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The orbital branches of the pterygopalatine ganglion and their relationship with internal carotid nerve branches in primates

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INTRODUCTION

Details of the distribution and function of numerous groups of autonomic nerves are still unknown; the rami orbitales or orbital branches of the pterygopalatine ganglion are among these. In man several rami orbitales issue from the dorsal surface of the pterygopalatine (sphenopalatine) ganglion and enter the orbit or the retro-orbital region through the inferior orbital fissure (Vitali, 1929; Andres & Kautzsky, 1955 and others). They have also been described in several animals (Ruskell, 1965).

A clear concept of the distribution of the rami orbitales cannot be obtained from the literature. The results of many dissection studies and a few histological studies obtained over a period of 150 years are remarkably inconsistent and, probably as a result, interest in the rami orbitales has lapsed. Current reviews either overlook the rami orbitales or mention their presence without elaboration; only one review has been found which refers to their distribution (Duke-Elder & Wybar, 1961).

Studies of the rami orbitales have provided little evidence of the identity of their nerve fibres or of their function. Müller (1848) implied that the protrusion of the eyeball effected by contraction of the orbital muscle was mediated by sympathetic nerve fibres of the rami orbitales. Prevost (1868) considered that this was not the case because stimulation of the cervical sympathetic chain in dogs after extirpation of the pterygopalatine ganglion still resulted in protrusion of the eyeball. In the ensuing 100 years no further evidence of the presence or absence of sympathetic nerve fibres in the rami orbitales has been produced, and subsequent comment on the function of these nerves has been rare and usually speculative. Evidence that the rami orbitales contain parasympathetic nerve fibres was recently presented (Ruskell, 1965, 1968).

Monkeys were used in the bulk of the work to be reported in this paper. The rami orbitales were examined by dissection, and electron microscopy was combined with conventional nerve degeneration techniques in order to determine the nature and the source of their nerve fibres. No adequate illustration of rami orbitales in man is available and therefore dissections of human material were undertaken for comparison with monkey material.

One or more rami orbitales anastomose with the internal carotid plexus in man (Vitali, 1929; Andres & Kautzsky, 1955), and a para-abducens plexus of nerves derived from these two sources was described in rabbits (Ruskell, 1965). A similar plexus in monkeys and man is described in this paper, together with an analysis of the nerve fibre content in monkeys. Other details of distribution and evidence of the functions of the rami orbitales will be presented in subsequent reports.

METHODS

Four monkey heads were used exclusively for dissection purposes. The heads of one vervet (*Cercopithecus aethiops*) and two cynomolgous (*Macaca irus*) monkeys, fixed by perfusion with buffered 5% formaldehyde, and the severed head of a pygmy marmoset (*Hapale pygmaea*), which was immersed in fixative shortly after death, were prepared for dissection. This material was perfused with saline and injected with red Neoprene latex through both common carotid arteries (see Ruskell, 1962) to assist in distinguishing between fine nerves and very small vessels. After a preliminary dissection to partially expose the pterygopalatine ganglion, the intracranial portions of the orbital somatic nerves, the petrosal nerves and the rami orbitales, the tissue was impregnated with silver by means of the Christensen (1936) technique, as modified by Grimes & von Sallmann (1960). Dissection data were also obtained from animals used in the electron microscopical studies. Unstained human material from four sides of three heads was also dissected. Dissections were confined to structures of the pterygopalatine fossa and the retro-orbital region.

Material from 11 adult monkeys was examined electron microscopically. Six were rhesus monkeys (*Macaca mulatta*), four were cynomolgous and one was a vervet. The superior cervical ganglion was removed at operation from one side of six of these monkeys (one vervet, three cynomolgous and two rhesus), although in two of the rhesus monkeys removal was incomplete, as the ganglion was partially lodged in the carotid canal and complete ganglionectomy would have presented a hazard to the internal carotid artery. The specimens were fixed 2, 8, 10, 15 and 21 d respectively after operation.

A second operation was performed on the opposite side of two of these monkeys (vervet and rhesus) and on two other monkeys (rhesus), in which a segment of the greater petrosal nerve was removed from its sulcus in the floor of the cranium. Details of this operation have been described elsewhere (Ruskell, 1969). These animals were fixed 3, 5, 16 and 58 d after operation respectively. The oculomotor nerve was also severed in two of these animals for the purposes of another experiment.

In two other rhesus monkeys an endeavour was made to destroy the pterygopalatine ganglion by a surgical approach through the infratemporal and pterygopalatine fossae, but in both cases the ganglion could not be found and attempts to destroy the tissue of the pterygopalatine fossa were made by manipulation of a sharp, hooked needle. Subsequent dissection revealed that the maxillary nerve and the internal maxillary artery had been severed in each case and that the pterygopalatine ganglion had been damaged, but the rami orbitales were not severed from the ganglion. These specimens were fixed 6 d after the operation. A length of the cervical sympathetic chain was removed from the opposite side of one of these animals below the superior cervical ganglion 11 d before fixation. One cynomolgous monkey was not operated upon.

Before operation the monkeys were sedated with 10 mg Sernylan (phenycyclidine hydrochloride) given parenterally in two doses. Anaesthesia was induced with 24–36 mg pentobarbital sodium through a saphenous vein.

Before fixation by perfusion, sedation and anaesthesia were induced in the same manner and approximately 1500 units of heparin sodium were injected, again through the saphenous vein. The common carotid arteries were exposed and cannulated and the external jugular veins were cut. After exsanguination, which was speeded by cutting the common carotid arteries below the points of cannulation, the cranial vascular system was perfused with warm 1% sodium nitrite in saline followed immediately by 5·5% cacodylate-buffered glutaraldehyde.

