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The distribution of autonomic post-ganglionic nerve fibres to the lacrimal gland in monkeys

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INTRODUCTION

Jendrássik (1893) and Goldzieher (1894) observed impairment of lacrimal secretion in cases of intracranial facial nerve lesion. Impairment was not observed when the lesion occurred in the region of the stylomastoid foramen. This led them to propose that lacrimal secretomotor fibres in man leave the facial nerve in the greater petrosal nerve and continue to the pterygopalatine ganglion in the nerve of the pterygoid canal. The results of many functional studies such as those of Köster (1900) and Golding-Wood (1964) substantiated this view. The same pathway has been demonstrated in various animals (see Gloster, 1961; Botelho, Hisada & Fuenmayor, 1966) including monkeys (Ruskell, 1969) and anatomical proof of the interruption of the pathway by a relay in the pterygopalatine ganglion in rabbits has been presented (Ruskell, 1965).

Because no alternative presented itself, Jendrássik (1893) and Goldzieher (1894) suggested that the secretomotor pathway continued in the pterygopalatine nerves and the maxillary nerve to reach the gland by way of the zygomatic branch of the maxillary nerve and an anastomosis between the zygomatic and lacrimal nerves. Their suggestion was generally adopted and it has prevailed until the present time, despite the inconstancy of the anastomosis between the zygomatic and lacrimal nerves in man (Testut, 1899). Supporting evidence is insubstantial or fragmentary. Campos (1897) described a copious secretion of tears induced by stimulating the zygomatic branch to the lacrimal nerve in a monkey but it is doubtful whether stimulation was confined to this nerve. Electrical potential changes in lacrimal gland cells and increased lacrimal secretion, induced by stimulation of the lacrimal nerve close to the gland, indicated that in cats the nerve contained secretomotor fibres (Botelho, Hisada & Fuenmayor, 1966).

The current concept of the post-ganglionic pathway has occasionally been questioned because of its unusual complexity and Howden (1920) suggested that secretomotor nerves might pass directly to the gland from the pterygopalatine ganglion. Such an arrangement was demonstrated in rabbits (Ruskell, 1965), in which branches of rami orbitales of the pterygopalatine ganglion passed to the gland directly or by way of the retro-orbital plexus. Although the possibility is strong that these nerves conducted parasympathetic fibres to the gland this was not established. A retro-orbital plexus was also demonstrated in monkey and human material (Ruskell, 1970)

and the main purpose of the present study is to show that the lacrimal gland in monkeys is served by nerves similar to those found in rabbits and that they alone conduct the parasympathetic post-ganglionic fibres to the lacrimal gland.

MATERIALS AND METHODS

Preparation for dissection

The heads of one vervet (*Cercopithecus aethiops*) and two cynomolgous (*Macaca fascicularis*) monkeys were fixed by perfusion with buffered 5 % formaldehyde through the common carotid arteries and used for dissection. Vessels were filled with red Neoprene latex and nerves were impregnated with silver by methods described earlier (Ruskell, 1970). One rhesus (*Macaca mulatta*), two more vervet and three cynomolgous monkeys were dissected after formaldehyde fixation but without further preparation.

Operative procedures

Surgical lesions were performed on both sides of a vervet monkey and on one side of nine other monkeys (six cynomolgous and three rhesus) using the opposite side as control in each case. The operations were designed to induce degeneration of fibres peripheral to the lesions and so provide a means of identification of the sources of fibres.

The superior cervical ganglion was removed from six of the monkeys (one vervet and five cynomolgous), which were fixed 7, 10, 15, 21 and 64 days after operation respectively. The ganglion was lodged in the carotid foramen in the rhesus monkeys and consequently its safe removal was not possible. A segment of the greater petrosal nerve was removed from its sulcus in the floor of the cranium in two of the monkeys, of which one was fixed 5 days and the other 16 days after operation. Details of this operation have been described elsewhere (Ruskell, 1969).

The pterygopalatine ganglion was damaged on one side in three monkeys. The ganglion was approached through the infratemporal and pterygopalatine fossae (Ruskell, 1969). In two monkeys the rami orbitales were not severed, as verified later by dissection, and in one of them the damage to the ganglion was slight, but in the third monkey all but two of the rami were found to be severed and ganglion damage was considerable. The monkeys were perfused 6, 6 and 14 days after operation respectively.

In order to preserve electron-dense granules in the small vesicles of sympathetic nerve terminals of the lacrimal artery, the sympathetic chain was severed below the superior cervical ganglion on the control sides of two monkeys 1 and 11 days prior to fixation respectively. To achieve the same purpose (Pellegrino De Iraldi, Zieher & De Robertis, 1965), from 150 and 300 mg of iproniazid (Marsilid: Roche Products) were administered intraperitoneally about 24 h before fixation in five monkeys and a second dose was given 1 h before fixation in three of the monkeys.

Before operation the monkeys were sedated with between 10 and 18 mg phencyclidine hydrochloride (Sernylan: Parke Davis) according to weight, given parenterally in one or two doses. Anaesthesia was induced with between 24 and 36 mg pentobarbital sodium through a saphenous vein.

Histological procedures

Before fixation of the monkeys by perfusion, sedation and anaesthesia were induced in the same manner as described above and approximately 1500 units of heparin sodium were injected through a 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 animals were perfused with warm 1 % sodium nitrite in saline followed immediately by 5·5 % cacodylate-buffered glutaraldehyde. This material was used to confirm dissection results and for light and electron microscopic inspection.

