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The development of the central–peripheral transitional zone of the rat cochlear nerve. A light microscopic study

J. P. FRAHER AND F. J. N. DELANTY
Department of Anatomy, University College, Cork, Ireland

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INTRODUCTION

Dorsal and ventral spinal nerve roots are attached to the cord surface by a number of rootlets. An outgrowth of central nervous tissue (the *central tissue projection*) extends distally into those dorsal rootlets that have been studied to date (Tarlov, 1937*a*, *b*; Nathaniel & Nathaniel, 1963; Steer, 1971; Sindou, Quoex & Baleydier, 1974; Berthold & Carlstedt, 1977; Schlaepfer, Freeman & Eng, 1979; Moll & Meier, 1983; Fraher & Sheehan, 1987) and also into lumbar ventral rootlets (Fraher & Kaar, 1986; Fraher & Bristol, 1987). However, ventral cervical spinal rootlets lack such a projection (Fraher, 1978; Fraher & Kaar, 1982). Central tissue projections have also been described extending into cranial nerves (Skinner, 1931; Tarlov, 1937*a*, *b*; Maxwell, Kruger & Pineda, 1969; Němeček, Pařízek, Špaček & Němečková, 1969; Gamble, 1976). Of these, the projection into the cochlear nerve is particularly extensive in adults of the species studied to date, such as man (Skinner, 1931; Tarlov, 1937*a*, *b*; Chandross, Adams & Bear, 1977; Chandross, Bear & Montgomery, 1977; Bridger & Farkashidy, 1980), cat (Berthhold, Carlstedt & Corneliusson, 1984), rat (Ross & Burkel, 1970), amphibians and reptiles (Wulfhekel, 1969). The present study surveys the development of the central tissue projection in the cochlear nerve of the rat.

MATERIALS AND METHODS

Wistar albino rats of the following ages were used: 15, 16, 17, 18, 19, 20 and 21 days fetal; newborn; 1, 2, 3, 4, 6, 13, 35, 72, 171 and 371 days postnatum. Five animals were studied at each age up to and including 13 days postnatum and two at each subsequent age. The ages of all animals were known to within ± 2 hours.

Fetal specimens were prepared as follows: the pregnant dam was anaesthetised using anaesthetic ether. Fetuses were delivered by Caesarean section through an abdominal hysterotomy and immediately killed by decapitation. The head was placed in fixative consisting of 2·5% paraformaldehyde and 2% glutaraldehyde in orthophosphate buffer at pH 6·6–6·8. Postnatal specimens were anaesthetised with anaesthetic ether and perfused through the left ventricle with the fixative described above. Perfusion was continued for 15–20 minutes. To optimise fixation of adult tissue, perfusate was introduced into the sacral part of the subarachnoid space and allowed to escape through a cranial burr-hole. Each specimen was then decapitated and the head placed in fixative. Heads of animals aged 13 days and over were decalcified in a solution of 5% trichloracetic acid and subsequently trimmed to a transverse segment which included the entire cochlea, the cochlear nerve and the associated brainstem. These slices, and the whole heads at younger ages, were

Table 1. *Length of central tissue projection (CTP) and transitional zone (TZ) at several stages postnatum and daily rates of increase in length (Δ/day) over the intervening periods*

	CTP		TZ	
Age	Length (μm)	Δ/day	Length (μm)	Δ/day
Newborn	125		125	
		140		20
2	405		165	
		103		150
4	610		465	
		12		−21
13	720		275	
		6·3		3·4
72	1090		475	
		2·0		1·4
171	1290		615	
		1·2		−0·3
371	1530		565	

dehydrated in ethanols and chloroform and then wax-embedded. Serial sections 7 μm thick, were made in planes transverse to the brainstem, using an American Optical rotary microtome. Calibration of the microtome showed that mean section thickness was accurate to within ±2%. Each series of sections included the entire cochlea, the cochlear and vestibular nerves and the associated length of brainstem to which these were attached. Sections were mounted serially on numbered glass slides and were stained either by Van Gieson's technique or with celestine blue-haemalum and counterstained with orange G-light green. The mounted and coverslipped sections were examined and photographed using a Reichert Polyvar photomicroscope.

