserve the original vertical alignment in the gyrus (Ferrer *et al.* 1987).

Taken together, these results suggest that cortical folding is a complex phenomenon, largely dependent on internal cortical forces, in which nerve cell recruitment, maturation of neurons, regional and interlaminar displacements of nerve cells and neuron loss harmoniously occur, at different rates, following rigid spatio-temporal patterns. However, the regular distribution of the sulci, together with the orderly spatio-temporal sequence of gyral growth, point to the likelihood that extracortical signals (i.e. thalamic afferents: Welker & Campos, 1963; Johnson, 1980) may play an important role in the guidance of these intracortical forces during the formation and growth of the cerebral convolutions.

SUMMARY

The postnatal development of the median-suprasylvian gyrus and adjoining sulci was studied in cats 1, 5, 15, 25 days and six months old. The median-suprasylvian

gyrus (G.S-Syl.) grows according to a lateral to medial intracortical gradient in which the adjoining sulci, sulcus lateralis (S.L.) and median-suprasylvian sulcus (S.S-Syl.), are considered to be fixed zones because of their relatively constant distance from the ventricular wall throughout the development. Thus the formation of the S.L. is a consequence of the increase in volume of the gyral region adjacent to this developing sulcus, whereas there is a smaller increase in volume of the gyral region adjacent to the almost fully formed, at birth, S.S-Syl. This increase in volume is associated with a regional increase in the number of nerve cells and with an increase in the density of neurons in the region adjacent to the S.L. as it fades in the region adjacent to the S.S-Syl. This process takes place from Day 1 until about Day 25 of postnatal life.

An intralaminar displacement of nerve cells also occurs during the process of cortical folding: nerve cell columns converge towards the hilum in the gyral region, but the columns progressively curve following the concavity of the infolding in the sulcal zones; as a result, although the length of nerve cell columns tends to be preserved to some extent along the gyrus, the cerebral cortex is progressively thinner in the sulci than in the gyri and the molecular layer is progressively thicker in the former than in the latter. This process also occurs following a lateral to medial gradient in the G.S-Syl.

The present observations may suggest that cortical folding is largely dependent on intracortical mechanical forces but the regular distribution of the sulci, together with the orderly spatio-temporal pattern of gyral growth, points to the conclusion that this process may be controlled by extracortical signals.

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