The heads were stored in the fixative at approximately 4 °C, and dissected immersed in buffered sucrose. With the aid of a binocular dissecting microscope and the application of needle dissection, portions of the internal carotid nerves (taken from within the carotid canal), deep petrosal and greater petrosal nerves and the nerve of the pterygoid canal were isolated and removed. Removal of all the rami orbitales of each specimen was attempted and their subsequent observation and handling were facilitated by leaving a piece of the pterygopalatine ganglion attached to each of them. Pieces of fine autonomic nerves, which formed a retro-orbital plexus through which the oculomotor, trochlear, ophthalmic and abducens nerves passed were dissected free and preserved. Connective tissue was left attached at one end of each piece of the plexus to increase visibility during subsequent manipulations. A total of 128 rami orbitales and 22 pieces of the retro-orbital plexus were preserved and examined electron microscopically.

The tissues were stained in 1% buffered or unbuffered osmium tetroxide for 60–120 min. After dehydration some of the preparations were stained for approximately 2 h in 1% phosphotungstic acid in ethanol. All preparations were embedded in Araldite and sections cut for electron microscopy. A few of the sections stained with phosphotungstic acid, and all sections lacking this stain were immersed on the grids in 0·4% lead citrate in N/10 sodium hydroxide for 6–20 min.

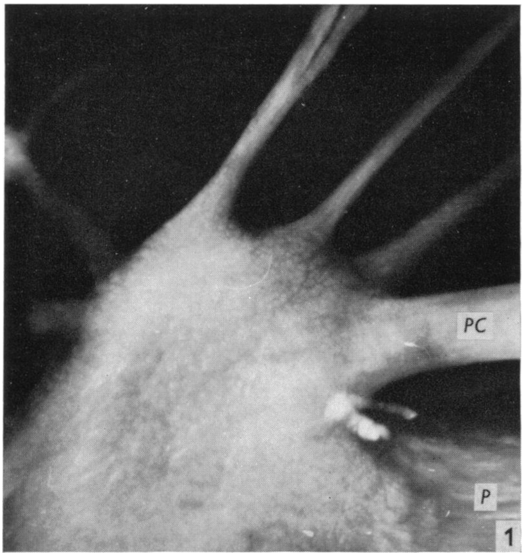
RESULTS

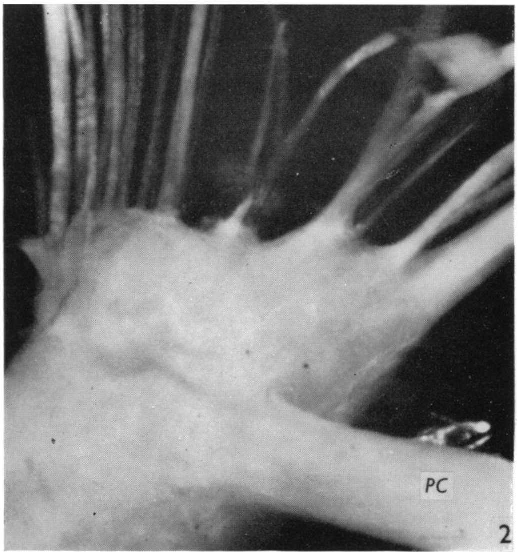
Dissections of monkey material

The deep petrosal and greater petrosal nerves joined to form the nerve of the pterygoid canal as in man. The pterygopalatine ganglion was positioned in the pterygopalatine fossa immediately anterior to the hiatus of the pterygoid canal. The ganglion was spheroid in shape with the long axis vertical or slightly inclined backwards dorsally. It occupied the full width of the single pterygopalatine nerve about 1 mm after the latter branched from the medial aspect of the maxillary nerve, but the bulk of the ganglion extended above both nerves (Figs. 1, 2). A short dorsal conical extension was usually present. In general, the short axis of the ganglion was 2 mm, the long axis was 3 mm and the central width was rather less than 1·5 mm. The nerve of the pterygoid canal joined the ganglion posteriorly at its broadest part above the level of the pterygopalatine nerve (Figs. 1, 2).

Between 5 and 16 rami orbitales issued from the apical region of the pterygopalatine ganglion, with the exception of one specimen in which 32 rami were observed. The ganglia with the least and the most rami orbitales are represented in Figs. 1 and

2. The rami varied between 30 and 130 μm in greatest diameter, the large majority measuring between 35 and 70 μm. All rami orbitales passed dorsally through the inferior orbital fissure and the largest group was also directed backwards, the most





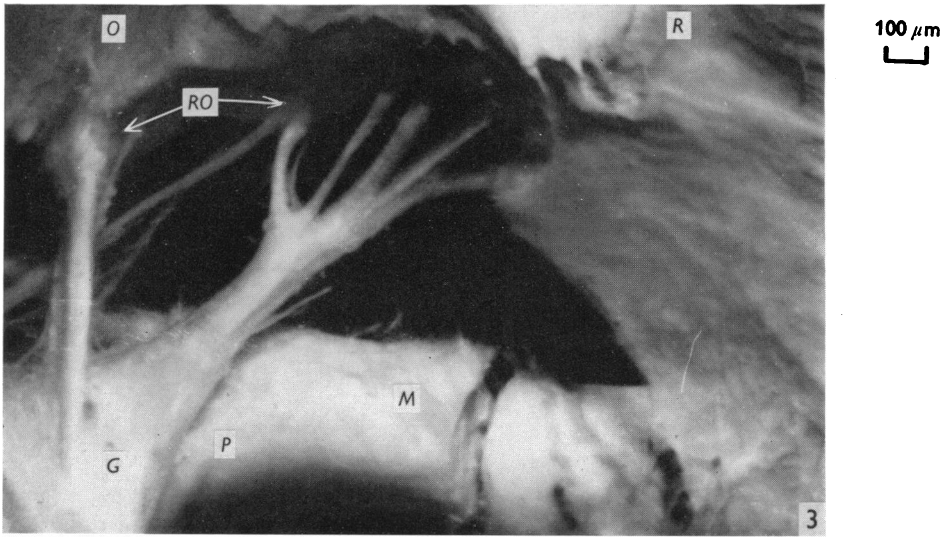


Fig. 1. Medial view of a pterygopalatine ganglion showing three large rami orbitales. Two finer rami had been severed. *P*, Pterygopalatine nerve; *PC*, nerve of the pterygoid canal. Rhesus, right side, unstained.

