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The tentorial nerve in monkeys is a branch of the cavernous plexus

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INTRODUCTION

Arnold (1851) gave the name *Nervus tentorii* to a nerve consisting of several bundles of fibres branching from the upper border of the ophthalmic division of the trigeminal nerve in man. It issues from the ophthalmic nerve about a centimetre anterior to the trigeminal ganglion, turns back close to or within the sheath of the trochlear nerve, then fans out in the tentorium to reach the straight and transverse sinuses, the falx, occipital dura and superior sagittal sinus. This distribution was confirmed by McNaughton (1938) but he experienced difficulty in locating the origin of the tentorial nerve bundles in dissections of silver-stained human preparations. Most of them appeared to leave the lateral surface of the trigeminal ganglion in common with monkeys which he found easier to study. Pain elicited by electrical stimulation of the tentorium and associated structures in man is attributed to tentorial nerve excitation (Ray & Wolff, 1940; Feindel, Penfield & McNaughton, 1960).

A resurgence of interest in structures responsible for head pain in recent years has led to a better understanding of intracranial sensory innervation but most experimental work has been concerned with innervation of the pial arteries rather than the dura mater and little has been added to Arnold's (1851) and McNaughton's (1938) gross anatomical descriptions of dural innervation. The possibility that these old accounts require revision became evident while studying the trigeminal contributions to the cavernous plexus and cerebral arteries in monkeys (Ruskell & Simons, 1987), when the tentorial nerve appeared to issue from the plexus rather than from the ophthalmic nerve or trigeminal ganglion. The trigeminal source of tentorial nerve fibres was consequently open to question. The nerve was duly tested and some fibres of trigeminal origin were found while others were autonomic.

MATERIALS AND METHODS

Nine young adult cynomolgus (*Macaca fascicularis*) monkeys of both sexes and one male rhesus (*Macaca rhesus*) monkey were used in the experiments and unoperated stock material was used from a further three cynomolgus and five rhesus monkeys. The animals were sedated parenterally with 2–3 mg/Kg ketamine and anaesthetised with 15–25 mg/Kg Sagatal (pentobarbital sodium) given via the saphenous vein or intraperitoneally. The calvaria was removed from seven of the monkeys, the dura mater split and the lateral lobe of the brain elevated on the left side to expose the trigeminal nerve. A piece of the maxillary nerve was removed close to its entry into the foramen rotundum. In four animals, including the rhesus monkey, the ophthalmic nerve was additionally sectioned. To minimise the risk of damage to adjacent nerves

and to the cavernous sinus, the ophthalmic nerve sheath was split parallel to the nerve axis close to the trigeminal ganglion, the nerve was freed from sheath attachments, separated from adjacent structures with a hook, divided and reflected, and a piece removed. Subsequent histological examination showed that this approach avoided damage to filaments of the cavernous plexus. In one of the animals the trochlear nerve was detached from the brainstem by avulsion in addition to maxillary neurotomy.

The superior cervical ganglion was removed from the left side of three cynomolgus monkeys. This procedure, simple in other animals, carries the risks of incomplete removal and internal carotid artery rupture in cynomolgus monkeys because the ganglion lies high in the neck, reaching the entrance to the internal carotid foramen tight against the artery. Examination of the excised tissue using a dissection microscope confirmed that the ganglion had been removed complete in each case.

The operations were designed to induce Wallerian degeneration so that fibres from the different sources could be traced and identified in the tentorial nerve. Maxillary neurectomy was included because earlier work on monkeys had shown that an extracranial branch of the maxillary nerve, the orbitociliary nerve, re-enters the cranium from the pterygopalatine fossa and in part joins branches from the internal carotid plexus (Ruskell, 1974). Consequently, the orbitociliary nerve is a potential source of tentorial nerve fibres.

From 3 to 20 days after operation (see Table 1) animals were sedated, anaesthetised and given an injection of the anticoagulant heparin sodium (1500 units). The external jugular veins and the inferior vena cava were cut and a 2% glutaraldehyde, 3% paraformaldehyde, cacodylate-buffered solution was perfused through the heart. The heads were stored in fixative at approximately 4 °C and dissected while immersed in buffered sucrose using a dissection microscope.

