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INNERVATION OF THE CAT LIP BY TWO GROUPS OF PARASYMPATHETIC VASODILATOR FIBRES

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SUMMARY

1. Electrical stimulation of the peripheral cut ends of the chorda tympani nerve proper (CTNP) and the chorda-lingual nerve (CLN) elicited a blood flow increase in the ipsilateral lower lip, tongue and submandibular gland in a stimulus intensity-dependent manner in anaesthetized cats.

2. Pretreatment with hexamethonium (1·0 mg kg^{-1}, I.V.), an autonomic ganglionic blocker, significantly reduced the CTNP-induced blood flow increases in all of the above three sites as well as the CLN-induced blood flow in the lower lip, but it had no effects on the CLN-induced blood flow increases in the tongue and submandibular gland.

3. The CTNP stimulation-induced lower lip blood flow was not influenced by sectioning the lingual nerve proper, but it was abolished by section of either the CLN or the inferior alveolar nerve (IAN) in the mandibular canal.

4. The lip blood flow increases elicited reflexly by electrical stimulation of the upper gingiva, the central cut ends of the mylohyoid nerve and CLN were not affected by cutting of the CTNP, but were markedly reduced by pretreatment with hexamethonium and abolished by the section of the inferior alveolar nerve just distal to the mylohyoid nerve. These observations imply that the parasympathetic vasodilator fibres involved in trigeminally induced reflex vasodilatation responses do not travel with the CTNP.

5. These results suggest that there is a dual innervation of the cat lower lip by two groups of parasympathetic vasodilator fibres; in one case fibres originating from the facial nerve root are distributed to the lower lip via the CTNP, CLN and IAN and in the other fibres emanating from the glossopharyngeal nerve root project to the lower lip via the mandibular nerve and the IAN.

INTRODUCTION

We have previously reported that electrical stimulation of the distal parts of the cut cranial facial and glossopharyngeal nerve roots in cats elicits vasodilatation in the facial areas such as gingiva and lip (Izumi & Karita, 1991*a*, 1992*a*,*b*). These fingings suggest that blood vessels in these areas might be innervated by two different groups of parasympathetic vasodilator fibres, ones originating from both the facial and glossopharyngeal nerves. However, if the vasodilator nucleus in the

brainstem extends forward to include the origins of both the facial and glossopharyngeal nerves, then the functional significance of the two groups of vasodilator fibres might be fundamentally the same.

Our recent observations (Izumi & Karita, 1992*a*) have shown that the trigeminally mediated reflex vasodilatation in the cat lower lip is abolished by section of the glossopharyngeal nerve root but not of the facial nerve root, suggesting a functional difference between these groups of parasympathetic vasodilator fibres supplying the lip. We have further shown by means of the HRP tracing technique that blood vessels in the lower lip are innervated by postganglionic fibres originating in the otic ganglion but not in the pterygopalatine ganglion (Kuchiiwa, Izumi, Karita & Nakagawa, 1992). Thus preganglionic fibres from the glossopharyngeal nerve enter the otic ganglion and synapse with postganglionic fibres that terminate in the cat lower lip, and this pathway makes a contribution to the trigeminally induced reflex vasodilatation.

During the course of studies regarding the pathways of these vasodilator fibres to the orofacial areas in cats (Izumi & Karita, 1990, 1991*a*, 1992*a*,*b*), we found that electrical stimulation of the peripheral parts of the cut chorda tympani nerve proper (CTNP) elicited a vasodilator response in cat lip. The available literature states that the CTNP is an important pathway for parasympathetic vasodilator and secretomotor fibres of the seventh cranial nerve to the submandibular and sublingual glands and tongue (Fitzgerald & Alexander, 1969; Gautvik, 1970; Hellekant, 1971*a*, *b*, 1977; Hellekant & Kasahara, 1973*a*,*b*; Farbman & Hellekant, 1978) as well as for gustatory and somatosensory fibres (Robinson, 1988), but there is no information available concerning vasodilator fibres travelling in the CTNP to the cutaneous skin of the cat lower lip. Accordingly, to obtain support for the idea that there is a dual parasympathetic vasodilator pathway to the cat lip, responses elicited by electrical stimulation of the distal parts of the CTNP were compared with those evoked reflexly. The effects of nerve sections at different sites and of the autonomic ganglionic blocker (hexamethonium) on the vasodilatation responses evoked by these means were compared.