Fig. 2. Medial view of a pterygopalatine ganglion showing most of the 32 rami orbitales. *PC*, Nerve of the pterygoid canal. Rhesus, right side, unstained.

Fig. 3. Medial view of the rami orbitales (*RO*) and part of the pterygopalatine ganglion (*G*). *M*, Maxillary nerve; *O*, orbital tissues; *R*, retro-orbital tissues. Man, right side, unstained.

posterior of them passing through the cavernous sinus towards the ophthalmic and abducens nerves. The small anterior group entered the orbit at its apex. The rami often divided at least once and occasionally anastomosed within the pterygopalatine fossa; they had invariably increased in number at the level of the inferior orbital fissure.

Upon emerging dorsally from the pterygopalatine fossa through the inferior orbital fissure close to its cranial end, the rami orbitales turned sharply, either towards the orbit or the cranium, to run approximately parallel with the oculomotor, trochlear, ophthalmic and abducens nerves. In this position the posterior group of rami orbitales anastomosed with the branches of the internal carotid *nerve*; anastomoses with the internal carotid *plexus* directly were not observed. The distinction made in this study between branches of the internal carotid nerves and the internal carotid plexus does not accord with the usual description of these structures in man and therefore needs to be elaborated. The internal carotid nerve branches within the carotid canal were embedded in the fibrous tissue lining the canal and this lining was clearly distinguishable from but loosely attached to the adventitia of the artery. The nerves clearly did not lie in the adventitial wall of the artery. Within the cranial cavity the separation of the two internal carotid nerve branches from the artery was maintained. These nerves divided infrequently upon emerging from the carotid canal, and anastomosed once or twice so that at any position along the artery no more than four branches were present. But, in addition, numerous very fine branches occured within the carotid canal and within the cranial cavity and these passed to the adventitia of the artery, in which they formed a network of fine nerves. In other words there were two layers around the internal carotid artery containing nerves; an outer layer of two to four relatively large branches and an inner layer of numerous fine branches which formed a plexus. The plexus of the inner layer, which will be called the internal carotid plexus, was probably composed of terminal fibres serving the artery or its branches. The branches of the internal carotid nerve located in the outer layer, in addition to being the sources of the internal carotid plexus, also distributed relatively large branches away from the internal carotid artery. The deep petrosal nerve was such a branch, and those (two or three) which anastomosed with the rami orbitales were others.

The nerves formed by the anastomosis of rami orbitales and branches of the internal carotid nerve were disposed in a loose plexus within and anterior to the cavernous sinus. The oculomotor, trochlear, ophthalmic and abducens nerves passed through the plexus immediately before they entered the orbit through the superior orbital fissure. In order to distinguish between this plexus and the internal carotid plexus, and because of its position, it will be called the retro-orbital plexus. A few very fine nerves branched from large somatic nerves and shortly rejoined the parent nerve or joined an adjacent somatic nerve. These occurred in a retro-orbital position and they were similar in size to branches of the retro-orbital plexus. Occasionally they were joined by a branch of the plexus. The parent nerves could not always be identified, but all of those which were identified issued from the ophthalmic nerve or one of its branches and in two instances they joined the trochlear nerve.

Very small accessory pterygopalatine ganglia were found in the rami orbitales and at their junctions with internal carotid nerve branches. Between two and five accessory ganglia were usually present; their identity was confirmed with both light and electron microscopy and they were estimated to contain between 10 and 40 nerve cells which were similar in appearance to those of the pterygopalatine ganglion. On one side of a cynomolgous monkey in which the pterygopalatine ganglion was exceptional in consisting of several parts, larger accessory ganglia were observed. These contained up to approximately 500 cells each.

Several fine nerves passed from the retro-orbital plexus and entered the orbit through the superior orbital fissure, and others joined the adjacent somatic nerves. Further details of the distribution of these fine nerves is beyond the scope of this paper.

Dissections of human material

The pterygopalatine nerve branched medially and inferiorly from the maxillary nerve within the pterygopalatine fossa. Within 2 mm of its source the single pterygopalatine nerve expanded into the pterygopalatine ganglion. The centre of the ganglion lay just below the level of the maxillary nerve in three specimens and opposite the nerve in a fourth. The shape of the ganglion was irregular, due to the variable size and position of conical extensions from which the palatine, nasal and orbital nerves branched. Figure 3 illustrates an example of a conical extension in relation to the rami orbitales; in this case the ganglion extended above the level of the maxillary nerve, but in the remainder it did not.

The numbers of rami orbitales passing dorsally from the pterygopalatine ganglion were 9, 9, 11 and 13 respectively in the four specimens. These varied in size between 40 and 400 μm. They passed through the inferior orbital fissure in one or two groups. Some appeared to be distributed within the inferior muscular position of the periosteum of the orbit and others penetrated the periosteum and entered the orbit; but the greater number passed towards the abducens and ophthalmic nerves in a retro-orbital position. Branches of the internal carotid nerve (the internal carotid nerve branches and the internal carotid plexus could be distinguished in the same way as in monkeys) were traced to the retro-orbital region. They passed forward from a sleeve of fibrous tissue surrounding the internal carotid artery, either in the wall of the cavernous sinus or in its trabeculae, and anastomoses between these nerves and branches of the rami orbitales were observed in the fibrous tissue surrounding the abducens and ophthalmic nerves. The condition of the material was too poor to establish whether or not a retro-orbital plexus as extensive as that found in monkeys was present, but the frequent division of both rami orbitales and internal carotid nerve branches retro-orbitally, and the passage of these branches between the adjacent somatic nerves, suggest that this was probably so.