On both sides the internal carotid artery was cut posterior to the trigeminal ganglion and again a few millimetres in front of its intracranial emergence from the cavernous sinus. The separated length of the artery, similar lengths of the trochlear, ophthalmic and abducent nerves, and the cavernous sinus in which they were embedded, were dissected free and processed in one piece or after division vertically into anterior and posterior halves. The orbitociliary nerve and the rami orbitales in the upper part of the pterygopalatine fossa were left attached to the sinus tissues. The hypophysis and, sometimes, the oculomotor nerve were removed and discarded. The inferior half of the trigeminal ganglion, the mandibular and, in some cases, the maxillary nerve were also removed and discarded.

The tentorium, complete from the cavernous sinus, where the embedded stump of the trochlear nerve was included, to the transverse sinus was dissected free and later

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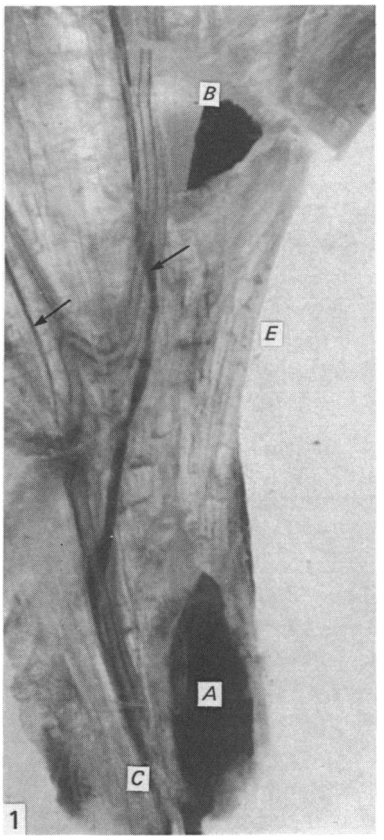
Fig. 1. Anterior tentorium showing the proximity of trochlear and tentorial nerves. Removal of a piece of dura mater at *A* reveals the buried trochlear nerve as it enters the cavernous sinus, and a window cut from the tentorium at *B* permits a view of the nerve proximally before entering the dura mater. The tentorial nerve, already separated from the trochlear at *C*, forms two branches (arrows). The free edge of the tentorium is shown at *E*. Stained with osmium tetroxide. ×21·5.

Fig. 2. The tentorium with widely dispersed tentorial nerve branches (arrows) directed towards the transverse sinus (not shown). The nerves mostly accompany blood vessels. The free edge of the tentorium is shown at *E*. Stained with osmium tetroxide. ×84.

Fig. 3. A branch of the cavernous plexus enters the trochlear nerve. ×346.

Fig. 4. Transverse section through part of the trochlear nerve with the colony of tentorial nerve fibres at the surface. Note the contrasting fibre sizes of the two groups with a greater proportion of smaller fibres in the tentorial nerve. ×440.



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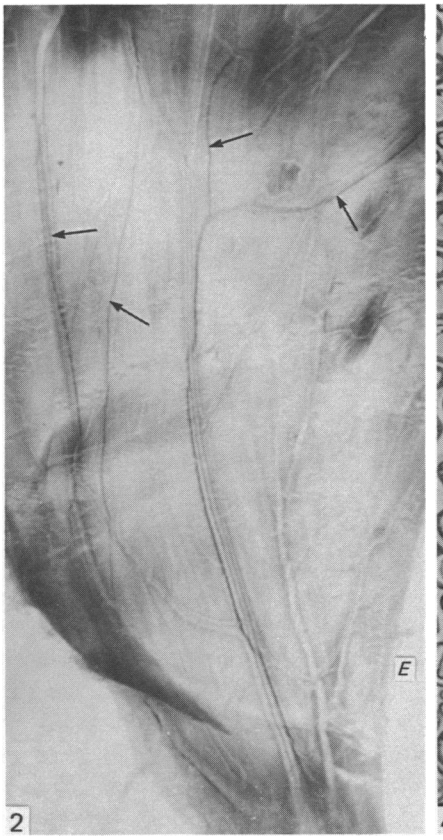