Central and peripheral nervous tissues were readily distinguishable from one another at all stages because of their different appearance and differential staining. The position and thickness of each section in its series was known. Consequently, for each specimen it was possible accurately to reconstruct the appearance of the cochlear nerve, its branches, its central tissue projection, the internal auditory meatus and the region of the brainstem to which the nerve was attached, as follows. Using every fourth section in the series, the profile of each of these tissues was traced on a transparent sheet. One sheet was used for each section examined. Sheets representing the entire series of sections through the nerve were aligned with one another and stapled together. In addition, a wax model of the central tissue projection was constructed for one specimen at 2, at 4 and at 13 days *postnatum*. Age changes in the three dimensional morphology and in the position of the central tissue projection were determined from these.

The growth of the central tissue projection of the cochlear nerve was studied by measuring its length at various postnatal stages (Table 1) and examining its position relative to the segment of the cochlear nerve which lay in the subarachnoid space (its *subarachnoid segment*) and/or to the modiolus of the cochlea.

Postnatal specimens aged 2, 3, 6, 10, 13, 21 and 30 days were plastic-embedded. At each age, between 10 and 20 specimens of cochlear nerve, together with the segment of brainstem to which they were attached, were dissected free, immersed for one and a half hours in the fixative described above, dehydrated in ethanols and epoxypropane and embedded in Araldite. Transverse and longitudinal 0·5 μm specimens were stained with toluidine blue and used to examine the vascularisation of the cochlear nerve.

OBSERVATIONS

General arrangement of the cochlear nerve

The cochlear nerve was attached to the brainstem as a single trunk. It ran across the subarachnoid space to the internal auditory meatus, where it entered the modiolus of the cochlea. In this, its branches fanned out to reach the spiral ganglion of the cochlea. In younger animals these traversed only loose connective tissue (Fig. 1*d*), but once the modiolus had been formed and ossified, each traversed first a cartilaginous and later a bony canal (Fig. 2).

The cochlear nerve was closely associated with the ventral trunk of the vestibular nerve (Fig. 2*a*, *b*), which entered the internal auditory meatus with it and turned dorsally through a foramen in its wall to innervate the vestibular apparatus. Some vestibular ganglion cells extended into the central part of the modiolus.

Developmental changes

15 *to* 21 *days fetal*

The cochlear nerve was attached to the brainstem on the caudal and ventrolateral aspect of the inferior cerebellar peduncle. At 15 days a shallow central tissue projection extended into it. This became more prominent up to 17 days but regressed somewhat between then and birth. It was asymmetrical within the nerve. Its medial part extended further distally than its lateral part (Fig. 1*b*, *c*). The cellularity of the projection was very low at first, but increased with age (compare Fig. 1*a* and *e*). However, it remained much less than that of the part of the nerve which consisted of peripheral tissue and in which nuclei were very densely packed in the early stages (Fig. 1*g–j*).