METHODS

Preparation of animals

Experiments were performed on twenty-three cats of both sexes weighing 1·0–4·0 kg on the day of surgery. Cats were initially anaesthetized with ketamine hydrochloride (30 mg kg^{-1}, I.M.) and then with an intravenous injection of Nembutal (sodium pentabarbitone) at a dose of 30 mg kg^{-1}, supplemented when necessary with additional doses of 10–20 mg. Local anaesthesia (2 % Lidocaine hydrochloride, Fujisawa Pharmaceutical Co. Osaka, Japan) was always applied to the areas of the skin that were cut. One cephalic vein was cannulated to allow drug injection and one femoral artery was cannulated and connected to a Statham pressure transducer to monitor systemic arterial blood pressure and heart rate. The anaesthetized animals were intubated, paralysed by intravenous injection of pancuronium bromide (Mioblock, Organon; 0·4 mg kg^{-1} initially followed by constant infusion at a rate of approximately 0·2 mg kg^{-1} h^{-1}), and artificially ventilated with air by a Harvard respirator through a tracheal cannula. Rectal temperature was maintained at 36–38 °C with a heating pad. The criteria for maintenance of an adequate depth of anaesthesia were the persistence of miotic pupils and the absence of heart rate changes during electrical stimulation of the tongue or upper buccal gingiva at 50 V. At the end of the experiment, the cat was killed with an overdose (about 150 mg) of Nembutal.

Blood flow monitoring

Blood flow changes in the lower lip adjacent to the canine tooth, in the tongue and in the submanibular gland were monitored using a laser Doppler flowmeter (Canon LC-1, Tokyo, Japan or Moor Instrument MBF3D, Devon) as described previously (Izumi & Karita, 1992*a*, *b*; Karita & Izumi, 1992*a*, *b*). Electrical calibration for zero blood flow was made in all recording session.

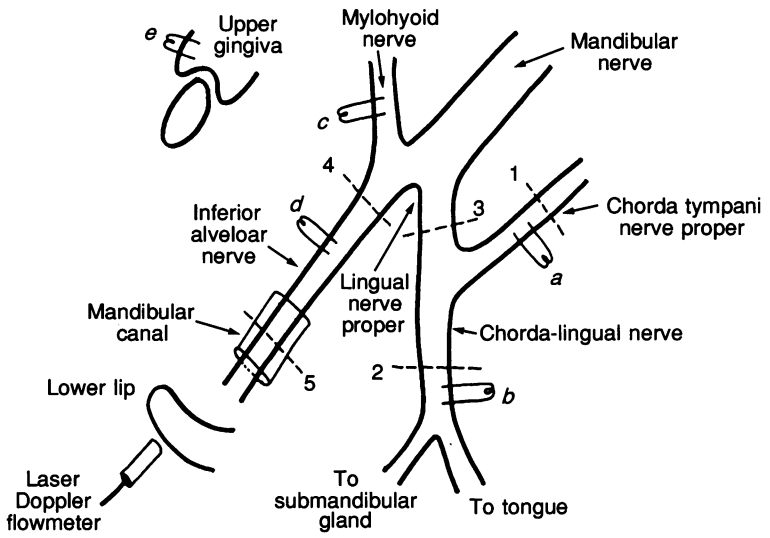

Fig. 1. Diagram showing the nerve sectioning sites (1–5) and the electrical stimulation sites (*a–e*) in the cat: 1, chorda tympani nerve proper (CTNP); 2, chorda-lingual nerve (CLN); 3, lingual nerve proper; 4, inferior alveolar nerve (IAN) just distal to mylohyoid nerve (MHN); 5, IAN in the mandibular canal; *a*, CTNP; *b*, CLN; *c*, MHN; *d*, IAN; *e*, upper buccal gingiva.

Several gains were selectable by switchers and the maximum output of a given gain level (defined electrically) was taken as 100 %. The gain was kept constant in each experiment. The analog output of the equipment gives no absolute values but relative changes of cutaneous blood flow (for technical details and evaluation of the laser Doppler flowmeter see Stern *et al.* 1977; Nilsson, Tenland & Oberg, 1980). Output of the device was continuously displayed on a multichannel chart recorder alongside that of the blood pressure transducer at a speed of 10 mm min^{-1}. The blood flow changes were measured by calculating the vasodilator areas with a planimeter, and were expressed as percentages of maximal blood flow increase (Fig. 2) and percentage changes compared to the corresponding control value (Figs 3 and 4).