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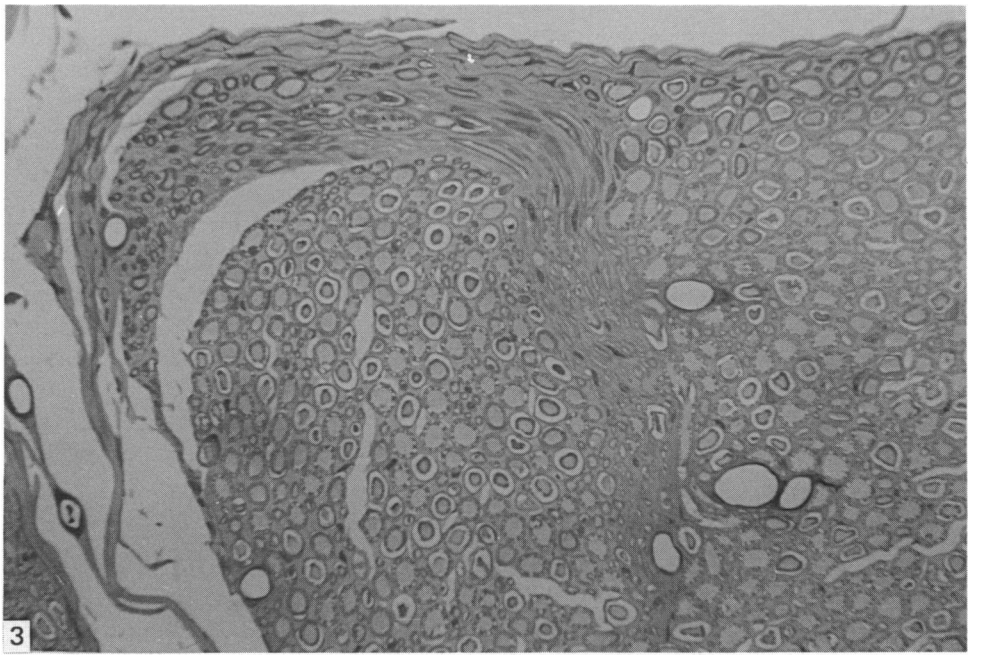
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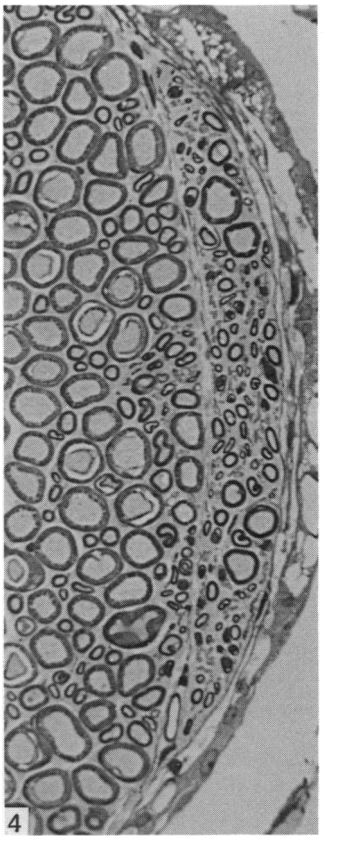
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(after treatment with osmium tetroxide) strips were cut from areas containing nerves and processed.

Tissues were post-fixed in 1 % unbuffered osmium tetroxide, dehydrated, embedded in Araldite and transversely sectioned using glass knives. Sections from the cavernous sinus blocks were cut 1 μm thick at intervals of 100–300 μm and in areas of special interest at 10 μm intervals, and stained with 1 % toluidine blue in an equal volume of 2·5 % sodium carbonate. The face of each large block of tissue was trimmed to present a small area for electron microscopical sampling. Sections were cut at intervals from the strips of tentorium and prepared for light and electron microscopy. Sections for electron microscopy were mounted on unfilmed copper grids, immersed in a saturated solution of uranyl acetate in 30–70 % ethanol for about 20 minutes, washed and immersed in 0·4 % lead citrate in 0·1 N sodium hydroxide for about 10 minutes.