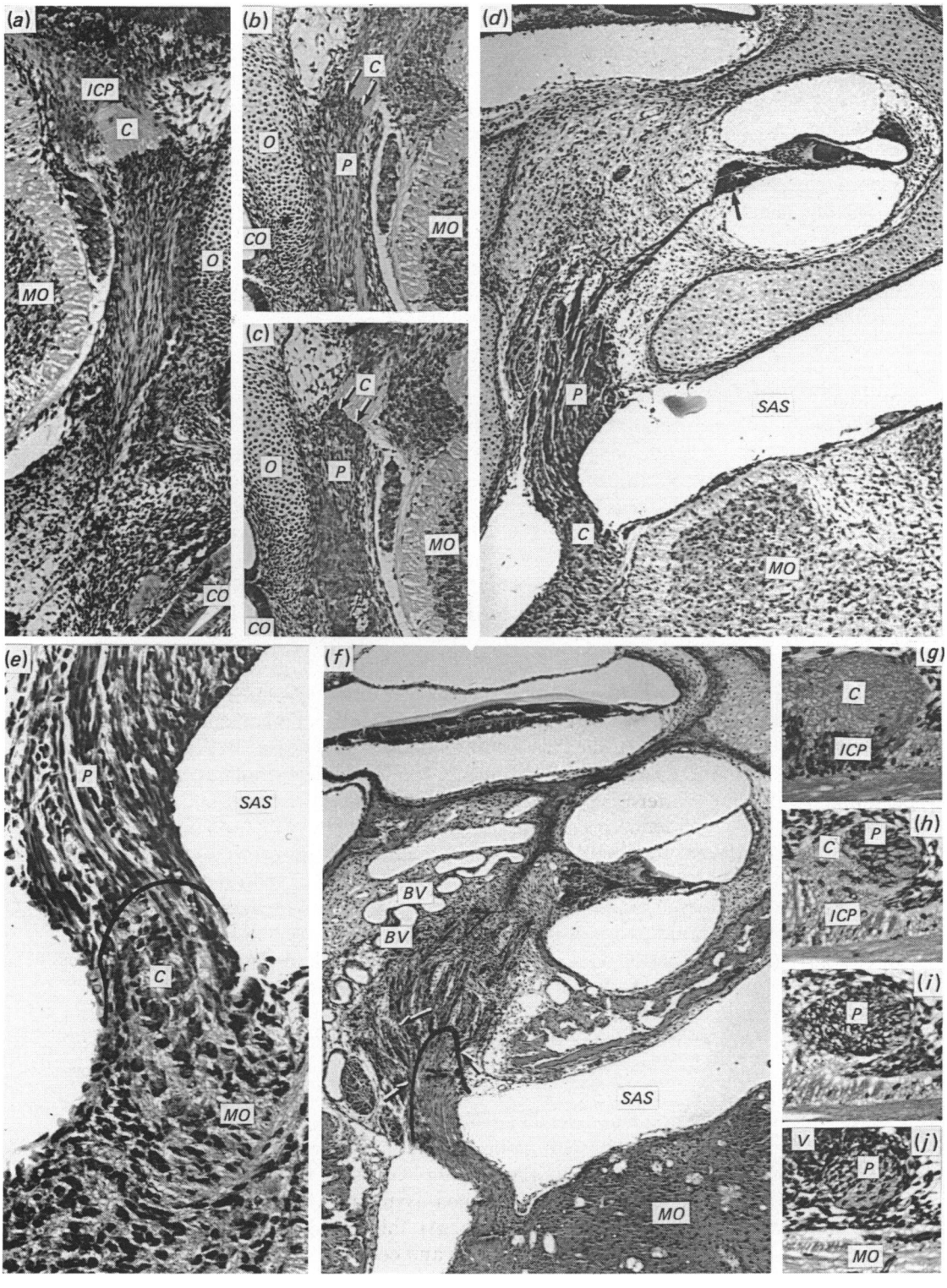
Newborn to 4 *days postnatum*

The central tissue projection grew distally into the nerve at its most rapid rate in the immediate postnatal period (Table 1; Fig. 1*d–f*). At 1 day its tip had come to lie about halfway along the segment of the nerve in the subarachnoid space. In some 2 day and in all 3 day animals it had reached as far as the internal auditory meatus. It was asymmetrical, being displaced medially and caudally within the nerve. Up to 2 days, peripheral tissue extended along the entire length of the nerve. It was more plentiful on the lateral than on the medial aspect of the central tissue projection. By 4 days, however, the most proximal part of the nerve consisted only of central tissue. The part of the nerve which was made up of peripheral tissue consisted of clearly defined fascicles. The most rapid phase of increase in transitional zone length also took place in the early postnatal period, but at a slightly later stage than that for central tissue projection length (Table 1). It decreased somewhat between 4 and 13 days.