Electron microscopy of rami orbitales, nerves of the pterygoid canal, deep petrosal and internal carotid nerves

A very large majority of the nerve fibres of the rami orbitales of monkeys were unmyelinated (Table 1, Fig. 4). The rami displayed no significant differences in form from other post-ganglionic autonomic nerves except that a slight majority (58%) of all nerve fibre bundles examined contained only one axon. The rami measured between 30 and 131 μm in greatest diameter with a content of between 54 and 1477 unmyelinated nerve fibre bundles, but the majority had a greater diameter of between 35 and 70 μm and contained between 180 and 600 unmyelinated nerve fibre bundles.

The total nerve fibre population of all the rami orbitales found in single pterygopalatine fossae are presented in Table 1. The Table is subject to two possible errors—firstly, all the rami may not have been found during dissection, and secondly, a full count of every ramus was not possible because of the occlusion of part of the field by the bars of the section mounting-grids. But only the very finest of rami were likely to have been overlooked and the estimations made are indicated.

Table 1. *Estimates of the total number of nerve fibres in all the rami orbitales found in single pterygopalatine fossae*

Monkey and side	Total rami orbitales	Estimated no. of myelinated nerve fibres	Estimated no. of unmyelinated nerve fibres		% of total area of rami counted
			Bundles	Axons	
Cynomolgous 3 R	12	302	6,727	10,226	76
Cynomolgous 4 L	16	217	3,689	4,913	84
Rhesus 1 L	10	76	3,615	9,437	68
Rhesus 5 R	6	97	1,799	4,099	82

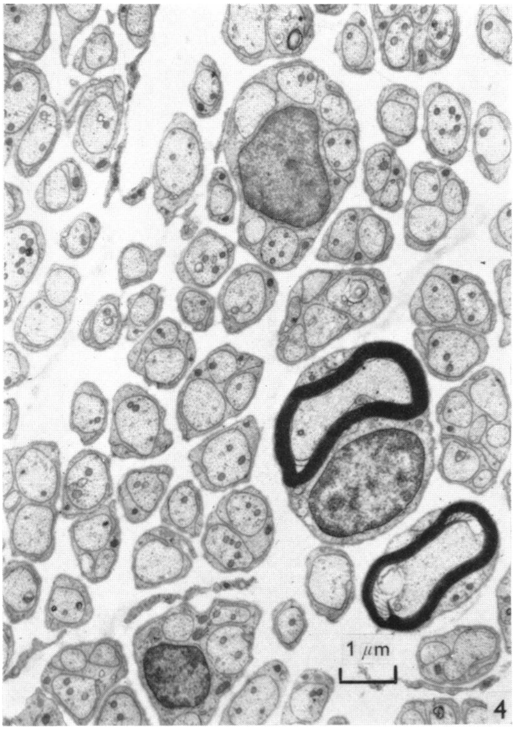
One or two Schwann cells without enclosed axons were present in a minority of control rami orbitales; between 0·2 and 1·4% of Schwann cell processes were without enclosed axons in the samples of rami orbitales examined (Table 2). The presence of the basement membrane surrounding the Schwann cells without enclosed axons afforded a simple means of distinguishing them from other cells of the endoneurium.

Superior cervical ganglionectomy

The superior cervical ganglion was completely removed from one side of each of four monkeys; this was confirmed by examining the excised tissue microscopically and the two internal carotid nerve branches of the carotid canal electron microscopically. All axons of unmyelinated nerve fibre bundles had disappeared from these nerves, but Schwann cells remained; these frequently occured as several separate cytoplasmic profiles within a single membrane boundary.

The appearance of the deep petrosal nerves from the operated sides of these animals was similar in all respects to that of the internal carotid nerve branches. The persistence of Schwann cell bundles after the degeneration of axons could therefore be interpreted as evidence that sympathetic axons had been present prior to operation. Schwann cells without enclosed axons were also seen in abundance scattered throughout the nerve of the pterygoid canal. This method was applied to identify sympathetic fibres in rami orbitales, subject to a correction made necessary by the occurrence of a few empty Schwann cells in control rami, as described earlier.

An analysis of the nerve fibre content of rami orbitales taken from monkeys after superior cervical ganglionectomy is represented in Table 2. The Table also includes data from one animal after partial ganglionectomy. The proportion of Schwann cells without enclosed axons varied between 1·0 and 5·3% in different animals and two examples are illustrated in Fig. 5. These proportions range marginally higher than



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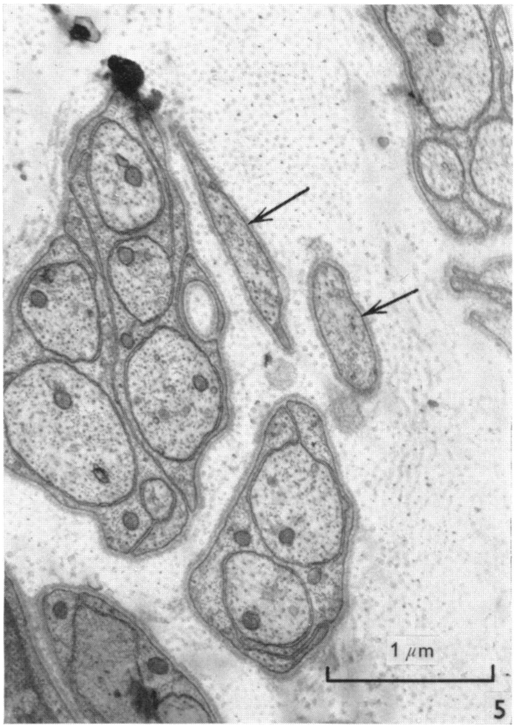