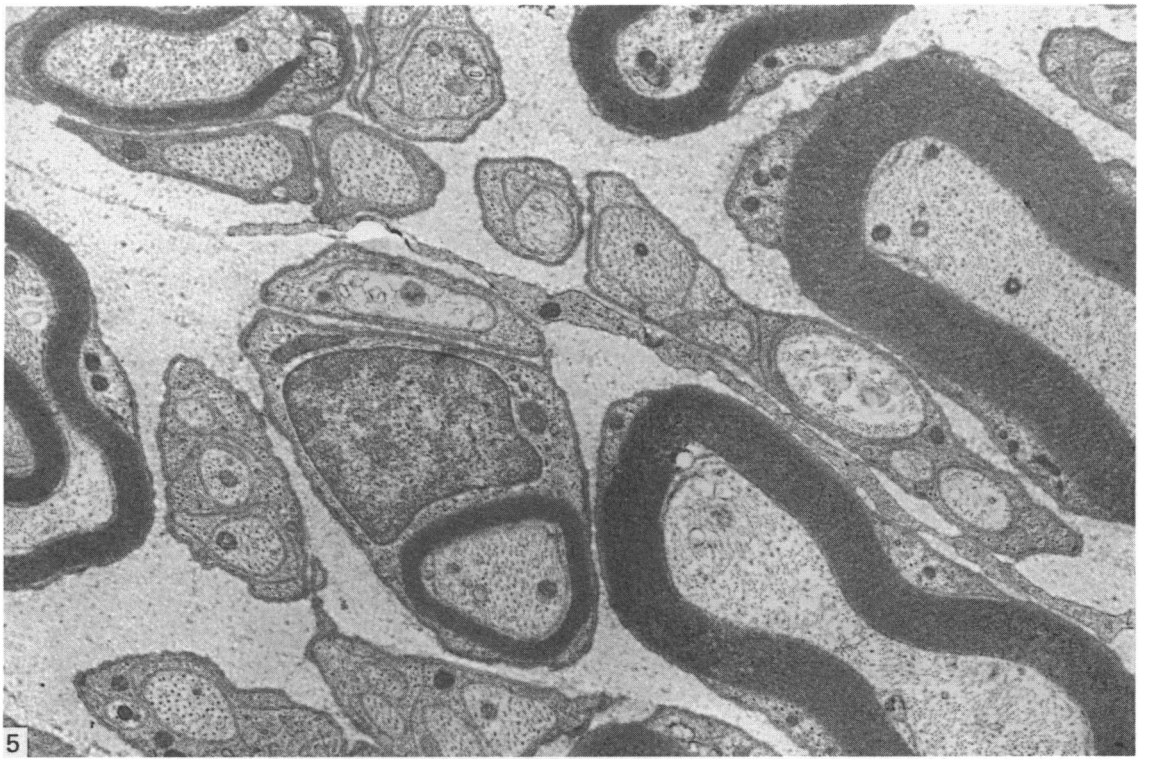
RESULTS

The cavernous plexus was revealed as the source of the tentorial nerve in both cynomolgus and rhesus monkeys. It was not a direct branch of the ophthalmic nerve in any of the preparations. Consequently the tentorial nerve might contain nerve fibres from a variety of sources. As reported earlier (Ruskell & Simons, 1987), the sympathetic nerves of the cavernous plexus are joined by two, three or more fine branches from the ophthalmic nerve and by one or two others from the orbitociliary branch of the maxillary nerve. The plexus is also joined anteriorly by parasympathetic rami orbitales from the pterygopalatine ganglion. Most of the plexus lies in the connective tissue surrounding the ophthalmic and abducent nerves in the lateral wall of the cavernous sinus and the tentorial nerve usually issued from a loop of the plexus lying above or medial to the ophthalmic nerve. It always arose distal to the junction of ophthalmic branches with the plexus and turned cranially and dorsally before joining the trochlear nerve in which it was directed towards the brainstem. Shortly before the trochlear nerve left the lateral wall of the sinus to reach the brainstem, the tentorial nerve separated from the trochlear (Fig. 1), remaining buried in dura mater and its branches were distributed in the tentorium cerebelli. Since no other nerves entered the tentorium from this direction it was obviously the equivalent of the nerve described in monkeys by McNaughton (1938) and identified as the *Nervus tentorii* of Arnold.

The tentorium was traversed by several arterioles radiating from the region of the stella turcica towards the transverse sinus, closely accompanied by one or two fine venules that appeared to connect the transverse and cavernous sinuses. The tentorial nerve branches were directed towards the transverse sinus mostly in the company of the vascular groups (Fig. 2). Attenuation of myelin with increasing distance from the trochlear nerve was noted but a few fibres still retained their myelin at the transverse sinus.