Over this period a small number of blood vessels of narrow calibre were found in the glial projection (Fig. 3*a*). They were more plentiful distal to the interface.

6 *days*

By 6 days the projection had extended distally well into the modiolus (Fig. 1*f*; Table 1). The segment of the nerve consisting purely of central tissue had lengthened further; it extended from the brainstem to the internal auditory meatus. The part of the projection lying within the modiolus remained asymmetrical: It tapered to an apex lying towards the medial side of the nerve. At this and at all subsequent stages, peripheral tissue was confined to the modiolus and cochlea. All branches arose within the modiolus, more arising laterally than medially. They contained extensions of central tissue. Consequently, the central–peripheral interface was irregular. The


(a)
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branches which arose close to the tip of the projection formed a loose bundle which curved rostrally within the modiolus. Blood vessels were plentiful within the projection at this stage and subsequently (Fig. 3*b*, *c*). Communications between these and vessels in the peripheral part of the nerve passed through the central–peripheral interface (Fig. 3*b*, *c*).

13 *days and older*

By 13 days the projection had attained its essential definitive form. Over most of its length it was relatively straight (Fig. 2*a*). The projection continued to make up the entire subarachnoid segment of the nerve and extended well into the modiolus (Table 1). In the distal part of the modiolus the projection bent rostrally (Fig. 2*b*). All branches arose within the modiolus and the most proximal of these arose from the lateral aspect of the projection. The surface of the projection was relatively smooth proximally but possessed large shallow undulations distally. Extensions from the projection passed distally into some of its branches (Fig. 2*c*).

After 13 days the projection continued to extend progressively further into the modiolus. Peripheral tissue retreated ahead of it and made up a progressively decreasing proportion of the length of the nerve in the modiolus. The extent to which its branches diverged from one another increased.

DISCUSSION

Development of the central tissue projection

The development of the central tissue projection is continuous but can be divided into four stages (Fig. 4): (1) A stage of initial outgrowth into the nerve from 15 to 17 fetal days when a shallow central tissue projection is established. (2) A stage of suspended growth or relative proximal regression over the last four days of fetal life, when the projection assumes the form which it retains during the subsequent period of most rapid elongation: its distal surface becomes convex, more so medially than laterally; it comes to lie medially and caudally within the nerve and is therefore asymmetrical within it. (3) A stage of pronounced glial outgrowth into the nerve, beginning immediately after birth and continuing at a diminishing rate into adult life (Table 1). (4) A stage of definitive organisation of the central tissue projection, during which it takes on its mature form; this is completed between 6 and 13 days *postnatum* and overlaps with the early part of Stage 3.

Between 2 and 6 days *postnatum* the nerve segment consisting entirely of central

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Fig. 1 (*a–j*). (*a–f*) Longitudinal sections through developing cochlear nerve. (*a*) 16 day fetus. The central tissue projection is much less cellular than the peripheral segment of the nerve. The inferior cerebellar peduncle is tangentially sectioned. ×66. (*b*, *c*) 17 day fetus. Serial longitudinal sections show variations in the form of the CNS–PNS interface (arrows). ×83. (*d*) 1 day *postnatum*. Cochlear nerve bundles traverse loose tissue to reach the cochlear ganglion (arrow). Left: lateral; right: medial. ×66. (*e*) 1 day *postnatum*. Enlargement of (*d*) showing the asymmetry of the central tissue projection (outlined) in the nerve. ×205. (*f*) 6 days *postnatum*. the distal limit of the central tissue projection (outlined) lies in the modiolus. Peripheral branches (arrows) arise directly from the projection. ×66. (*g–j*) 16 day fetus. Transverse sections (*g*) through the almost acellular central tissue projection where it is attached to the inferior cerebellar peduncle; (*h*) through the part of the nerve including the interface between central (relatively acellular) and peripheral (relatively highly cellular) tissues; (*i*) through the highly cellular peripheral tissue segment of the nerve (*P*) immediately distal to the central tissue projection; (*j*) through the distal part of the nerve (*P*) where it lies close to the vestibular ganglion (*V*) and is less cellular than at more proximal levels. ×103. *C*, central tissue projection; *P*, peripheral nervous tissue segment of the cochlear nerve; *MO*, medulla oblongata; *O*, otic capsule; *CO*, developing cochlea; *ICP*, inferior cerebellar peduncle; *SAS*, subarachnoid space; *BV*, blood vessel.