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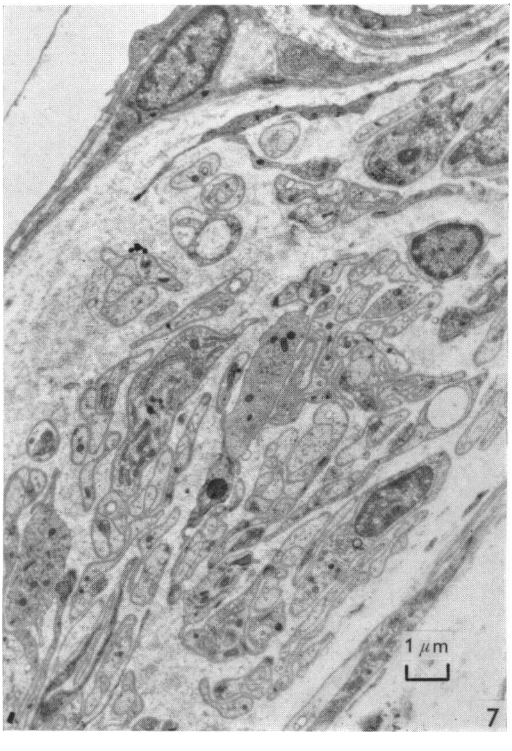

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those obtained from control material which suggests that very few fibres of the rami orbitales were sympathetic. However, if the operated and control sides of individual animals represented in Table 2 are compared, it will be seen that in one monkey the control side figure was in fact slightly higher than that of the operated side (1·3% and 1·0% respectively in cynomolgous 3). These figures suggest that sympathetic fibres were not present in this animal.

Table 2. *Analysis of the nerve fibres of the rami orbitales*

Monkey and side	Operation and interval before fixation (days)	No. of rami orbitales (branches)	myelinated nerve fibres	Unmyelinated nerve fibre bundles (Schwann cell units)	Schwann cells without enclosed axons	%
Cynomolgous 1 R	None	2	14	411	6	1·4
3 L	None	4	160	1,935	26	1·3
4 R	None	5	68	2,758	8	0·3
5 R	None	5	97	1,799	9	0·5
6 L	None	4	211	2,077	2	0·2
Vervet 1 R	Superior Cervical Ganglionectomy (10)	3	84	525	23	4·2
Cynomolgous 1 L	Superior Cervical Ganglionectomy (21)	7	57	593	33	5·3
Cynomolgous 3 R	Superior Cervical Ganglionectomy (15)	12	247	5,092	51	1·0
Cynomolgous 4 L	Superior Cervical Ganglionectomy (15)	16	186	3,097	71	2·2
Rhesus 6 R	Partial Ganglionectomy (8)	7	391	2,512	14	0·5
Rhesus 3 R	Cervical sympathectomy below Superior Cervical ganglion (11)	5	68	993	9	0·9
Vervet 1 L	Greater Petrosal Neurectomy (3)	2	49	671	5	0·7
Rhesus 1 L	Greater Petrosal Neurectomy (16)	10	54	2,449	16	0·6
Rhesus 4 L	Greater Petrosal Neurectomy (58)	3	16	1,121	8	0·7
Rhesus 5 L	Greater Petrosal Neurectomy (5)	2	9	214	1	0·5

(The numbers and percentages of Schwann cells without enclosed axons are shown and grouped according to the operation performed. Left and right sides of the same monkey may be identified by the species and number code in the first column.)

Fig. 4. Unmyelinated and two myelinated nerve fibres of a ramus orbitalis. Between one and six axons are present in the unmyelinated nerve fibres. Rhesus, control.

Fig. 5. Two Schwann cell processes without enclosed axons (arrows) in a ramus orbitalis. Fixed 15 d after superior cervical ganglionectomy. Cynomolgous.

Fig. 6. Nerve fibres of a ramus orbitalis showing many induced alterations including Schwann cells without enclosed axons (arrows). Fixed 6 d after pterygopalatine ganglion damage. Rhesus.

Fig. 7. Part of a nerve of the retro-orbital plexus with many Schwann cell processes but very few axons. Fixed 15 d after superior cervical ganglionectomy. Cynomolgous.

In some of the rami of the monkey fixed 2 days after partial superior cervical ganglionectomy one or two conspicuously altered axons were found. These were much enlarged and possessed few or no organelles of normal appearance. The axoplasm was mostly composed of small clumps of fine granular material. Axons of this appearance were abundant in the ipsilateral internal carotid nerve branches of this animal.

Myelinated nerve fibres were of normal appearance in all specimens and no evidence of degenerating myelin was seen.

Cervical sympathectomy below the superior cervical ganglion

A few Schwann cells without enclosed axons were observed in the rami orbitales of the single rhesus monkey used (Table 2). No control data were available for this animal, as the pterygopalatine ganglion had been damaged on the other side, but the 0·9% of Schwann cell bundles without enclosed axons was of the same order of magnitude as that observed in the controls of other animals.

Greater petrosal neurectomy.

Similar results were obtained after greater petrosal neurectomy (Table 2). In none of the samples of rami orbitales examined was the proportion of Schwann cells without enclosed axons greater than 1%. It was anticipated that this lesion would induce degeneration of myelinated nerve fibres of the rami, assuming that they were continuations of fibres of the greater petrosal nerve which passed through the pterygopalatine ganglion and terminated in the accessory ganglia. But this was not so; all myelinated nerve fibres were of normal appearance and no signs of degenerated myelin were found.

Inspection of the deep petrosal nerves revealed no degeneration of nerve fibres. The passage of centrifugal nerve fibres from the greater petrosal nerve to the nerve of the pterygoid canal was proved by the presence in the latter of Schwann cells without enclosed axons.