Fig. 5. A typical example of tentorial nerve fibres with a variety of myelinated nerve fibre diameters and a majority of unmyelinated nerve fibre bundles. × 15800.

Fig. 6. Tentorial nerve fibres fixed three days after ophthalmic/maxillary neurotomy. Normal axoplasmic organelles are replaced by an irregularly disposed flocculent material and circular profiles of various densities in the myelinated fibres. Early signs of disruption of the myelin sheaths are apparent. A Schwann cell process without enclosed axons is arrowed; and another with induced change is marked with an asterisk; other unmyelinated bundles have a normal appearance. × 13300.



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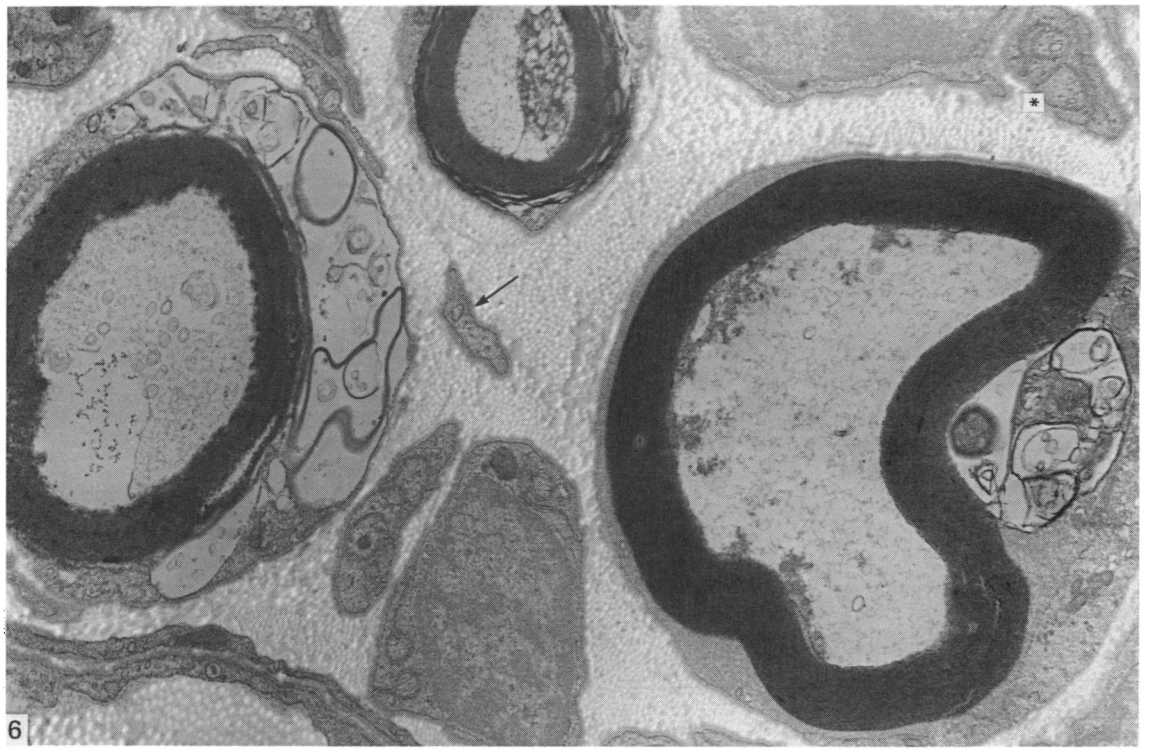

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Histological examination showed that upon joining the trochlear nerve, the tentorial nerve usually stayed at or close to its surface, sometimes after initially penetrating deep into the nerve (Fig. 3). The tentorial nerve typically persisted as a single colony of fibres easily distinguishable from those of the trochlear (Fig. 4). Myelinated fibres of various diameters were present together with numerous unmyelinated nerve fibre bundles (Fig. 5; Table 1), whereas many of the myelinated fibres of the trochlear nerve were substantially larger, and unmyelinated fibres very infrequent. The smallest of the tentorial nerves from unoperated sides contained 43 myelinated fibres and 87 unmyelinated fibres, the largest 206 and 142, with means of 85 ± 42 and 133 ± 65 ($n = 18$). In five preparations the tentorial nerve was double and in a sixth, three nerves were present. In each of these instances the nerve fibres remained aggregated within the trochlear nerve and, in three of them, one of the branches passed directly to the tentorium without joining the trochlear nerve.