Electrical stimulation of the CTNP, chorda-lingual nerve (CLN), mylohyoid nerve (MHN) and inferior alveolar nerve (IAN)

Using a binocular microscope a bipolar electrode was inserted into the distal ends of the CTNP (*a* in Fig. 1), the proximal ends of the mylohyoid nerve (*c* in Fig. 1) and both the distal and proximal ends of the chorda-lingual nerve (*b* in Fig. 1) and inferior alveolar nerve (*d* in Fig. 1). These nerves and the upper buccal gingiva were stimulated for 10 s with 0–50 V, 40 Hz pulses of 2 ms duration using a Nihon Koden model SEN-7103 stimulator.

Section of nerves

To trace the peripheral pathway of the parasympathetic vasodilator fibres, the CTNP-induced vasoldilator responses and the trigeminally mediated reflex vasodilator responses following electrical stimulation of MHN, CLN and IAN were observed before and after section of the following nerves: (a) the CTNP was cut close to the CLN (1 in Fig. 1; Fig. 4); (b) the CLN was cut close to the CTNP (2 in Fig. 1; 4 experiments); (c) the lingual nerve proper was cut close to the IAN (3 in Fig. 1; Fig. 6*A*; 4 experiments); (d) the IAN was cut close to the MHN (4 in Fig. 1; Fig. 6*C* and *D*; 5 experiments); and (e) the IAN in the mandibular canal (5 in Fig. 1; Fig. 6*B*; 3 experiments).

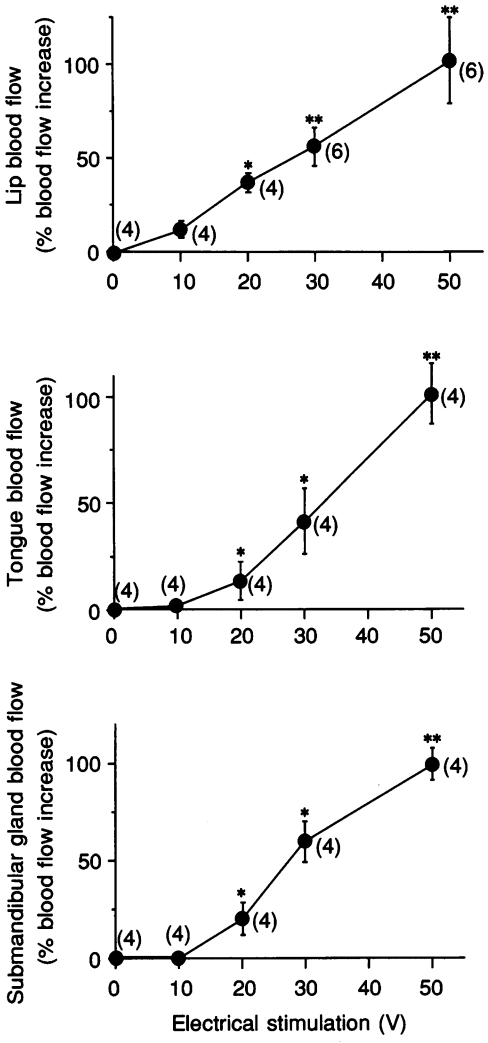

Fig. 2. Stimulus intensity–response relationships for changes in the blood flow in response to electrical stimulation of the peripheral parts of the cut chorda tympani nerve proper in the ipsilateral lower lip, in the tongue and in the submandibular gland. The peripheral cut ends of the chorda tympani nerve proper were electrically stimulated at 0, 10, 20, 30, 40 and 50 V with stimulation parameters of 40 Hz, 2 ms for 10 s. The number of experiments is shown in parentheses. Values on the ordinate have been expressed as percentages of the blood flow increase elicited by electrical stimulation at 50 V and are given as means ±S.E.M. Statistical significance was calculated according to the unpaired t test. Asterisks indicate the statistical difference from control. *$P < 0.05$; **$P < 0.01$.

Autonomic ganglionic blockade

To examine whether the reflexly evoked vasodilatation responses were mediated via activation of the autonomic nervous system or whether the vasodilator fibres stimulated were either preganglionic or postganglionic efferent fibres to the target tissues, hexamethonium (1·0 mg kg^{-1}, I.V.), an autonomic ganglionic blocker, was used before and after stimulation; the magnitude of the responses obtained were shown as percentages of the corresponding control response.