The heads were stored in the fixative at approximately 4 °C and dissected immersed in buffered sucrose. Earlier study of the material used for dissections only had revealed fine orbital nerves of pterygopalatine ganglion origin which passed close to the lacrimal artery and nerve. Consequently, all the tissue lying between the extraocular muscle cone and the periorbita in the vicinity of the lacrimal artery and nerve was preserved in one piece with the artery and nerve. Most of the fine nerves were then identified and dissected free but some were preserved together with the artery or the nerve. A total of 119 fine nerves (some of which were not identified until the artery preparations were examined in section), 11 lacrimal nerves and 14 lacrimal arteries were preserved and examined electron microscopically.

Internal carotid nerves were preserved from each side of the six monkeys from which the superior cervical ganglion was removed unilaterally.

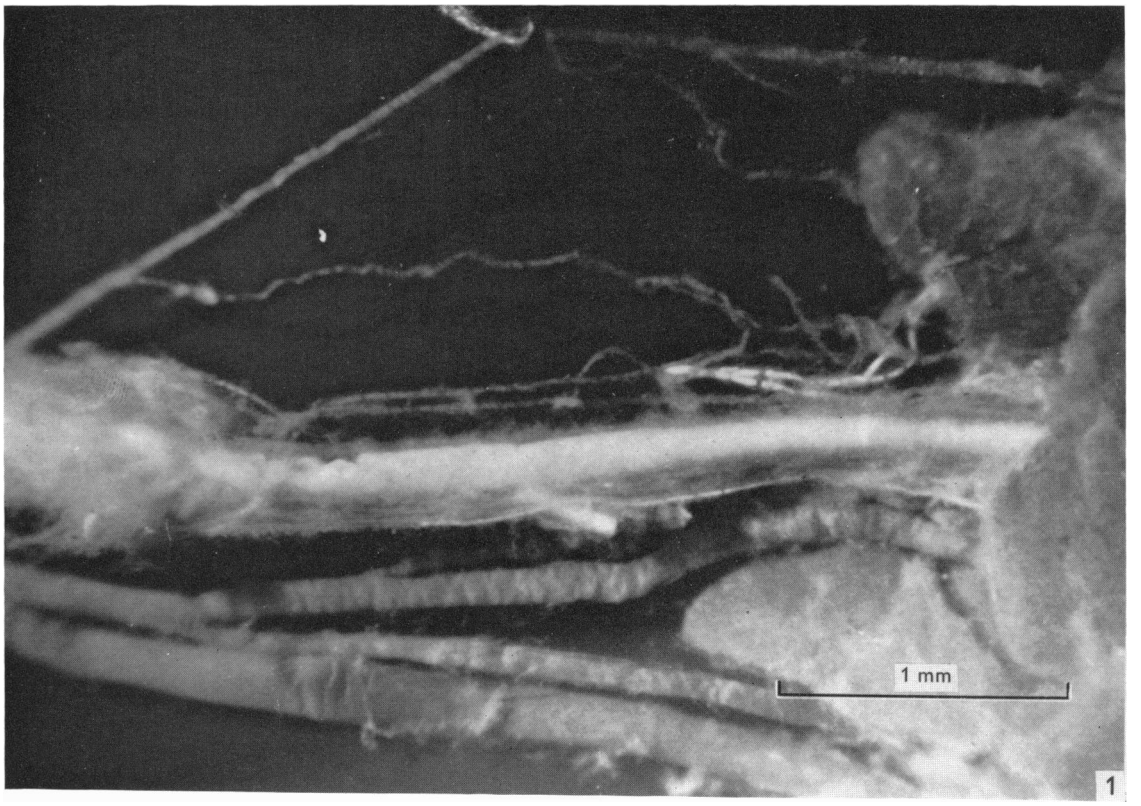
The tissues were stained in 1 % osmium tetroxide for 60–120 min. After dehydration some of the preparations were stained for approximately 2 h in 1 % phosphotungstic acid (PTA) in ethanol. All preparations were embedded in Araldite and ultra-thin sections cut for electron microscopy. A few of the sections stained with PTA 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. Thicker Araldite sections were cut from many of the same specimens, mounted on glass slides and used for light microscopy; these were stained with 1 % toluidine blue in 2·5 % sodium carbonate for 30 to 90 min.

RESULTS

Dissections and light microscopy

Between 4 and 6 fine nerves from the retro-orbital plexus entered the orbit close to the oculomotor nerve and numerous branches, the rami oculares, passed to the eyeball (Ruskell, 1971). Other, rather larger, branches passed close to the lacrimal nerve and advanced in the orbit on each side of the lacrimal artery, mostly between the artery and the lacrimal nerve. They were joined by one or two divisions of rami orbitales which passed from the pterygopalatine ganglion directly into the orbit through the superior orbital fissure. The name *rami lacrimales* will be adopted to describe these fine nerves.