Within the tentorium a reduction was observed in the number of myelinated and unmyelinated fibres with increasing distance from the cavernous sinus, consistent with the appearance of nerves in the gross preparations. In addition, nerve terminals were present in the walls of arterioles and venules close to the nerve trunks. They occasionally displayed varicosities filled with small agranular vesicles and a few mitochondria. Terminals were not found in avascular regions of the tentorium.

Identification of the sources of fibres contributing to the tentorial nerve in control material was facilitated by the marked difference of the fibre content of ophthalmic and autonomic groups. Apart from the absence of the largest myelinated fibres, the content of the cavernous plexus branches of the ophthalmic nerve was representative. Accordingly, many of the fibres were myelinated and their diameter range, although slightly diminished, was large and contrasted sharply with the predominantly unmyelinated fibre population of the autonomic elements. Consequently the ophthalmic groups were followed in the complex meshes of the cavernous plexus without difficulty for some distance through the serial sections. However, the ophthalmic groups tended to split up at the numerous plexus filament junctions and become dispersed among the abundant autonomic fibres. A large myelinated fibre or a small group of them still offered adequate expression of ophthalmic presence but not of their number because other ophthalmic fibres, the unmyelinated and smaller myelinated fibres, were indistinguishable from the autonomic groups. Although cavernous plexus branches of maxillary origin had a similar appearance to ophthalmic branches, tracing their passage through the plexus in control material was impractical because of their smallness and their complex course commencing anteriorly in the plexus, remote from the origin of the tentorial nerve. Ophthalmic fibres, on the other hand, were often traced with more or less confidence through the plexus to the tentorial branch and when this was not possible the fibre spectrum in the branch permitted the conclusion that fibres of trigeminal origin were present. The nearly uniform unmyelinated groups of autonomic fibres could also be traced through the plexus to the tentorial nerve when they remained aggregated but in most cases they were dispersed and only the evidence of the high overall incidence of unmyelinated fibres was available to suggest an autonomic contribution.

The results of combined ophthalmic and maxillary neurotomy confirmed the presence of trigeminal fibres in the tentorial nerve and, as expected, most of the myelinated fibres were degenerated (Fig. 6; Table 1). Maxillary neurotomy alone failed to induce degeneration in any of the fibres in two preparations and a very small fraction of the fibres in a third.

Ophthalmic/maxillary neurotomy also induced degeneration in a proportion of the

Table 1. *Tentorial nerve fibre analysis*

Reference and survival time in days	Operation	Myelinated fibres normal/degenerated	% Degenerated	Unmyelinated fibres normal/degenerated/mixed*	% Degenerated
CL 11–15	Superior cervical ganglionectomy	59/1	1	53/46/8	47
CL 35–7	Superior cervical ganglionectomy	59/2	2	117/104/13	43
CL 67–20	Superior cervical ganglionectomy	60/0	0	107/99/78	49
CL 43–6	Ophthalmic and maxillary neurotomy	1/43	98	44/21/10	35
RL 44–4	Ophthalmic and maxillary neurotomy	17/43	72	108/18/33	16
CL 83–3	Ophthalmic and maxillary neurotomy	18/43	80	119/23/3	17
CL 84–3	Ophthalmic and maxillary neurotomy	2/92	98	113/24/7	19
CL 46–6	Maxillary neurotomy	77/1	1	95/5/2	6
CL 80–4	Maxillary neurotomy	96/0	0	108/0/0	0
CL 82–4	Maxillary neurotomy	38/0	0	57/0/0	0

Counts were made at trochlear or tentorial level (before division) and were complete in most cases. No degeneration was observed in contralateral tentorial nerves.
* Bundles with most obvious signs of degeneration but containing one or more axons of normal appearance and given half value in the degeneration percentages.