Statistical analysis

All numerical data are given as the means ± S.E.M. The significance of changes in blood flow data was tested using Student's paired or unpaired t test. Differences were considered significant at a level of $P < 0{\cdot}05$.

RESULTS

Figure 2 shows the effects of electrical stimulation of the peripheral cut end of the CTNP on the blood flows of the ipsilateral lower lip, submandibular gland and tongue of the cats. Electrical stimulation of less than 10 V had no significant effect on these three blood flows, while increasing the stimulus voltage from 20 to 50 V caused successively bigger vasodilator responses. Ipsilateral and bilateral sympathectomies or vagotomies in the neck did not influence these blood flow responses (data not shown).

The blood flow increases in all three sites measured following electrical stimulation of the peripheral part of the cut CTNP were abolished by section of the

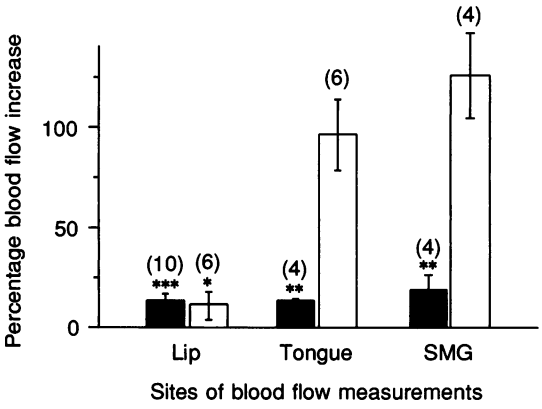

Fig. 3. Effects of hexamethonium on vasodilator responses to stimulation of the chorda tympani nerve proper (filled columns) and chorda-linual nerve (open columns) in the ipsilateral lower lip, tongue and submandibular gland (SMG). The distal cut ends of the chorda tympani nerve proper and the chorda-lingual nerve were stimulated at 50 V, 40 Hz, 2 ms for 10 s. Values after hexamethonium have been expressed as a percentage of the corresponding control response and given as means ± S.E.M. The number of experiments is shown in parentheses. Statistical significance was calculated according to the paired t test. $^{*}P < 0{\cdot}05$; $^{**}P < 0{\cdot}01$; $^{***}P < 0{\cdot}001$.

CLN (2 in Fig. 1; 4/4 experiments, data not shown) and were significantly reduced by pretreatment with hexamethonium, an autonomic ganglionic blocker, at a dose of 1·0 mg kg^{-1} (Fig. 3). On the other hand, the effect of pretreatment with hexamethonium on the lip blood flow increase in response to electrical stimulation of the peripheral cut CLN differed from those in the tongue and submandibular gland; hexamethonium significantly reduced the lip blood flow increase, but had no effect on the tongue and submandibular gland blood flow increases (Fig. 3).

Figure 4 shows the effect of section of the CTNP and of hexamethonium on the trigeminally mediated reflex vasodilatation in the lower lip following electrical

stimulation of the upper gingiva, and of stimulation of the central cut ends of the mylohyoid and chorda-lingual nerves. The lip blood flow increases elicited by these methods were not affected by sectioning the CTNP, but they were markedly reduced by pretreatment with hexamethonium.

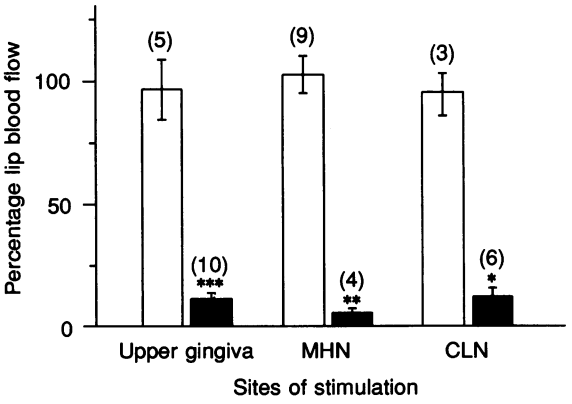

Fig. 4. Effects of section of the chorda tympani nerve proper (open columns) and of hexamethonium (filled columns) on the trigeminally mediated reflex vasodilatation elicited by electrical stimulation of the upper buccal gingiva, central cut ends of mylohyoid nerve (MHN) and the chorda-lingual nerve (CLN) in the ipsilateral lower lip of the cats. The upper buccal gingiva, the central cut end of the MHN and the CLN were stimulated at 50 V with 40 Hz, 2 ms for 10 s. Values after section of the chorda tympani nerve proper of hexamethonium have been expressed as percentages of the corresponding control response (open column) and given as means ± S.E.M. The number of experiments is shown in parentheses. Statistical significance was calculated according to the paired t test. $^{*}P < 0{\cdot}05$; $^{**}P < 0{\cdot}01$; $^{***}P < 0{\cdot}001$.