The rami lacrimales usually divided once and sometimes twice before entering the lacrimal gland. Between 5 and 9 rami lacrimales could be discerned at the gland by dissection (Fig. 1) but other smaller rami were identified by light microscopy close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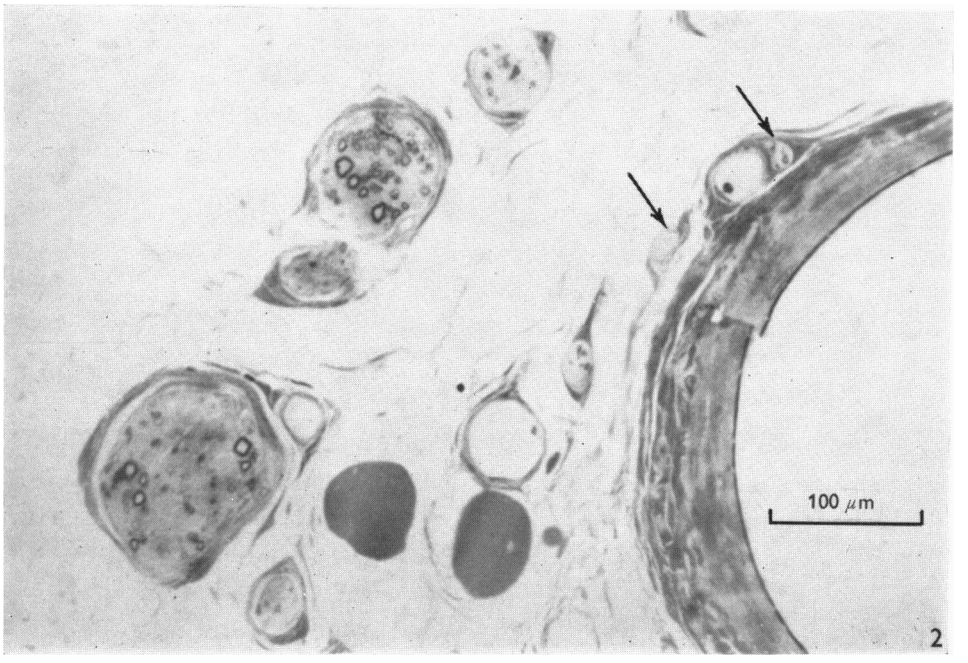
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to the adventitia of the lacrimal artery to bring the total up to a maximum of 14 (Fig. 2). One and sometimes two rami lacrimales joined very small branches of the lacrimal nerve and these appeared to terminate in the gland. None joined the lacrimal nerve or its major branches which continued distal to the gland. Up to 3 rami passed very close to the lacrimal artery and sent fine branches towards the adventitia where they could be traced no further. Their presence was confirmed by light microscopy. Rami lacrimales could not be traced beyond the gland by dissection or by microscopic inspection of the connective tissue surrounding a single, large lacrimal artery branch which passed beyond the gland.

The zygomatic nerve or nerves and its branches were dissected and in no instance was an anastomosis with the lacrimal nerve observed; nor did any branch enter the lacrimal gland.

Electron microscopy

Rami lacrimales

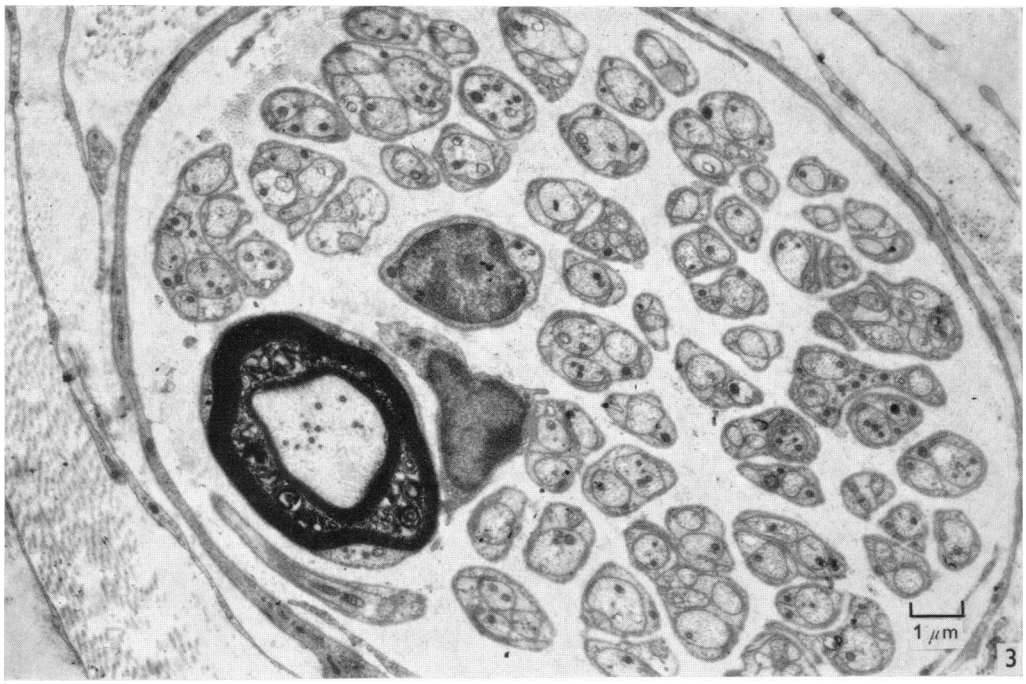
The rami lacrimales were composed largely of unmyelinated nerve fibre bundles (Fig. 3). Myelinated nerve fibres were not present in approximately one-third of the rami and only one to three were present in most of the others; a few contained more, up to a maximum of 39 (Fig. 4). In four preparations of fine lacrimal nerve branches which each received a ramus lacrimalis, 12, 16, 24 and 110 myelinated nerve fibres, respectively, were present but they constituted a minority of the total nerve fibres in each case.

The average size of rami lacrimales was 26×20 μm, the smallest measuring 7×5 μm and the largest 62×53 μm. The smallest ramus contained 6 unmyelinated nerve fibre bundles and the largest 424, with 18 myelinated nerve fibres. There was no significant species difference in ramus size or number. All the rami of several of the orbits of rhesus and cynomolgous monkeys were examined. The total number of unmyelinated nerve fibre bundles in these varied between 740 and 1186. A minority of rami lacrimales of control orbits contained either one or two Schwann cell processes without enclosed axons (Table 1). They were also found earlier in some rami orbitales and rami oculares of monkeys (Ruskell, 1970, 1971).

The appearance of rami lacrimales after superior cervical ganglionectomy was similar to that of control rami except that 0·9 to 1·1 % of Schwann cells were without enclosed axons in 4 out of 6 animals, compared to 0 to 0·4 % in the controls. The proportion was lower than that of the control side in another (1·2 % compared to 3·2 %) and in the vervet monkey the exceptionally high proportion of 9·6 % of Schwann cells contained no axon. As a check on the efficacy of the ganglionectomies the internal carotid nerves were examined and the axons of unmyelinated nerve fibre bundles were found, with rare exceptions, to be degenerated.