Fig. 7. Tentorial nerve fibres fixed twelve days after superior cervical ganglionectomy. Several Schwann cell bundles without enclosed axons include numerous processes of various shapes with development of spaces within the basal lamina – all signs of degenerated unmyelinated nerve fibre bundles. A rounded mass of flocculent material suggests retention of degenerated axoplasm in one bundle (arrow). Induced changes are displayed in one bundle containing two axons of normal appearance (double arrow) – such bundles are counted as 'mixed' in Table 1. Myelinated and several unmyelinated fibres are unchanged by the lesion. × 11 700.

unmyelinated fibres (mean 22%) and it remained to identify the sources of the majority that survived.

Superior cervical ganglionectomy resulted in degeneration of nearly half (mean 46%) of the unmyelinated bundles but, at most, only one or two small myelinated fibres degenerated. Every specimen displaying degenerated fibres included some unmyelinated bundles with induced changes yet containing one or more good axons (Fig. 7), indicating that fibres from different sources occasionally shared the same Schwann cell investment (Table 1).

The appearance of the trochlear nerve subsequent to its surgical avulsion offered the clearest evidence that the fibre colony constituting the cavernous plexus tentorial branch was not native to the trochlear nerve and that passage within it was transient. The tentorial group retained a normal appearance while the somatic fibres, severed from their brainstem origin, were degenerated. All other experimental procedures used in this study preserved the integrity of somatic trochlear fibres.

One rhesus monkey was used experimentally and the result was consistent with cynomolgus data (Table 1). Additionally, five tentorial/trochlear nerves from unoperated sides of stock rhesus material produced counts and spectra similar to those of cynomolgus monkeys. The source of two of these was traced back to the cavernous plexus. Hence the nature of the tentorial nerve is likely to be the same in the two species.

DISCUSSION

Previous descriptions of the tentorial nerve were mainly derived from dissections of human material and represented by drawings or photographs of gross preparations

(Arnold, 1851; McNaughton, 1938; Feindel *et al.* 1960). McNaughton was able to trace the tentorial nerve with less difficulty, even without dissection, in monkeys and he concluded that it issued from the trigeminal ganglion. The osmium tetroxide-stained material of the present study and McNaughton's silver preparations are similar and without proceeding beyond gross observations one would have been misled into accepting his account, with the rider that the trigeminal ganglion and the trochlear nerve appeared equally likely sources of the tentorial nerve. But histological examination consistently showed that the tentorial nerve passed close to the ophthalmic nerve and the trigeminal ganglion without joining either of them; the cavernous plexus was regularly the immediate source.

It borders on presumption to question the work of Arnold whose astute observations on human material have been echoed with little dissent over a century and a half but an adjustment is necessary if we are to understand the unhomogeneous nature of the tentorial nerve and the cavernous plexus which, incidentally, he described and named (Arnold, 1831). The adjustment is made on the assumption that the nerve in the monkey and man is similar.

The cavernous sinus origin of the tentorial nerve differs from the classical view because it introduces the possibility that autonomic nerve fibres contribute to the nerve and so it proved. Trigeminal fibres, all or practically all from the ophthalmic division, entered the nerve but the degeneration experiments showed that many fibres survived trigeminal branch lesions. At least some of the survivors were sympathetic as a proportion of the unmyelinated fibres and, at most, one or two small myelinated fibres were degenerated following superior cervical ganglionectomy. If the pattern of degeneration had been approximately reciprocal following the two manoeuvres the analysis of the fibre content would have been complete. This was so for the myelinated fibres, as all but one or two survived ganglionectomy in all three animals and were degenerated with combined ophthalmic/maxillary neurotomy in two of four animals; in the other two, 20% and 28% of the myelinated fibres were undegenerated. These survivors were probably also largely trigeminal in origin. Failure of the lesions to produce degeneration can be accounted for, in part at least, by the fact that cell bodies are commonly present in the ophthalmic nerve two millimetres or more distal to the trigeminal ganglion (Ruskell & Simons, 1987); peripheral fibres of neurons lying distal to the lesion would not be damaged by ophthalmic neurotomy. In one of the two cases the ophthalmic nerve was incompletely transected which helps to explain the fraction of surviving myelinated axons. The validity of these explanations is supported by the presence of intact nerve fibres amid the masses of degenerated fibres of the ophthalmic nerve itself distal to the lesions and, moreover, the diameter spectrum of the surviving fibres in the tentorial nerve matched that of the ophthalmic branches joining the cavernous plexus.