Typical examples of the effects of hexamethonium on the lip and tongue blood flow increases elicited by electrical stimulation of the peripheral cut end of the CTNP, and of direct stimulation of the IAN and CLN are shown in Fig. 5. The CTNP-induced blood flow increases in both lip and tongue were reduced by pretreatment with hexamethonium (Fig. 5*a* and *d*; for lip, 13·1 ± 3·0 % *vs.* before hexamethonium, $n = 10$, $P < 0{\cdot}001$; for tongue, 13·0 ± 3·6 % *vs.* before hexamethonium, $n = 4$, $P < 0{\cdot}01$), while the effects of hexamethonium on the IAN- or the CLN-induced blood flow increases were different depending on the site of blood flow measurements. Pretreatment with hexamethonium had no effect on the IAN-induced blood flow increases in the lip (Fig. 5*c* and *f*; 116·5 ± 10·2 % *vs.* before hexamethonium, $n = 5$, not significant) or the CLN-induced blood flow increase in the tongue (Fig. 5*b* and *e*; 97·7 ± 17·3 % *vs.* before hexamethonium, $n = 6$, not significant), despite a marked reduction in the tongue blood flow increase elicited by IAN stimulation (Fig. 5*c* and *f*; 10·9 ± 1·8 % *vs.* before hexamethonium, $n = 6$, $P < 0{\cdot}001$) and in the lip blood flow increase caused by CLN stimulation (Fig. 5*b* and *e*; 10·8 ± 7·1 % *vs.* before hexamethonium, $n = 6$, $P < 0{\cdot}05$). These inhibitory effects of hexamethonium disappeared 1 h after administration. With these

stimulation procedures, slight increases in systemic blood pressure were observed but there was no relationship between the blood flow increase and the blood pressure increase.

Figure 6 shows the effects of sectioning the lingual nerve proper (Fig. 6*A*) and the IAN in the mandibular canal (Fig. 6*B*) on the lip blood flow increase in response to

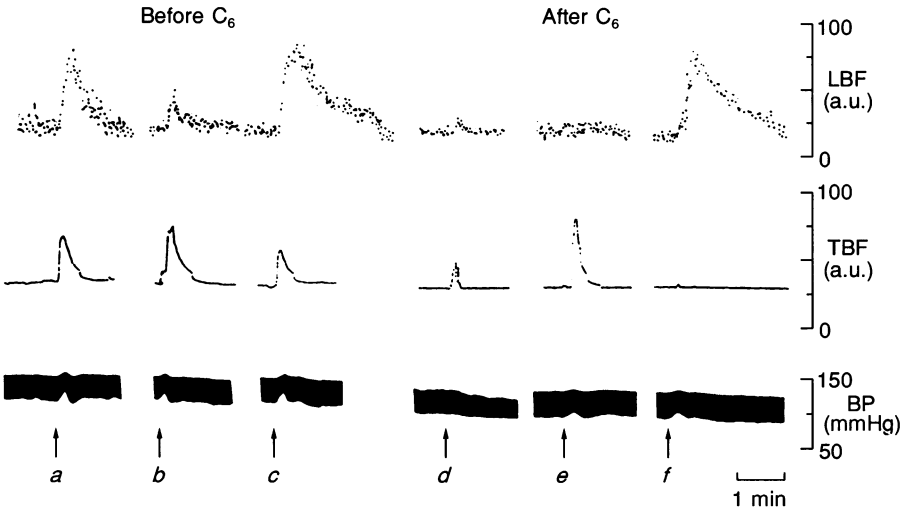

Fig. 5. Typical examples of the effects of hexamethonium (C_6) on the ipsilateral lower lip and tongue blood flow increases elicited by electrical stimulation of the peripheral cut end of the chorda tympani nerve proper, and direct stimulation of the chorda-lingual nerve and inferior alveolar nerve (IAN). The distal cut ends of the chorda tympani nerve proper, and the cut chorda-lingual nerve and the IAN were stimulated at 50 V, 40 Hz and 2 ms for 10 s where indicated by the small letter: (*a* and *d*) chorda tympani nerve proper; (*b* and *e*) chorda-lingual nerve; (*c* and *f*) IAN. Abscissa: time (min). Ordinate: lip blood flow (LBF), tongue blood flow (TBF) and blood pressure are shown in arbitrary units (a.u.) and systemic arterial blood pressure is in mmHg.