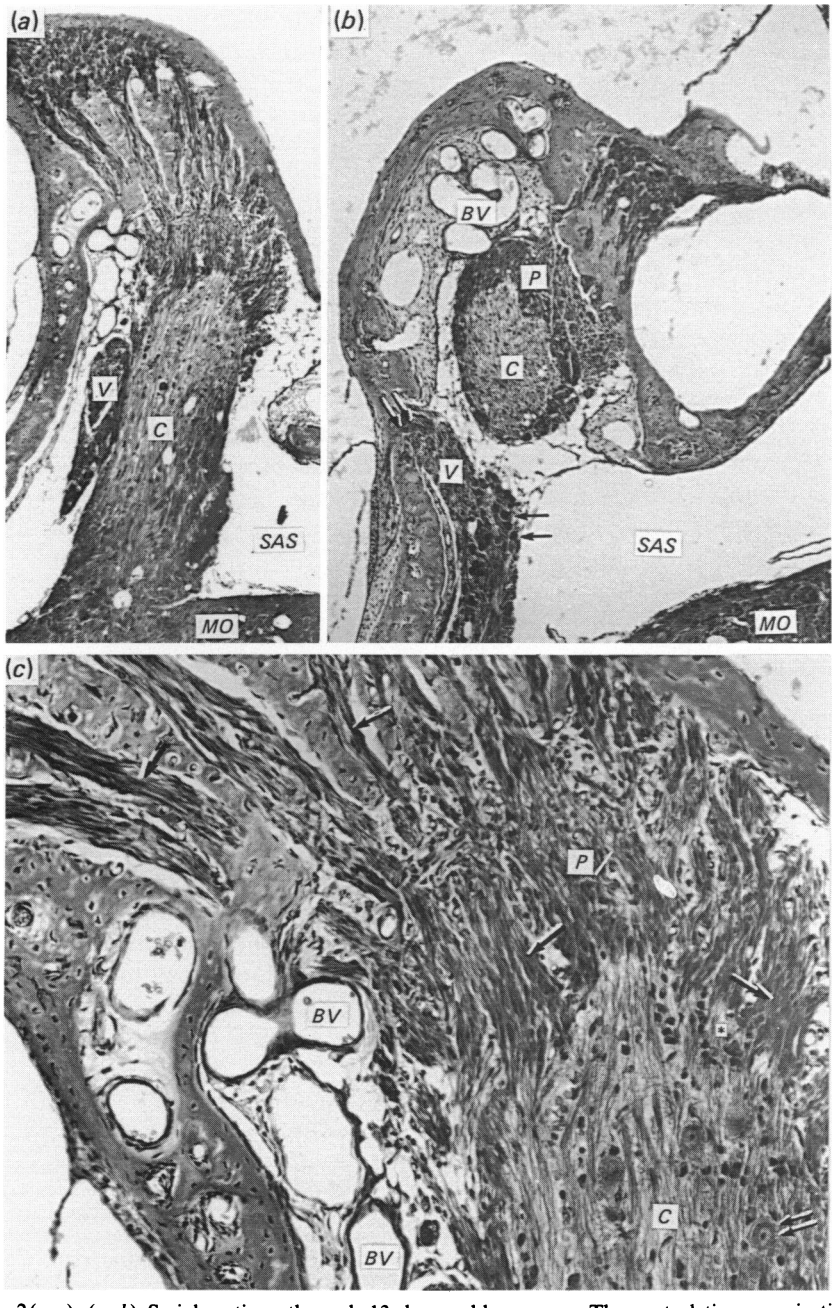

Fig. 2(*a–c*). (*a*, *b*) Serial sections through 13 day cochlear nerve. The central tissue projection is curved. As a result its proximal part (*a*) is sectioned longitudinally and its distal part (*b*) obliquely. The ventral division of the vestibular nerve (*V*) enters the modiolus (*a*) and leaves it through a foramen in its dorsal wall (*b*, double arrow). Associated ganglion cells (*b*, arrows) also lie in the modiolus. ×66. (*c*) Enlargement of (*a*) showing cochlear nerve branches (arrows) consisting of peripheral nervous tissue arising directly from the central tissue projection. Short projections of central tissue (*) extend into these. Occasional neuronal somata (double arrows) lie in the central