Regarding the unmyelinated fibres the results of the two different operations were clearly not reciprocal. The proportion of unmyelinated fibres surviving combined ophthalmic and maxillary neurotomy was substantially greater (mean, 78%) than that of the degenerated fibres following superior cervical ganglionectomy (mean, 46%). This disparity may be accounted for in one or more of three ways.

(1) Ophthalmic neurotomy does not produce degeneration in all ophthalmic fibres distal to the lesion for the reasons mentioned above. But this technical limitation cannot be used for the disparity because the fibres unaffected by either lesion were almost exclusively unmyelinated whereas a large proportion of ophthalmic fibres in the tentorial nerve were shown to be myelinated.

(2) All sympathetic fibres may not suffer degeneration with removal of the superior

cervical ganglion as autonomic microganglia are found on the cranial side of the ganglion (Mitchell, 1953), some in the cavernous sinus itself (Gibbins, Brayden & Bevan, 1984; Ruskell & Simons, 1987). But too little is known of the microganglia to apply a reasonably estimated correction factor.

(3) The unmyelinated fibres unaccounted for may be postganglionic parasympathetic fibres.

Support for the third possibility is tangible but inconclusive. Postganglionic parasympathetic fibres of the pterygopalatine ganglion pass dorsally in the rami orbitales and join the nerves of the cavernous plexus in monkeys and man (Ruskell, 1970*a*). These fibres, like the unidentified group in the tentorial nerve, are unmyelinated and one is encouraged to suspect that, in common with plexus efferents to the orbit (Ruskell, 1970*b*), the tentorial efferent contains parasympathetic fibres from the pterygopalatine ganglion. The cerebral arteries also receive plexus efferents and they too may include parasympathetic fibres originating in the ganglion; VIP-ergic fibres, characteristic of parasympathetic nerves (Larsson *et al.* 1976), are eliminated from the adventitia of these vessels when the ganglion is destroyed in rats (Hara, Hamill & Jacobowitz, 1985). Against this must be set Edvinsson's (1980) claim that ganglionectomy fails to alter the vascular pattern of VIP-ergic fibres in cats. Horseradish peroxidase tracer studies support a pterygopalatine ganglion origin for adventitial nerve fibres of the middle cerebral artery in rats (Walters, Gillespie & Moskowitz, 1986) and invoke the otic ganglion as an additional source. Definitive work on this aspect of cavernous plexus and tentorial nerve fibre content is required.

The present study was not primarily intended to address the question of where tentorial nerve fibres terminate but the gross and histological preparations of the tentorium revealed some information worthy of comment. Nerves were followed to the vicinity of the transverse sinus where some of the fine branches presumably terminated close to the sinus. Whether or not others passed beyond the sinus could not be ascertained because the dense staining of the sinus region obscured the nerves. However, the vesicle-filled varicosities of the sparsely distributed terminals in the walls of arterioles and venules evidently issued from the tentorial nerve branches as their content reduced with increasing distance from the cavernous sinus. The terminals were presumably vasomotor but the possibility of a trigeminal identity cannot be excluded especially as myelinated fibres, degenerated following ophthalmic/maxillary neurotomy, were also reduced in number with distance from the cavernous sinus. On the other hand, Ray & Wolf (1940) observed that pressure on the tentorium in man was not painful unless applied close to sinuses.

SUMMARY

The origin and content of the tentorial nerve in cynomolgus and rhesus monkeys were studied using light and electron microscopic inspection of interrupted serial sections of the trigeminal/cavernous sinus region combined with selective nerve degeneration. The nerve was invariably a branch of the cavernous plexus rather than a branch of the trigeminal ganglion or ophthalmic nerve as described in earlier reports. The cavernous plexus branch forming the tentorial nerve joined and passed back in the trochlear nerve while it remained in the lateral wall of the cavernous sinus, then left the trochlear to be distributed in the tentorium cerebelli. It was composed of trigeminal fibres mainly from the ophthalmic division together with sympathetic fibres

from the superior cervical ganglion. The source of another group of unmyelinated fibres was unidentified but they are likely to be parasympathetic.

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