electrical stimulation of the distal cut ends of the CTNP. The CTNP stimulation-induced lip blood flow increase was not influenced by cutting the lingual nerve proper (Fig. 6*A*; 4/4 experiments), but it was abolished by section of the IAN in the mandibular canal (Fig. 6*B*; 3/3 experiments). Cutting the IAN near MHN (Fig. 6*C* and *D*) completely abolished the lip blood flow increase elicited by the proximal MHN stimulation (Fig. 6*C*; 5/5 experiments) and by the upper buccal gingiva stimulation (Fig. 6*D*; 5/5 experiments) but it did not show a clear-cut attenuation of the CTNP stimulation-induced blood flow increase in the lip (data not shown).

DISCUSSION

Until recently it was believed that the calibre of cutaneous vessels of the face was controlled primarily by vasoconstrictor fibres from the cervical sympathetic chain. The general view was that vasodilatation was brought about through an inhibition of the sympathetic vasoconstrictor tone. However, we have recently reported the

presence of parasympathetic vasodilator fibres in the orofacial area of the cat (Izumi & Karita, 1991*a*, 1992*a*,*b*). These findings are consistent with the results obtained by Matthews & Robinson (1980), Kaji, Shigematsu, Fujita, Maeda & Watanabe (1988) and Kaji, Shigematsu, Maeda & Watanabe (1991). Matthews &

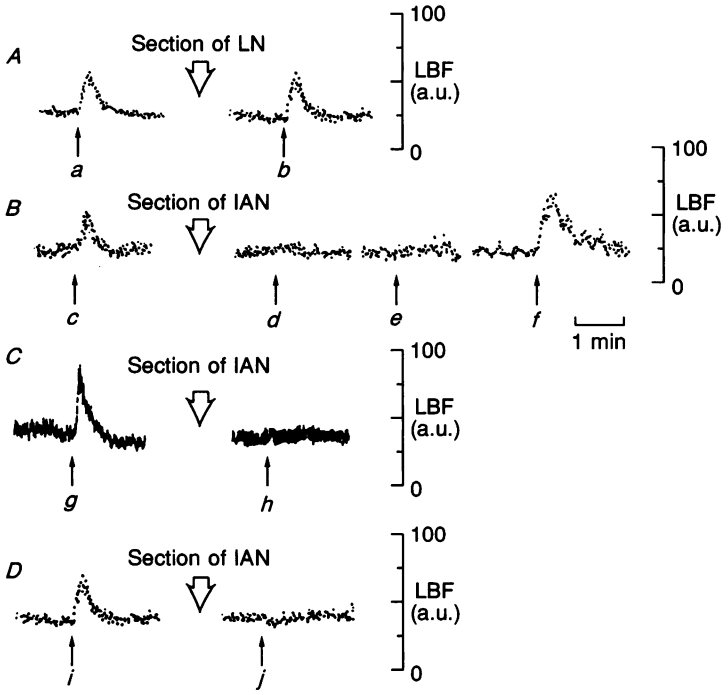

Fig. 6. Effects of section of lingual nerve proper (LN) and inferior alveolar nerve (IAN) on the chorda tympani nerve proper stimulation (*A* and *B*) and the central MHN stimulation (*C*) and the upper buccal gingiva stimulation (*D*). The distal cut ends of the chorda tympani nerve proper (*a*–*d*), the central (*e*) and peripheral (*f*) cut ends of IAN, the central cut ends of the MHN (*g* and *h*) and the upper buccal gingiva (*i* and *j*) were electrically stimulated at 50 V, 40 Hz and 2 ms for 10 s where indicated by the small letter. Abscissa: time (min). Ordinate: lip blood flow (LBF) expressed in arbitrary units (a.u.).