Pterygopalatine ganglion damage

Rami orbitales from the least damaged specimen contained a large number of Schwann cells without enclosed axons and fibroblasts were unusually abundant. These changes were more common in the rami of the severely damaged specimen, which also displayed a variety of other induced changes. A majority of the unmyelinated nerve fibre bundles contained more Schwann cell processes (up to 8) than found in controls, and they did not conform to the usual pattern; the processes were large and rounded or of grossly irregular shape and they failed to invest the axons. Axons and Schwann cell cytoplasm were easily confused because the latter, staining less heavily than in controls, had become similar in density to axons. Further, many axons had also assumed an irregular shape. Groups of axons were often sandwiched between adjacent Schwann cell processes, and some processes and axons displayed an atypical abundance of organelles; a few axons were unusually large and composed of aggregated fine granular material and a few irregularly shaped vacuoles. Degenerating myelin was identified and no normal myelinated nerve fibres were present. Many of the induced alterations are illustrated in Fig. 6, which adequately conveys the marked contrast between the altered rami and that of controls as shown in Fig. 4.

Electron microscopy of the retro-orbital plexus

Most of the branches of the retro-orbital plexus examined were dissected free without observing their relationship with rami orbitales or internal carotid nerve branches. But the relationship of several preserved branches with one or other of these sources was known. A few rami orbitales which did not join the plexus but which entered the orbit directly were also examined.

In control material nearly all the fine rami of the plexus were found to be populated by unmyelinated nerve fibres, but a few were entirely different in character, possessing a predominance of medium-sized (4–9 μm) myelinated nerve fibres. These were presumably the fine somatic nerve divisions described earlier. The perineurium of the retro-orbital plexus branches was seldom more than one or two cells thick. Evidence of junctions between elements of the plexus was frequently apparent in single nerves by the presence of single cell processes extending from the perineurium across the nerve from one side to the other. Examination of an accessory ganglion revealed somata all of similar appearance with several axon terminals apposed to each soma in single sections. The terminals were more or less packed with small agranular vesicles and mitochondria.

After superior cervical ganglionectomy several branches of the plexus contained only Schwann cells without enclosed axons. Such branches were clearly exclusively sympathetic. In others only an occasional axon of normal appearance was encountered (Fig. 7). Some nerves displayed single large or small groups of normal unmyelinated nerve fibres in an otherwise degenerated nerve, thus probably indicating a nerve of mixed origin. But the most common form of nerve encountered contained Schwann cells with or without enclosed axons, with no large aggregations of one or the other (Fig. 8).

In three branches nearly all the nerve fibres were myelinated and of medium size. In these, all the nerve fibres including the few unmyelinated nerve fibres were of normal appearance, with the exception of a small group of Schwann cells without enclosed axons at the surface of one of them. This identified them as fine divisions of the somatic nerves as described earlier. Evidently one had been joined by a fine sympathetic ramus.

In the two nerves taken from the retro-orbital plexus of the rhesus monkey fixed only 2 d after partial superior cervical ganglionectomy, unmyelinated nerve fibres showing distinct alterations were scattered throughout. The axons in these were much enlarged and contained few or no organelles of normal appearance. The organelles replaced by scattered clumps of fine granular material.

The appearance of nerves of the retro-orbital plexus after pterygopalatine ganglion damage was complementary to their appearance after superior cervical ganglionectomy. Some nerves were of completely normal form whilst others contained only nerve fibres with induced alterations similar to those found in rami orbitales after this operation. Others contained both normal nerve fibres and fibres with induced changes. In one specimen, fibres with induced changes were observed on the orbital side of a junction with a ramus orbitalis, but no changes were present on the cranial side of the junction (Fig. 9).

Two rami orbitales were sectioned close to their entry into the orbit. No anastomoses


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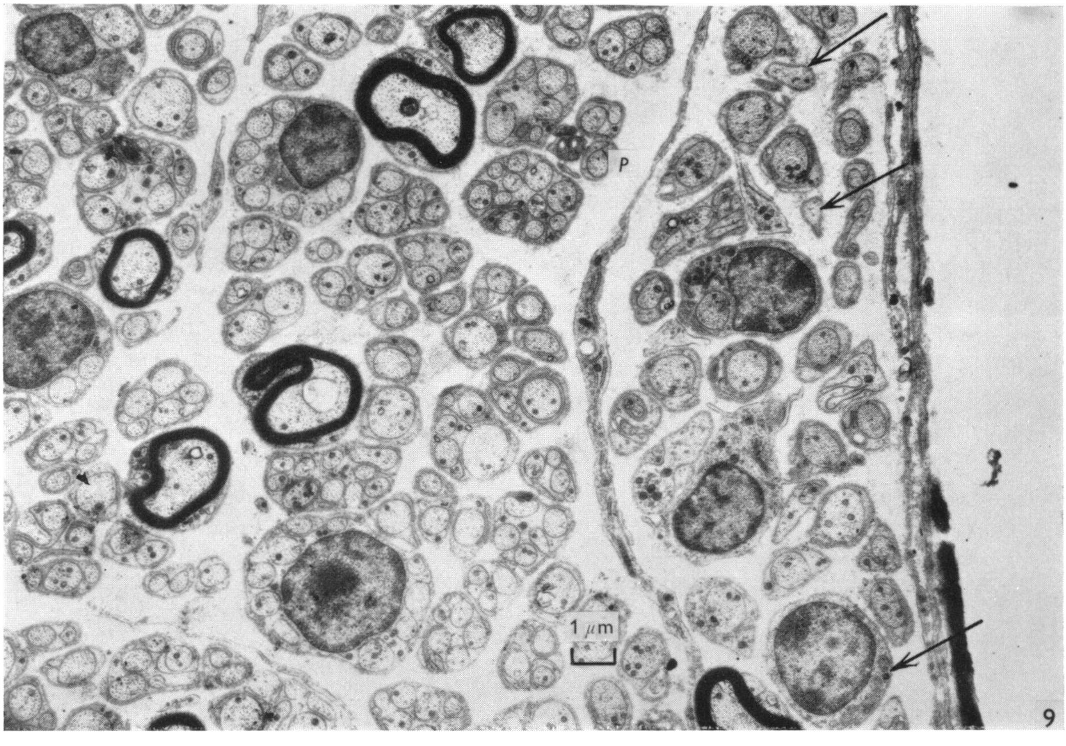
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with the retro-orbital plexus had been observed in these. Their appearance was precisely the same as that of rami orbitales sectioned at pterygopalatine fossa level.