Fig. 1. Rami lacrimales. Four fine rami are seen at the top of the figure. The largest of them is under tension from a hooked pin at the point at which it divides before entering the lacrimal gland to the right. The Neoprene-filled lacrimal artery is central and the lacrimal nerve branches lie below it. Cynomolgous, silver nitrate.

Fig. 2. Transverse section through eight rami lacrimales. The two largest contain unusually large numbers of myelinated nerve fibres. The two smallest rami lie on opposite sides of the small vessel adjacent to the adventitia of the lacrimal artery on the right (arrows). Rhesus, toluidine blue.



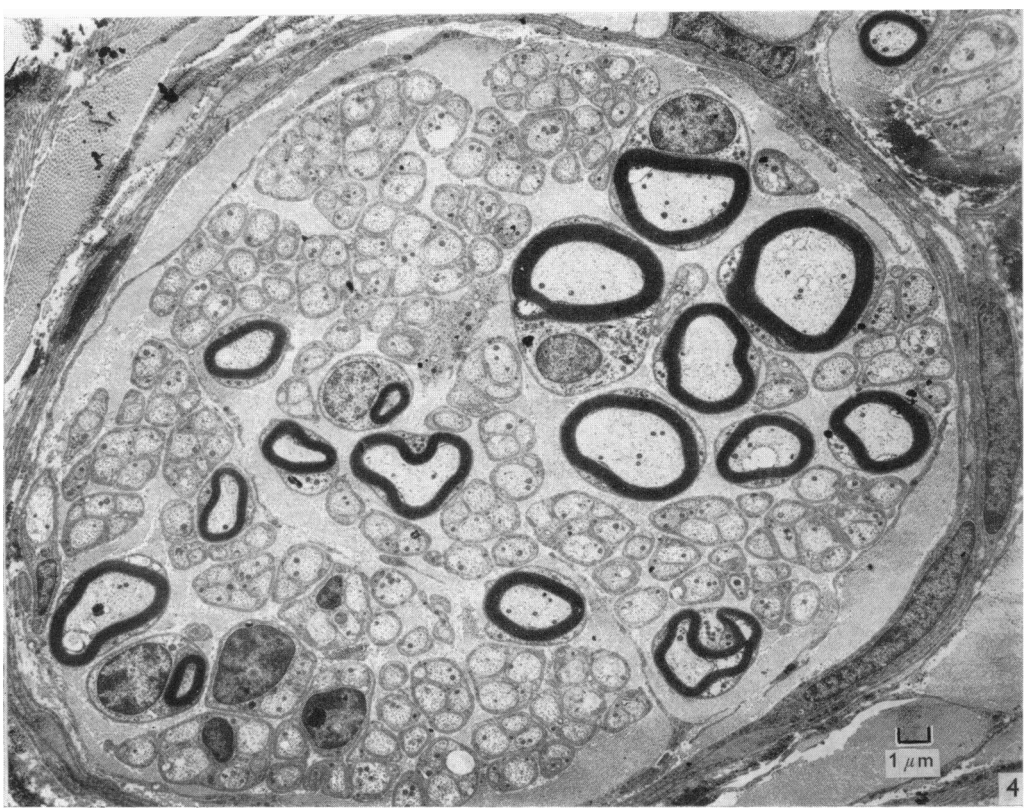


Fig. 3. A ramus lacrimalis of average size and content. Rhesus, control.
Fig. 4. A large ramus lacrimalis from a control side with numerous myelinated fibres. Cynomolgous.

Rami lacrimales, taken from the operated sides of the three animals in which the pterygopalatine ganglion had been damaged, displayed marked and widespread differences from controls in one rhesus and one cynomolgous monkey, and limited differences in all but two of the rami of a second rhesus monkey (Fig. 5). The dissimilarity of the results in these monkeys was expected as the second rhesus monkey suffered little damage of the ganglion compared with the others. More than 23 % of the Schwann cells lacked enclosed axons (Table 1) and other gross changes were seen in many of the persisting fibre bundles. These changes included altered axon and Schwann cell profiles and the occurrence of several Schwann cell processes in single nerve fibre bundles (Figs. 5 and 6). They were the same as those described earlier in rami orbitales and rami oculares (Ruskell, 1970, 1971). All myelinated nerve fibres were of normal appearance.

After greater petrosal neurectomy the rami failed to display differences from control rami. Schwann cells without enclosed axons were found but they were rare and their proportion of the total compared with those of controls (Table 1).

Table 1. *Summary of the incidence of Schwann cells without axons in rami lacrimales*