Robinson (1980) showed that tonically active, non-sympathetic and atropine-resistant vasodilator fibres to the cat lip are present in the inferior alveolar nerve. Kaji *et al.* (1988, 1991) have demonstrated that vasoactive intestinal polypeptide (VIP)-immunoreactive nerve fibres exist around blood vessels in the lip skin of rats and that they originate from the parasympathetic otic ganglion. Furthermore, it was suggested from our previous data that there would be two neural pathways for parasympathetic nerve vasodilator fibres supplying the cat lower lip, one consisting of fibres originating from the glossopharyngeal nerve and another of fibres from the facial nerve (Izumi & Karita, 1992*a*).

Chorda tympani nerve proper

In view of the statements in textbooks that the CTNP from the facial nerve supplies parasympathetic efferent vasodilator and secretomotor fibres to only the submandibular and sublingual glands and tongue, the vasodilator effect of CTNP

stimulation on lip blood flow we have found deserved further investigation. As shown in Fig. 2, electrical stimulation of the peripheral part of the cut CTNP elicited a stimulus intensity-related vasodilatation response not only in the tongue and submandibular gland but also on the lower lip of the ipsilateral side.

The vasodilator response elicited by stimulation of the cut chorda tympani nerve was abolished by section of the CLN (data not shown) and was markedly reduced by pretreatment with hexamethonium (Fig. 3), but was unaffected by section of the lingual nerve proper (Fig. 6*A*). On the other hand, the trigeminally induced reflex vasodilatations elicited by electrical stimulation of the upper gingiva and central part of the cut MHN were not affected by cutting the CTNP and lingual nerve proper, although these reflex vasodilatations were consistently reduced by pretreatment with hexamethonium (Fig. 4) and by sectioning the IAN near MHN even though the CTNP was intact (Fig. 6*C*). It seems safe to conclude, therefore, that the vasodilator fibres in the CTNP constitute an efferent preganglionic pathway but they make little contribution to the reflexly evoked vasodilatation response. This also suggests that this set of parasympathetic vasodilator fibres is separate from those travelling in the glossopharyngeal nerve which contribute to reflex vasodilatation induced via activation of the trigeminal sensory nerve.

The vasodilator responses elicited by stimulation of nerves containing both nociceptive C fibres and parasympathetic vasodilator fibres were resistant to hexamethonium (Fig. 5*b* and *e* in tongue blood flow and *c* and *f* in lip blood flow) (Izumi, Kuriwada, Karita, Sasano & Sanjo, 1990). Hexamethonium pretreatment largely abolished the CTNP-induced blood flow increases in the lower lip, tongue and submandibular gland (Fig. 3), suggesting that nociceptive C fibres which are considered to contribute to antidromic vasodilatation (Izumi & Karita, 1990; Izumi *et al.* 1990) and axon reflex vasodilatation (Izumi & Karita, 1988, 1991*b*,1992*c*) are not present in the CTNP to the lip, tongue and submandibular gland of the cat. This is in accordance with previous studies which have demonstrated no capsaicin-sensitive, nociceptive fibres in the mouse CTNP (Hiura, Ishizuka & Sakamoto, 1990). On the other hand, the blood flow increases in the tongue and submandibular gland following electrical stimulation of the distal cut ends of the CLN were not affected by pretreatment with hexamethonium, while the lip blood flow increase was markedly reduced by this procedure (Fig. 3). It seems likely that the CLN, unlike the CTNP, contains nociceptive C fibres supplying the tongue and submandibular gland but not the lower lip of the cat. Apparently, there is no spontaneous tone in these nerve fibres in animals under general anaesthesia; without electrical stimulation the blood flow was the same on both sides of the lips in spite of unilateral section of the CTNP.

Dual innervation

The parasympathetic vasodilator fibres involved in reflexly evoked vasodilatation responses do not travel with the CTNP (Fig. 4), although both sets of fibres travel by the same final route, namely the inferior alveolar nerve in the mandibular canal (Fig. 6*B*; Izumi & Karita, 1992*a*) as illustrated in Fig. 7. This observation suggests that two groups of parasympathetic vasodilator fibres may have different functions. In view of the present data, we are inclined to suggest that there is a dual innervation of the cat lip by two different groups of parasympathetic vasodilator fibres, although

the physiological function of the vasodilator fibres in the CTNP emanating from the facial nerve to the lip remains to be established.