The nerve of the pterygoid canal was also examined after pterygopalatine ganglion damage. This nerve displayed some minor changes among a few of the unmyelinated nerve fibres. The axons were occasionally slightly mis-shapen and neurotubules were obliquely orientated in a few axons. However slight, these changes appeared to have been induced by the operation because they could not be observed in the controls. None of the gross changes induced in the rami orbitales after this operation was duplicated in the nerve of the pterygoid canal.

After superior cervical ganglionectomy, degenerated nerve fibres were more numerous than fibres of normal appearance in the retro-orbital plexus branches when considered collectively, and after pterygopalatine ganglion damage a majority were normal. This suggests that sympathetic nerve fibres predominated in the plexus.

DISCUSSION

The rami orbitales of the human material were found to be more numerous (9 to 13) than reported hitherto. Their number has seldom been stated explicitly but some authors have implied that one or only a few are present; Vitali's (1929) figures of 6 to 8, obtained from histological examination of 26 sides, are the highest previously reported.

The pterygopalatine ganglion and the rami orbitales in monkeys, which have not been described previously, were of strikingly similar appearance to those of man but the ganglion invariably lay medial to and slightly above the maxillary nerve in monkeys. In man the ganglion lay slightly below the maxillary nerve in three of the four specimens, which was the position most commonly found in a study of 60 ganglia by Tanaka (1932). Primate tissue contrasts with that of rabbit which does not usually possess a pterygopalatine nerve and in which the ganglion is flat and long (Ruskell, 1965).

The persistence of Schwann cells after the degeneration of axons induced by sympathetic ganglionectomy provides an excellent method for tracing the distribution of unmyelinated sympathetic nerve fibres. By this means it was made evident that many sympathetic nerve fibres passed to the pterygopalatine ganglion in the nerve of the pterygoid canal. But because of the occurrence of a few Schwann cells without enclosed axons in unoperated material (Table 2), one is not free to conclude that all examples of such cells represent remnants of sympathetic nerve fibres. This factor presents a particular difficulty in analysing the fibre content of the rami

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Fig. 8. Part of a nerve of the retro-orbital plexus with a mixture of normal unmyelinated nerve fibre bundles and Schwann cells without enclosed axons. Fixed 15 d after superior cervical ganglionectomy. Cynomolgous.

Fig. 9. Part of a nerve of the retro-orbital plexus sectioned close to the orbital side of a junction with a ramus orbitalis. Induced alterations are present in the portion contributed by the ramus orbitalis (to the right of the perineurium cell process, *P*). The nerve fibres of normal appearance to the left are presumably sympathetic. Three Schwann cells without enclosed axons are arrowed. Fixed 6 d after pterygopalatine ganglion damage. Rhesus.

orbitales in which the difference in numbers of Schwann cells without enclosed axons between control and operated specimens was not marked. However, the difference between the proportions 5·3% and 1·4% (cynomolgous 1 of Table 2), and between 2·2% and 0·3% (cynomolgous 4) of operated and control material respectively must be indicative of the presence of a few sympathetic nerve fibres. The presence of degenerating axoplasm in fibres of the rami orbitales 2 d after superior cervical ganglionectomy confirmed that a few fibres were sympathetic. Yet, as noted earlier, in one of the six monkeys in this series, Schwann cells without enclosed axons were more numerous in the control group (1·3% compared with 1·0%), indicating that sympathetic nerve fibres were probably not present in this case.

It follows that at least an overwhelming majority of the nerve fibres of the rami orbitales were other than sympathetic. These were not affected in significant numbers, if at all, by greater petrosal neurectomy, as the proportion of Schwann cells without enclosed axons after this procedure (0·5 to 0·7%) compared with that of controls. Yet there is no doubt that the greater petrosal nerve and rami orbitales are parts of a common nerve pathway; for example, it was shown that greater petrosal neurectomy induces a radical reduction in lacrimal gland secretion in monkeys (Ruskell, 1969), and that the rami orbitales are the only nerves relating the greater petrosal nerve with the gland in monkeys (Ruskell, 1968), which is also the case in rabbits (Ruskell, 1965). Consequently, the absence of induced alterations in fibres of the rami orbitales after greater petrosal neurectomy can only be explained by the presence of a relay in the pterygopalatine ganglion. The failure of pterygopalatine ganglion lesions to induce significant alterations in the nerve of the pterygoid canal whilst inducing pronounced alterations in the rami orbitales is consistent with this explanation; the lesion would be expected to affect post-ganglionic nerve fibres of damaged pterygopalatine ganglion cells but comparable retrograde changes in the preganglionic fibres in the nerve of the pterygoid canal would not be expected. Hence, most of the nerve fibres of the rami orbitales are identified as parasympathetic motor of pterygopalatine ganglion origin. The identification of parasympathetic motor nerve fibres in the rami orbitales with cell bodies in the pterygopalatine ganglion was demonstrated in rabbits earlier (Ruskell, 1965, 1968).

The presence of nerve fibres other than the parasympathetic and the few sympathetic motor fibres in the rami orbitales cannot be ruled out. For example, the identity of the small myelinated nerve fibres of the rami orbitales has not been revealed by this study. They were unaffected by superior cervical ganglionectomy and greater petrosal neurectomy. They degenerated after pterygopalatine ganglion damage. These results limit their identity to the possibilities of: 1. post-ganglionic fibres of the pterygopalatine ganglion; (2) a maxillary nerve origin; or, (3) a greater petrosal nerve origin with unipolar or bipolar cell-bodies in the pterygopalatine ganglion.