tissue projection. ×205. *C*, central tissue projection; *P*, peripheral nervous tissue segment of the cochlear nerve; *MO*, medulla oblongata; *SAS*, subarachnoid space; *BV*, blood vessel.

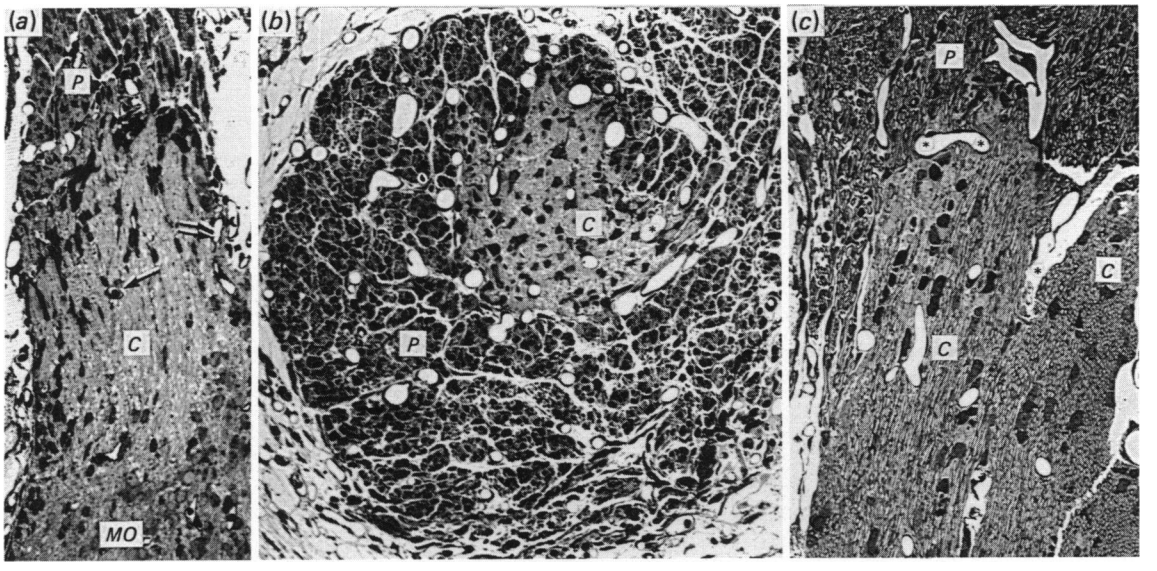

Fig. 3(*a–c*). Semithin Araldite sections. (*a*) Longitudinal section through 1 day *postnatum* cochlear nerve. The central tissue projection contains small calibre blood vessels (arrow). One vessel (double arrow) is entering it from the pial surface. × 205. (*b*, *c*) Transverse (*b*) and longitudinal (*c*) sections through 13 day *postnatum* cochlear nerves showing blood vessels in both peripheral and central parts of the cochlear nerve. Communicating vessels (asterisks) traverse the central–peripheral interface. × 205.