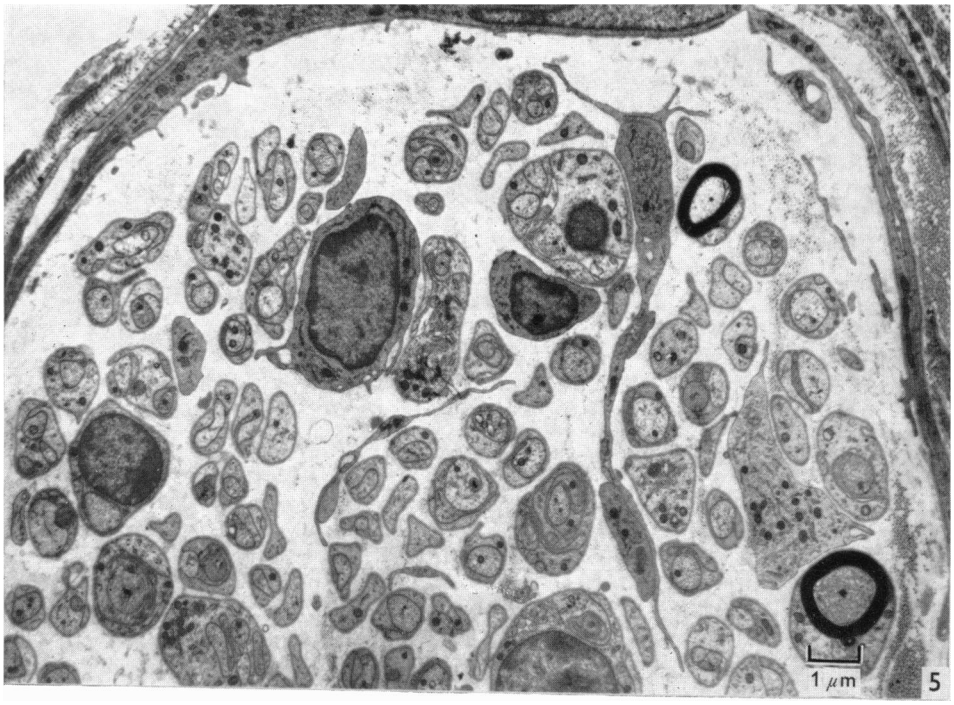
Operation	Number of animals	Number of rami lacrimales	Unmyelinated nerve fibre bundles	Schwann cells without axons	Percentage of Schwann cell units without axons
Controls	7	54	4337	36	0·6
Superior cervical ganglionectomy	6	38	3263	42	1·3
Pterygopalatine ganglion damage	3	19	1893	437	23·1
Greater petrosal neurectomy	2	8	833	5	0·6

Lacrimal nerves

The number of unmyelinated nerve fibre bundles in lacrimal nerves either approximately equalled or exceeded the number of myelinated nerve fibres. Schwann cells without enclosed axons were absent or rare in the 5 control nerves examined. In counts made from a quarter to one-third of each nerve they amounted to 0 to 0·54 % of the total Schwann cell units (excluding those of myelinated nerve fibres). The proportion was similar after pterygopalatine ganglion damage (0·13 and 0·29 %) and in no respect were the lacrimal nerves different from the controls. After superior cervical ganglionectomy, however, the proportions of Schwann cells without axons were 4·3, 3·9 and 3·0 % respectively (Fig. 7). Counts revealed that the increment in such units of operated material was significant at $P \leqslant 0{\cdot}0001$ using the binomial test. A similar proportion was found in a nerve distal to the gland.

Lacrimal arteries

Several small nerves containing up to 12 unmyelinated nerve fibre bundles were present in the adventitia of most arteries. The adventitia also contained separate, scattered, randomly orientated nerve fibre bundles. Most separate nerve fibre bundles lay at the junction of media and adventitia and these were distinguishable from the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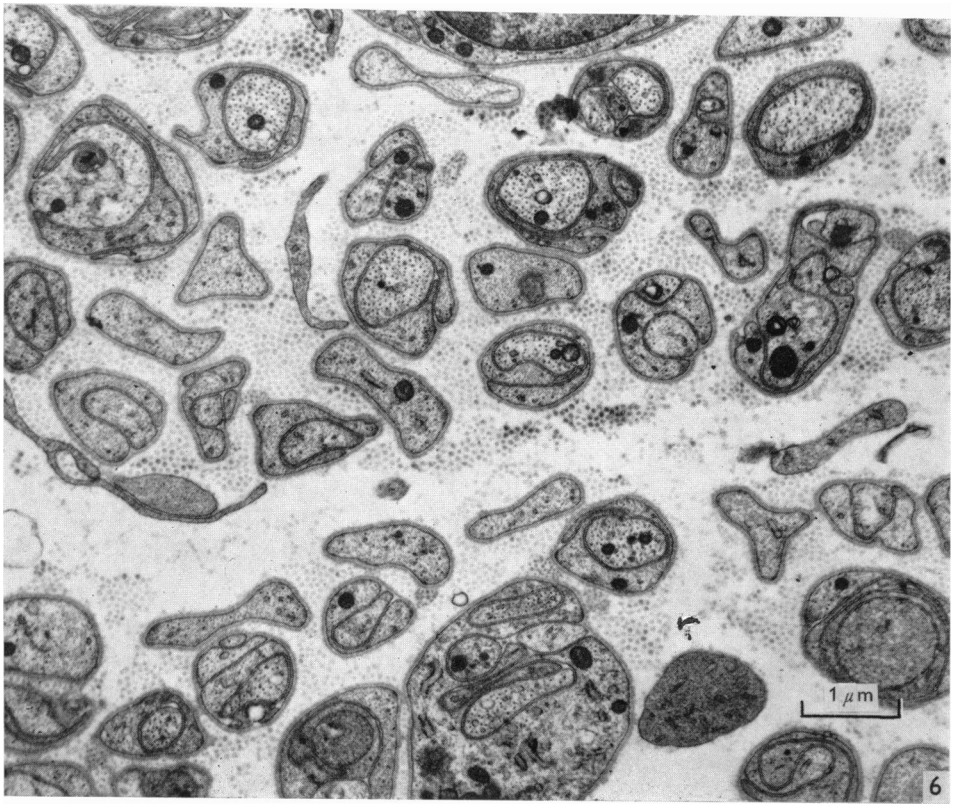
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others by their abundance of varicosities containing aggregations of many vesicles and a few mitochondria. None penetrated into the muscle layer. The varicosities contained vesicles of three types: small agranular vesicles (30–50 nm), large granular or dense-cored vesicles (65–100 nm) and the small granular vesicles (30–50 nm) characteristic of sympathetic terminals (Fig. 8). Varicosities containing small granular vesicles were more common in animals treated with iproniazid or in which pre-cervical ganglion neurectomies were performed. They were present in the walls of all control lacrimal arteries.