Similar dual innervation of target tissues by more that one group of parasympathetic fibres has previously been reported concerning secretomotor fibres

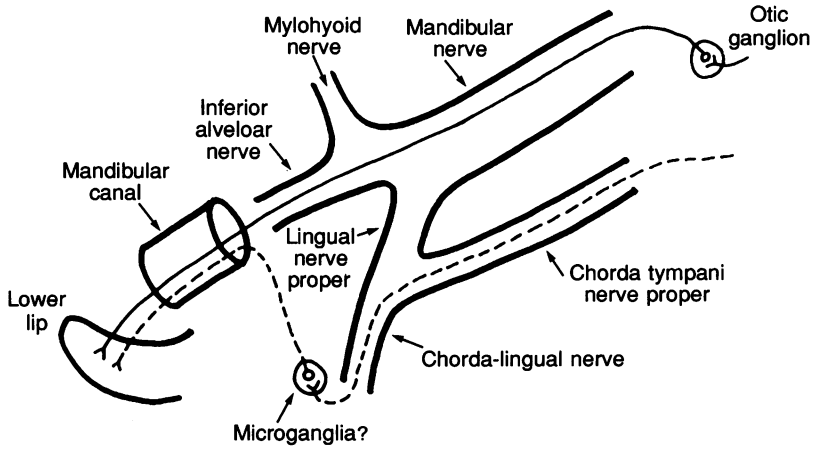

Fig. 7. Schematic illustrations of our working hypothesis on the course of two groups of parasympathetic vasodilator fibres to the cat lower lip.

to the submandibular gland of the rat and monkey by Hellekant & Kasahara (1973*a*, *b*). They showed that electrical stimulation of the peripheral part of the trigeminal portion of the CLN as well as of the facial portion elicited secretion in the submandibular gland. This finding is supported by studies showing that cutting the chorda tympani in man does not abolish salivation from the submandibular gland in response to acid (lemon juice) (Diamant, Enfors & Holmstedt, 1958; Laage-Hellman, Stromblad & Charles, 1960). Data showing there was no difference in the composition of saliva caused by CTNP stimulation and that by lingual nerve proper stimulation (Hellekant & Kasahara, 1973*a*) suggest that the influence of these two nerves on the secretion of the gland were essentially the same. These results also indicate that there is an unknown path for secretomotor fibres to the submandibular gland. Furthermore, it is stated in textbooks (e.g. Williams & Warwick, 1980) that postganglionic parasympathetic fibres leave the otic ganglion via branches of the auriculotemporal nerve, but recent evidence from stimulation experiments indicates that not all these branches are crucial for activation of the parotid gland (Al-Hadith & Breen, 1986), suggesting the presence of other neural secretomotor pathways that supply the parotid gland. At the present time the physiological function of the two sets of parasympathetic vasodilator fibres as well as that of two sets of secretomotor fibres on the orofacial areas remains unclear.

Ganglion

The finding that vasodilatation in response to electrical stimulation of the peripheral parts of the cut CTNP was significantly reduced by pretreatment with hexamethonium indicates that the CTNP is the route taken by preganglionic

efferent vasodilator fibres to the cat lip. As shown in Fig. 6*B*, the vasodilator response elicited by stimulation of the cut CTNP was abolished by section of the inferior alveolar nerve in the mandibular canal. Recent fibre tracing studies using the horseradish peroxidase (HRP) method have shown that blood vessels in the lower lip are innervated by postganglionic fibres originating in the otic ganglion but not in the pterygopalatine ganglion (Kuchiiwa *et al.* 1992). Although the exact site of the ganglion associated with the parasympathetic vasodilator fibres in the CTNP is uncertain at the moment, it seems unlikely that it is the otic ganglion, from the topographical anatomy of the nerves. Recently Gibbins, Brayden & Bevan (1984) and Gibbins (1990) have suggested that microganglia which might contain VIP-immunoreactive perikarya are present in the orofacial areas associated with the facial and glossopharyngeal nerves. If this is so, the preganglionic fibres from which the facial nerve could enter the microganglia via the CTNP and the VIP-containing postganglionic fibres terminate in the cat lower lip after running via the inferior alveolar nerve as shown in Fig. 7. This may account for why we could not determine the site of the ganglion for the parasympathetic vasodilator fibres originating from the facial (chorda tympani proper) nerve and why atropine, a muscarinic cholinoceptor antagonist, was without effects on the reflex vasodilatation and vasodilatation elicited by electrical stimulation of the seventh and ninth cranial nerves (Izumi & Karita, 1991*a*, 1992*a*). Efforts aimed toward understanding more about the sites of these microganglia and characterizations of these vasodilator fibres are presently under investigation in our laboratory.

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