THE PERIPHERAL INNERVATION OF THE VESSELS OF THE EXTERNAL EAR OF THE RABBIT.

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Although the demonstration of the alteration of the calibre of the vessels in the rabbit's ear furnished one of the earliest proofs of the existence of vaso-constrictor fibres, there still remains considerable uncertainty as to the precise nervous supply of the vessels of this organ. The object of the present research was to clear up these uncertainties as far as possible, both with regard to vaso-constrictor and vaso-dilator fibres.

The external ear is provided with nerves from the V and VII cranial nerve and with nerves from the spinal cord as follows:

(1) The facialis supplies the ear muscles, some branches of which leave the Fallopian canal before reaching its termination; these are known as the facialis posterior.

(2) The trigeminus gives to the ear the ramus auricularis temporalis.

(3) Nerves from the II and III cervical form the great auricular (or auricularis anterior) and the posterior auricular. The sensory nerve supply of the ear consists of these fibres with the addition of the auriculo-temporal branch of the trigeminus.

Langley has suggested that the anterior auricular should be called the ventral auricular and similarly, that the posterior auricular should be called the dorsal auricular. His reason was that the anterior auricular supplies the posterior part of the ear, and the posterior auricular supplies the anterior part of the ear. They were given their names because the anterior (ventral) auricular came chiefly from the anterior (ventral) branches of the II and III cervical and the posterior (dorsal) auricular from the posterior (dorsal) branch of the II cervical. In this paper we shall use the terminology suggested by Langley[1].

We could not find that the first cervical nerve sends any fibres to the ear.

[1] Shortly before his death, Prof. Langley worked on the problem of the peripheral innervation of the vessels of the rabbit's ear. He intended that his work and mine should be published together. After his death I finished the experiments alone.

Method. The animals were in all cases anæsthetised and tracheotomised. We observed the vessels with the naked eye by transmitted light—usually electric light but occasionally daylight. In all cases we were careful to eliminate the factor of warmth.

We employed both electrical and mechanical stimulation, usually the former. Mechanical stimulation was simply made by compressing the nerve with forceps for either 10–20 sec. or else for several short intervals.

The extirpation of the superior cervical ganglion. This was made under chloroform-ether anæsthesia. The dilatation of the ear vessels after the extirpation of the ganglion disappeared in a few days. Even the next day only the central artery showed a small dilatation especially in its lower part. Under normal conditions this dilatation disappeared also in a few days. In the few cases, where the wound took some time to heal, the central artery remained dilated for a longer time. Similar observations on the denervated hind-legs are described by Goltz(1).

A fortnight to two months elapsed between the extirpation of the ganglion and the observation of the effect. During the process of cutting the hair on the operated and normal sides respectively it was noticed that the manipulation due to this procedure made the ear red more rapidly on the operated side than on the control, and the red colour was longer maintained. Later on, when we began the chloroform-ether anæsthesia (the rabbits were put under a glass bell) the ear vessels of the operated side dilated more quickly than the vessels on the normal side. They remained also longer dilated after the administration of the anæsthetic was stopped. On several occasions no dilatation on the sound side took place if the anæsthetic was removed at the moment when the vessels on the operated side became dilated. There appears to be a contrast between the effects of chloroform-ether and those of amyl nitrite (Eugling(2)).

The extirpation of the ganglion stellatum. We found no mention in the literature of this operation on the rabbit. Dr Anderson(3) (whom I have consulted) described an extra-pleural method for taking away the ganglion from the first intercostal space in the cat. The exact description of the preparation of the ganglion is given by Sherrington(4). In the rabbit it is impossible to uncover the whole ganglion from here and to draw it out without causing extensive bleeding. The ganglion, which is very long, lies mostly under the first rib and cranial to it. After some practice on the dead rabbit it was easy to take it away from above the first rib without injuring the pleura. The vessels in this region presented the only difficulty. This may be obviated by cutting each branch of the ganglion separately before drawing it out. The exact course of the operation was as follows:

One hour and a half before the commencement of the operation 90–100 mg. luminal were injected subcutaneously so that but little chloroform-ether was needed. The rabbit lay on its side. The skin was cut between the dorsal edge of the scapula and the spinal vertebræ, the front end of the incision reaching some cm. above the anterior border of the scapula. The slender transversus muscle was cut. The scapula with its muscles was raised a little and drawn down, so that the upper part of the chest lay free. The scapula was held in its position by a hook. The first rib is covered by the musculus scalenus medius, which was cut at this level. Under this muscle lies the small musculus scalenus anterior which was gently torn across. The roots of the brachial plexus were now exposed. We dissected deeper with a small forceps between the first two branches of the plexus, which issue in front of the first rib and join a little later to form a triangle. The upper part of the ganglion stellatum was then always found at once by keeping quite near to the first rib and not too ventral. Each fibre of the ganglion was separately cut through, first the upper branches, then slowly drawing out the ganglion we cut the rest one fibre after the other. At last it tore off, usually with a small piece of the sympathetic remaining on the lower end. We sewed the musculus scalenus medius and transversus with two sutures and then the skin. The operations were made under strict asepsis. The animals always recovered very quickly apart from a slight limp of the fore-leg on the operated side.

The post-mortem examination showed that the ganglion was always completely removed and that the wound had thoroughly healed. We made in all five operations on the right side and two operations on the left side.