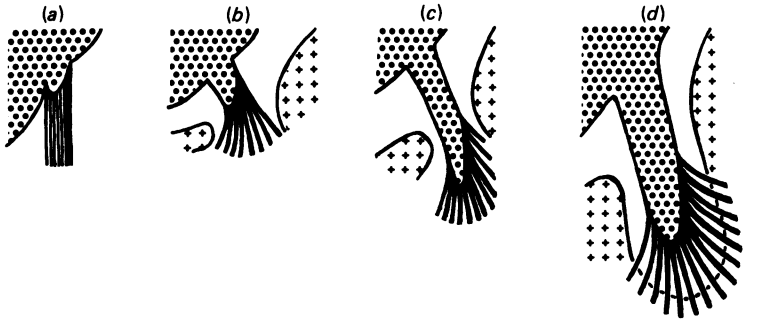

Fig. 4(*a–d*). Diagrammatic longitudinal sections through the cochlear nerve and associated brainstem at (*a*) 17 days fetal, (*b*) 1 day, (*c*) 6 days and (*d*) 13 days *postnatum*, showing age changes in the form of its central tissue projection. The modiolus has formed at 13 days and its outline is shown (see Text). Central nervous tissue, dotted area; Peripheral nervous tissue, black lines; Otic capsule/developing skull, crosses.

tissue is established and increases very rapidly in length (Table 1). This may involve interstitial growth of the initially short central segment, or active regression distally of peripheral tissue, vacating axon segments which are enveloped by distal migration of central tissue. The latter process is likely to occur in cervical ventral spinal nerve roots (Fraher & Kaar, 1982).

The tapering terminal segment of the projection within the modiolus is asymmetrical in so far as its apex lies towards the medial side of the nerve. The most proximal cochlear nerve branches arise from its lateral aspect and run to the basal turn of the cochlea. Branches arising from its medial aspect originate further distally and run to more distal turns of the cochlea. Thus the asymmetry of the projection correlates with

the origin of its branches and their relationship to the cochlea. It is noteworthy that this asymmetry develops during the late stages of fetal life. It thus anticipates the definite arrangement and is maintained throughout the phase of rapid elongation.

With maturation, the projection comes to occupy a progressively increasing proportion of the length of the modiolus. Preliminary quantitative studies suggest that the length of that peripheral segment of the nerve between the projection and the ventromedial part of the basal turn of the spiral ganglion decreases over this period by 50 to 75 %. This true decrease would seem to be highly unusual, if not unique in peripheral nerve development.

Comparison with central tissue projections in other nerves

Developmental studies of the rat central–peripheral transitional region have been carried out on cervical ventral (Fraher, 1978; Fraher & Kaar, 1982), cervical dorsal (Fraher & Sheehan, 1987), L5 ventral (Fraher & Kaar, 1986) and L6 ventral (Fraher & Bristol, 1987; Fraher, Kaar & Bristol, 1987) rootlets. Although the growth phases of the central tissue projection of the cochlear nerve resemble those of some of the above, there are substantial differences as well. The period of most rapid cochlear outgrowth is between birth and 4 days *postnatum*. This takes place slightly earlier than the most rapid outgrowth phases of the projections in rat lumbar ventral (Fraher & Kaar, 1986) and cervical dorsal (Fraher & Sheehan, 1987) rootlets, both of which occur between 3 and 6 days. However, in both of these locations this phase occurs at the beginning of the outgrowth period, whereas in the cochlear nerve the projection has already been present for one week before the most rapid outgrowth occurs. Proximal regression is a general feature of central tissue projection development in all areas studied to date in the rat (see references above). In the rootlets mentioned above, the phase of rapid growth is followed by one of proximal regression of the projection. By contrast, in the cochlear nerve the sequence of these phases is reversed and regression is less marked than in the other locations. Quantitative studies on spinal nerve roots (Fraher & Kaar, 1982, 1986; Fraher & Sheehan, 1987) are consistent with the occurrence of differential distal overgrowth of central tissue as a cause of proximal regression. The inferior cerebellar peduncle is closely related to the cochlear nerve and expands rapidly in diameter during later fetal stages. Associated growth changes may result in distal overgrowth of central tissue. As a result of this, segments of the nerve originally in the subarachnoid space may therefore be engulfed and come to lie deep to the surface of the inferior cerebellar peduncle.