Varicosities were defined for the purposes of determining their density and analysing their vesicle content, as areas of axons containing aggregates of 3 or more vesicles. Counts were made from single sections or from 2 or 3 sections from widely separate positions on the arteries. Between 350 and 1213 μm lengths of vessel walls were examined. A varicosity occurred on average each 7–13 μm of vessel wall in 6 control arteries and the proportion containing one or more small granular vesicles was 10, 14, 20, 21, 32 and 42 % respectively.

After superior cervical ganglionectomy clear evidence of induced changes in terminal bundles was not seen in any of the specimens: surviving terminals of normal appearance were numerous but none contained small granular vesicles. The density of terminal varicosities was lower in the 5 arteries examined than in the control arteries. Expressed as ratios of the density in each pair from operated and control sides the counts were 0·19, 0·48, 0·52, 0·71 and 0·90. The small adventitial nerves were of normal appearance.

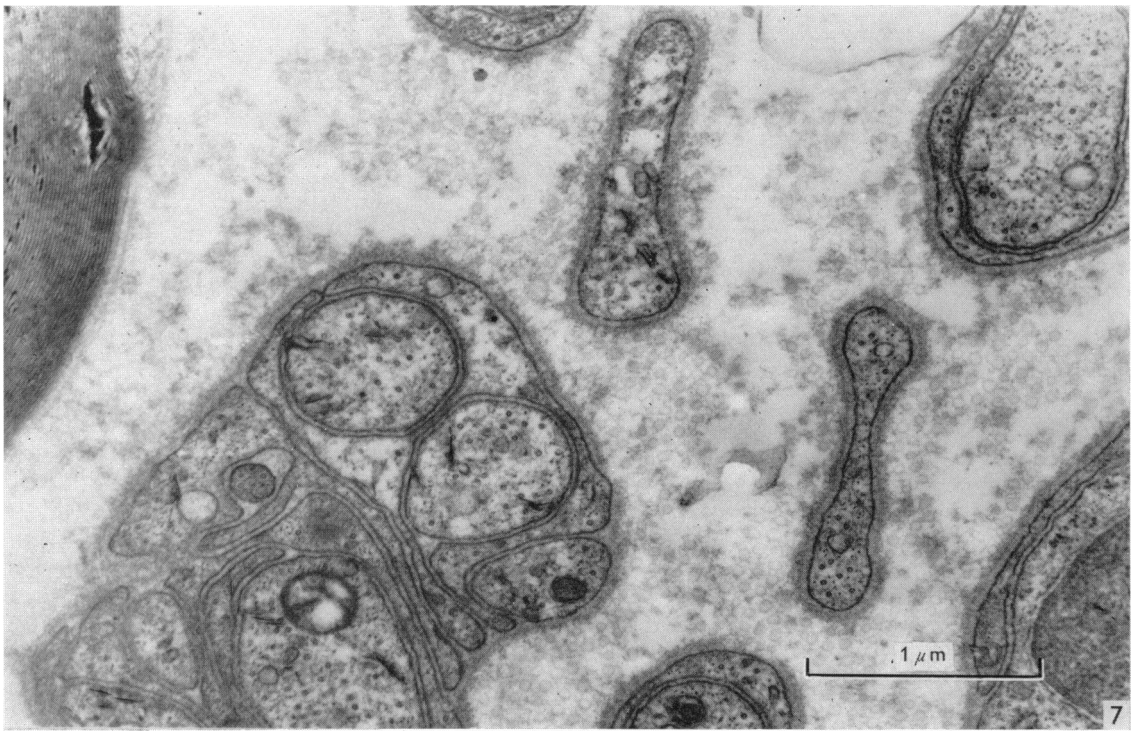
The evidence of dissection studies indicated that lacrimal arteries might be served by nerve fibres of pterygopalatine ganglion origin, which would account for those fibres that remained after the destruction of sympathetic fibres, but terminals were of normal appearance after pterygopalatine ganglion damage. However, arteries from both operated and control sides of one animal were examined and the density ratio of varicosities was 0·52 operated/control. An unusually high proportion of 70 % of varicosities contained small granular vesicles, compared with 32 % in the control artery. Only one other artery from this series was examined. It was from an operated side and the varicosity density (1 per 7 μm of artery wall) and the proportion of varicosities containing small granular vesicles (14 %) were comparable with controls of other series. Three of ten small adventitial nerves of two arteries from operated sides displayed differences from controls similar to those seen in rami lacrimales.

DISCUSSION

Widespread changes in unmyelinated nerve fibre bundles of the rami lacrimales were clearly induced by pterygopalatine ganglion damage and it may be predicted that all or practically all of the bundles would have been affected had the ganglion

Fig. 5. Part of a large ramus lacrimalis with induced changes. It was fixed 6 days after pterygopalatine ganglion damage. Only a small minority of nerve fibres, including the two myelinated fibres, are of normal appearance. Many Schwann cells without enclosed axons are present. Axon and Schwann cell profiles are so changed in other units that they are distinguished with difficulty. A few units contain several Schwann cell processes of which some are unusually large. Rhesus.