The first possibility seems unlikely on morphological grounds. Apart from their distinguishing feature of myelination, their axon size invariably dwarfed that of the largest unmyelinated nerve fibres and it is therefore improbable that these two groups would share the same functional classification as post-ganglionic parasympathetic motor fibres. A maxillary nerve origin also appears unlikely in view of observations made on rabbits (Ruskell, 1965, 1968). In this animal the pterygopalatine ganglion was not usually connected to the maxillary nerve through a pterygopalatine nerve yet the rami orbitales were similar to those of monkeys in possessing a minority of myelinated nerve fibres. Some evidence of the presence of sensory nerves which fit the third possibility has been found (Ruskell, 1968), and the presence of more than one type of cell in the pterygopalatine ganglion has been demonstrated histochemically in cats (Koelle & Koelle, 1959). Acetylcholinesterase was demonstrated at synapses around many cells which were identified as autonomic motor, but the staining reaction was absent from the surfaces of other cells. The latter cells presumably lacked synapses at ganglion level, which is in keeping with the argument that unipolar or bipolar sensory cells are present in the pterygopalatine ganglion.

A retro-orbital plexus was originally described in rabbits (Ruskell, 1965), but because much of the plexus in this animal was disposed around the abducens nerve, the name 'para-abducens plexus' was used. The relationship of the plexus with the abducens nerve in monkeys is no more marked than with other somatic nerves of the region and the same is true in man. Hence the term 'retro-orbital plexus' is preferred. The earlier dissections on rabbits indicated that the plexus was probably composed of both parasympathetic fibres of pterygopalatine ganglion origin and sympathetic fibres of superior cervical ganglion origin, and the same conclusion was conveyed by the dissections of monkey and human material in this study. The nerve degeneration experiments in monkeys amply confirmed that this is the case; evidence that retro-orbital plexus branches are purely sympathetic, parasympathetic or a mixture of the two has been presented. Sympathetic nerve fibres appear to be more numerous but the evidence is not conclusive because of the small samples taken from single sides of monkeys. On the assumption that all the nerve branches of the internal carotid nerve contributing to the plexus are sympathetic and those from the rami orbitales parasympathetic, there can be little difference in the size of the contributions of each to the plexus.

The difficulty of interpreting the degeneration experiments because of the possible presence of ectopic sympathetic cells along the internal carotid nerve (Mitchell, 1953, and others) was overcome by applying other experimental techniques in addition to sympathectomy. Indeed, small ectopic groups of cells were recognized regularly in the rami orbitales and the retro-orbital plexus but only very occasionally in the internal carotid nerve branches in monkeys. They have also been observed in the rami orbitales of adult (Vitali, 1929) and foetal (Andres & Kautzsky, 1955) man, and in the rami orbitales and retro-orbital (para-abducens) plexus of rabbits (Ruskell, 1965).

An important implication of establishing that both parasympathetic and sympathetic nerve fibres are present in the retro-orbital plexus is that all autonomic nerves distributed from the plexus may be composed of both types of fibres. This replaces the concept, so often presented, that any autonomic nerve of this region is necessarily sympathetic. One's attention is drawn to the structures which may be served by these nerves. On the evidence presented, there are three possible distributions from the retro-orbital plexus. These are: (1) to the structures of the orbit; (2) to the adjacent somatic nerves; (3) to the cerebral arteries by way of the internal carotid plexus.

Some evidence of the first two possibilities has been presented in this paper but each of these represents a broad topic and they will be described in detail in later papers.

Definite evidence that parasympathetic fibres were directed towards the wall of the internal carotid artery from the retro-orbital plexus was not obtained, but it is clearly a possibility. Several observers noted that stimulation of the facial nerve produced dilation of the arteries of the cerebral pia mater (see Cobb & Lennox, 1944), and it has been claimed that the responsible parasympathetic nerve fibres passed from the greater petrosal nerve to the deep petrosal (Chorobski & Penfield, 1932). The evidence for this was based on histological observations of normal material and the presence of a small ganglion at the junction of the greater petrosal and deep petrosal nerves in monkeys. These observations are unsupported by the results of this study. The ganglion at the junction of the greater and deep petrosal nerves was not present in any of the monkeys used and all nerve fibres of the deep petrosal nerve degenerated as a consequence of superior cervical ganglionectomy. Greater petrosal neurectomy failed to induce degeneration of deep petrosal nerve fibres. This leaves no doubt that all the nerve fibres of the deep petrosal nerve are sympathetic. Therefore, cerebral vasodilatation induced by facial nerve stimulation has not been explained satisfactorily, but parasympathetic fibres of the retro-orbital plexus could mediate this activity.

SUMMARY

The orbital branches (rami orbitales) of the pterygopalatine ganglion were studied by dissection in monkeys and man. A majority of the rami orbitales were joined by branches of the internal carotid nerve to form a retro-orbital plexus. Before entering the orbit through the superior orbital fissure, the oculomotor, trochlear, ophthalmic and abducens nerves passed through the plexus within and anterior to the cavernous sinus.

Various autonomic nerve lesions were used in conjunction with electron microscopy to analyse the nerve fibres of the rami orbitales and the retro-orbital plexus in monkeys. A very small proportion of nerve fibres of the rami orbitales were sympathetic post-ganglionic, and in one of five monkeys none were sympathetic. The rami orbitales conducted parasympathetic nerve fibres, which issued from cells of the pterygopalatine ganglion, to the retro-orbital plexus. The plexus received sympathetic nerve fibres from branches of the internal carotid nerve. Single branches of the retro-orbital plexus were composed of either sympathetic or parasympathetic nerve fibres or both. In the samples examined sympathetic nerve fibres predominated. All nerve fibres of the deep petrosal were sympathetic.

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