The cochlear nerve differs significantly from the other nerves mentioned above in additional ways. Firstly, it possesses no segment where the nerve trunk consists entirely of peripheral tissue. Instead, its terminal branches arise directly from the surface of the central tissue projection. Although some of these initially run close together, especially where they surround the distal end of the central tissue projection, they do not reunite to form a compact peripheral cochlear nerve trunk, as occurs in the cat (Berthold *et al.* 1984). Secondly, while the rat cochlear nerve possesses a substantial segment consisting only of central tissue, rat spinal nerve rootlets lack this. In these, peripheral tissue extends proximally around the projection to a level close to or at the central nervous system surface. During development the projection of the cochlear nerve resembles that of the lumbar ventral and the cervical dorsal rootlet in having an irregular surface and in being displaced towards the side of the nerve closest to the central nervous system surface.

Central tissue projection length (Table 1) in the mature cochlear nerve (approximately 1·5 mm) is much greater than that in other rat nerves examined. It averages

around 70 μm in L5 ventral rootlets (Fraher & Kaar, 1986), 135 μm in L4 ventral rootlets (Fraher & Bristol, 1987) and 425 μm in C7 dorsal rootlets (Fraher & Sheehan, 1987). It reaches around 300 μm in mouse cervical dorsal rootlets (Moll & Meier, 1983). However, the length of the transitional zone, along which central and peripheral tissues overlap, differs little from that of rat cervical dorsal rootlets (Fraher & Sheehan, 1987).

Tarlov (1937*b*) suggested that differential tension on the intrathecal segments of developing nerves, due to differential growth between the neuraxis and the skeleton, may cause marked variation in the degree of central tissue projection into them. Carlstedt (1981) supports this hypothesis to explain the rostrocaudal increase in projection length between spinal nerve roots. It seems very unlikely that such a mechanism operates in developing cochlear nerve, since the length of its peripheral segment probably undergoes an absolute decrease during development.

Blood vessels

Reports regarding the existence of anastomoses between blood vessels of peripheral nerve roots and the central nervous system are at variance: Berthold & Carlstedt (1977) found that vessels at the cat dorsal rootlet transitional zone lack continuity with those of the underlying cord. However, such communications have been found at rat cervical dorsal rootlet attachments (Fraher & Sheehan, 1986, unpublished observations), and at rat cervical (Fraher, 1976, unpublished observations) and lumbar (Kaar & Fraher, 1987) ventral rootlet attachments. The present study also demonstrates extensive anastomoses between central and peripheral vascular territories in the cochlear nerve (Fig. 3).

The morphological relationships of vessels to spinal nerve rootlets and to the cochlear nerve differ. The latter enter the projection and are completely surrounded by central tissue. The former generally run to the central nervous system surface in connective tissue spaces between the central tissue projections of neighbouring nerve rootlets (Kaar & Fraher, 1987) and are therefore not immediately surrounded by central tissue. Furthermore, the presence of blood vessels within the cochlear projection ensures that its tissues are sufficiently close to them for metabolic purposes. In the adult rat, its radius (around 250 μm) is five times greater than the upper limit of the range (Guyton, 1981) of distances of cells in general from blood vessels.

SUMMARY

A projection of central nervous tissue extends for a short distance into the proximal part of the cochlear nerve trunk during the last week of fetal life but regresses slightly as birth approaches. During the first two weeks after birth it again grows distally at a very rapid rate and reaches well into the modiolus of the cochlea. The segment of the cochlear nerve trunk which lies in the subarachnoid space comes to consist entirely of central nervous tissue. The central tissue projection continues to grow further distally into the cochlea up to the end of the first year of life. Cochlear nerve branches consisting of peripheral nervous tissue arise directly from the central tissue projection. The cochlear nerve trunk lacks a compact segment which consists only of peripheral nervous tissue.

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