Fig. 6. Detail of part of the ramus illustrated in Fig. 5.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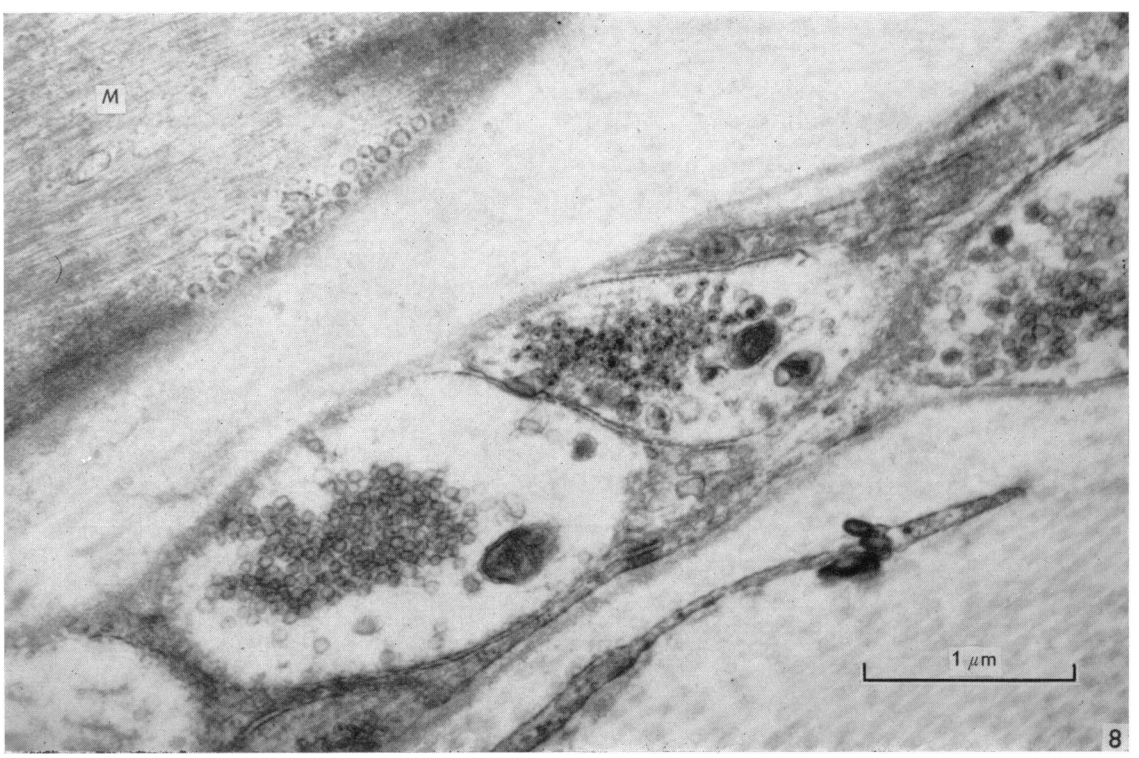
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been removed. The pterygopalatine ganglion is the only cell station between the greater petrosal nerve and the rami lacrimales (Ruskell, 1970) and the cell bodies of the fibre bundles must therefore lie in the ganglion, as greater petrosal neurectomy failed to induce changes in the fibres. Had the fibres originated proximal to the lesion changes would have been seen. A majority of rami issued from the retro-orbital plexus, which was shown to consist of sympathetic and parasympathetic fibres (Ruskell, 1970), and consequently the presence of sympathetic fibres in the rami lacrimales was expected. But the number of Schwann cells without axons after superior cervical ganglionectomy, although slightly raised compared with controls in most monkeys, was insufficient to conclude that sympathetic fibres were present. Sympathetic fibres were probably present in the rami lacrimales of the vervet monkey, in which 9·6 % of Schwann cells were without enclosed axons. Evidence of a small minority (about 7 %) of sympathetic fibres was also found in rabbits (unpublished observations).

Induced changes similar to those seen in rami lacrimales were previously found in the rami orbitales of the pterygopalatine ganglion and in the retro-orbital plexus of monkeys after ganglion damage (Ruskell, 1970), and the present dissection studies demonstrated the origin of rami lacrimales directly from the rami orbitales or from the plexus. Parasympathetic fibres are therefore distributed to the lacrimal gland from the pterygopalatine ganglion by each of these pathways and it has been shown that they serve a secretomotor function in monkeys (Ruskell, 1969). However, it is currently assumed that parasympathetic fibres reach the gland by successively passing in the pterygopalatine, maxillary, zygomatic and lacrimal nerves (for example see Duke-Elder & Wybar, 1961). The present study shows that parasympathetic fibres do not reach the gland by this route. Firstly, there is no connexion between the zygomatic and lacrimal nerves in monkeys, which is also the case in rabbits (Ruskell, 1965) and sometimes in humans (Testut, 1899 and others), and secondly, changes were not induced in the lacrimal nerve by damaging the pterygopalatine ganglion.

The basis for this current view of the post-ganglionic parasympathetic pathway is that no other pathway is available (see Introduction) and the only tenable supporting evidence is derived from studies in which the lacrimal nerve was stimulated. For example, by this means Botelho *et al.* (1966) recorded electrical potential changes in lacrimal gland cells of cats together with an increased lacrimal secretion. But if rami lacrimales are present in cats, stimulation of the lacrimal nerve could hardly be achieved without also stimulating some of the rami. In the likely event that rami lacrimales are present in species other than the various monkeys used in this study and rabbits (Ruskell, 1965), then the zygomatic nerve pathway may be abandoned as the conductor of parasympathetic fibres to the gland in favour of the rami lacrimales (Fig. 9). It is of interest that endeavours to reduce lacrimal secretion in patients

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Fig. 7. A group of unmyelinated nerve fibres of a lacrimal nerve fixed 15 days after superior cervical ganglionectomy. Two Schwann cells without axons are present. Cynomolgous.

Fig. 8. Nerve fibre terminal varicosities at the junction of the media and adventitia of a lacrimal artery. The small granular vesicles in one of the varicosities identify it as sympathetic. The other two varicosities contain only small agranular and large granular vesicles. *M*, smooth muscle cell. Rhesus, control.

suffering from epiphora by severing the zygomatic nerve branch to the gland have produced equivocal results (Whitwell, 1958; Royer, 1963). These results are consistent with the view that the zygomatic nerve does not conduct secretomotor fibres to the gland and that the limited success of the operation was due to the incidental involvement of rami lacrimales.

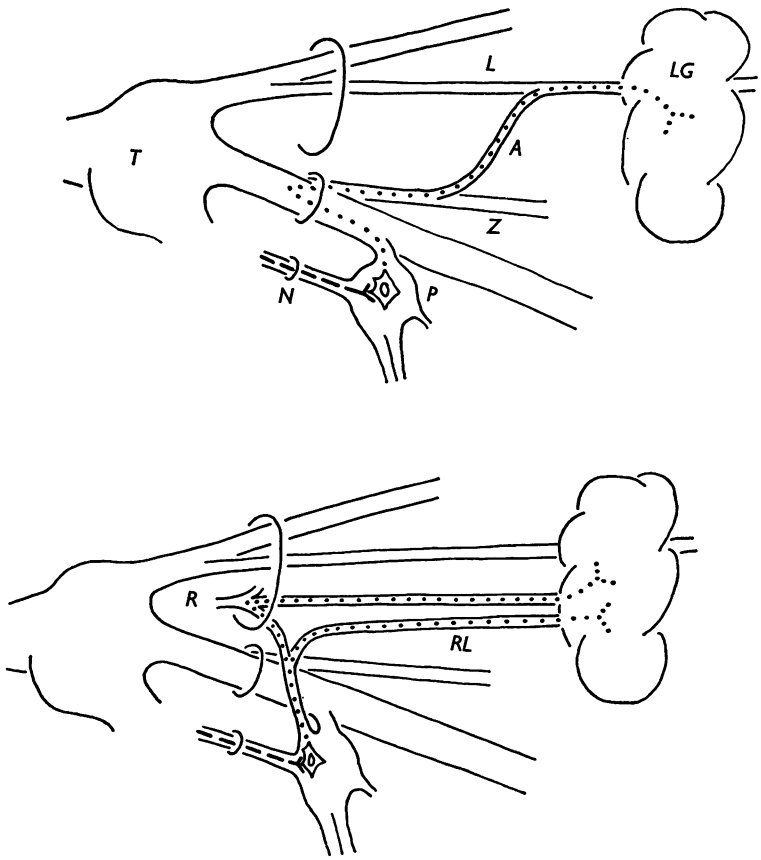

Fig. 9. The upper diagram shows the conventional post-ganglionic pathway for lacrimal secretomotor nerve fibres. It has been shown not to apply to monkeys.

The lower diagram summarizes the results of this study on monkeys. The post-ganglionic fibres pass from the pterygopalatine ganglion in the rami orbitales and pass to the lacrimal gland in the rami lacrimales either directly or by way of the retro-orbital plexus. This pathway is likely to apply to rabbits and it may also apply to humans and other species. *A*, anastomosing ramus between the zygomatic and lacrimal nerves; *L*, lacrimal nerve; *LG*, lacrimal gland; *N*, nerve of the pterygoid canal; *P*, pterygopalatine ganglion; *R*, retro-orbital plexus; *RL*, rami lacrimales; *T*, trigeminal ganglion; *Z*, zygomatic nerve. The relative size of autonomic nerves is exaggerated.

The presence of small granular vesicles in many of the terminal varicosities in the wall of the lacrimal artery is proof of its sympathetic innervation (Bondareff & Gordon, 1966; Ruskell, 1967) and, predictably, small granular vesicles were eliminated and varicosity density reduced after superior cervical ganglionectomy. Presumably, sympathetic fibres continue forward in the wall of the artery to the gland, which

possesses an abundance of sympathetic terminals (Ehinger, 1966) especially in the walls of arterioles (Ruskell, 1967). As argued above, sympathetic fibres are unlikely to pass to the gland in the rami lacrimales of cynomolgous monkeys but some probably do so in vervet monkeys and rabbits. A small number of sympathetic nerve fibre bundles was shown to be present in the lacrimal nerve, and although it is possible that some of them passed into the gland the majority were unlikely to have done so. The bulk of the lacrimal nerve passed beyond the gland, and the Schwann cells without enclosed axons resulting from superior cervical ganglionectomy were widely scattered in the nerve and equally numerous distal to the gland.

The vascular nerve fibre terminals that persisted after superior cervical ganglionectomy probably derived from the branches of rami lacrimales traced to the lacrimal artery wall. But, if this was so, the lack of induced changes in terminals after pterygopalatine ganglion damage was surprising, especially as changes were seen in arteriolar walls of the lacrimal gland after the same operation (Ruskell, 1969). On the other hand, the presence of parasympathetic terminals was supported by the observation of a reduced density of terminals and an increased proportion of varicosities containing small granular vesicles after ganglion damage. Furthermore, the identification of the pterygopalatine ganglion origin of some of the small adventitial nerves is consistent with this view.

SUMMARY

Fine nerves passing from the retro-orbital plexus or directly from the pterygopalatine ganglion were traced by dissection to the lacrimal gland in cynomolgous, rhesus and vervet monkeys. Up to 14 of them were found at the gland in single orbits. Examination of the fine nerves (the *rami lacrimales*) by electron microscopy showed that they were largely composed of unmyelinated nerve fibre bundles. Induced changes in the rami after pterygopalatine ganglion damage but not after greater petrosal neurectomy identified the fibre bundles as parasympathetic, originating from cells of the ganglion. Changes induced by superior cervical ganglionectomy provided evidence that in a vervet monkey a small minority of the fibres were sympathetic: in five cynomolgous monkeys sympathetic fibres were probably absent.

The doubtful validity of the current concept of the parasympathetic post-ganglionic pathway to the lacrimal gland is discussed and an argument for its replacement by the rami lacrimales is presented.

Both sympathetic and parasympathetic terminals were present in the wall of the lacrimal artery but, of the two, only sympathetic fibres were identified in the lacrimal nerve and they were few.

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