After the removal of both the superior cervical ganglion and stellatum on one side, the vessels did not return to their original degree of contraction. Even four weeks after the operation the vessels showed a small but distinct dilatation compared with the vessels of the normal side. The same difference in the calibre of the vessels was found in two of the three experiments, in which only the ganglion stellatum had been removed. This is not the case after the extirpation of the superior cervical ganglion. It should be remembered, however, that the extirpation of the ganglion stellatum also removes the whole central supply of the superior cervical ganglion, so that the influence from the central nervous system on the constrictor tonus of the ear vessels remains. This incomplete return of tonus agrees with isolated observations of Eugling (2) and with those of Krogh (5) on the capillaries.

The preparation of the auriculo temporalis (V). In the dead rabbit this rather thin nerve is best found at its origin, where it leaves the trunk of the maxillaris inferior. From here it comes up towards the surface behind the posterior border of the ramus mandibularis of the mandible and soon divides into its branches to the facialis, to the regio temporalis and to the ear. In one animal the nerve was still divided at its origin.

The preparation of this nerve in the living animal is easy if the rabbits used are not too fat and muscular. The most suitable are young female animals. The skin and fascia were cut between the base of the ear and the zygoma. We dissected behind the posterior border of the mandibularis ascendens close to the border of the medial part of the masseter muscle and reached the vena facialis posterior. In front of this vein we went deeper. The branch to the ear runs under and behind the vein. The trunk of the nerve is enclosed with the pterygoid muscle above, the fat of Bichat below, the ramus mandibularis ascendens in front and the tympanic bulla behind. The nerve was freely exposed, tied and cut as deeply as possible.

The preparation of the auricularis ventralis and dorsalis and of the facialis posterior. The skin was cut 2 cm. from the basis of the ear obliquely to the neck. After cutting the fascia the auricularis ventralis was to be found behind the vena auricularis posterior. The nerve comes out behind the posterior border of the musculus sternocleidomastoideus and runs in an oblique direction to the base of the external ear. To find the auricularis dorsalis we went towards the back and under the two next muscles. The branches of the facialis posterior were found between both the auricular nerves on the base of the ear.

THE PERIPHERAL DISTRIBUTION OF THE VASO-CONSTRICTORS OF THE EAR.

The vaso-constrictor fibres run in the nervi facialis posterior, auricularis ventralis and auricularis dorsalis. We could not confirm the observation of Lowen(6) that fibres run directly from the superior cervical ganglion in close connection with the arteries which distribute to the ear: for after having cut both the cervical nerves and all branches of the facialis posterior, stimulation of the cervical sympathetic did not cause the slightest constriction of the vessels of the ear.

The nerves each supply special parts of the ear with vaso-constrictor fibres. These areas overlap, particularly those supplied by the facialis and the cervical nerves. We may leave out of consideration the individual variations because they do not alter the nature of the distribution.

The auricularis ventralis. Cutting this nerve always caused a marked dilatation of the ear. The dilatation took place chiefly on the distal part and the posterior border or the side of the ear. The basal part of the central artery was only slightly dilated as also the anterior border of the ear.

Very strong currents were needed to give a vaso-constriction on stimulating this nerve. This was pointed out first by Morat and is due to the thickness of the sheaths of this nerve (Fletcher(7)). In our experiments the secondary coil was between 10–6 cm.; at 7–10 cm. the current was unbearable on the tongue. The constriction took place chiefly on the distal part and posterior border of the ear. The anterior border was only contracted on the tip (see Fig. 1). The basal part of the central artery was only weakly affected even with very strong current. From 5 to 15 sec., after ceasing the stimulation, an after-flush occurred. This gradually increased and faded slowly after some minutes.

Similar observations about the distribution of this nerve were made by Dastre and Morat(8), Fletcher(7), Langley(9), Lowen(6) and Schiff (quoted by Langley). Fletcher, however, states that he also found "the proximal third of the artery to show marked constriction equal in one case to that in the distal third."

Auricularis dorsalis. Cutting this nerve always caused a strong dilatation on the anterior border of the ear; the electrical stimulation caused a strong constriction in this region (see Fig. 3). If the ventral auricular had been cut previously, the contracted vessels were sharply marked against the remaining dilated ear.

Facialis posterior. The cutting of all the branches of this nerve caused a marked dilatation of the proximal part of the ear.

Electrical stimulation of this nerve always caused a marked constriction of the same region. It is impossible to stimulate all branches of this nerve together. In order to observe the exact distribution of the whole nerve, we stimulated the peripheral end of the cervical sympathetic after having cut previously the ventral and dorsal auricular. The facialis posterior receives, as we shall see later, all its vaso-constrictor fibres from the superior cervical ganglion, so that stimulation of the sympathetic nerve involves all the fibres of the facialis posterior, and these fibres only, since the cervical nerves are cut. Under this condition the stimulation of the cervical sympathetic caused a contraction of the proximal half of the ear, the contracted part reaching higher in the middle of the ear than on both sides (see Fig. 5).

THE ORIGIN OF THE POST-GANGLIONIC FIBRES OF THE VASO-CONSTRICTORS OF THE EXTERNAL EAR.

Fletcher's(7) work showed that the ventral auricular obtains vaso-constrictor fibres from the ganglion stellatum, but did not make it clear whether all its vaso-constrictor fibres have this origin, and Fletcher did not deal with the question whether the dorsal auricular, which supplies only the small anterior part of the ear, obtains any fibres from the ganglion stellatum.

In order to ascertain which nerves receive fibres from the superior cervical ganglion, we cut all the nerves of the ear, except the one we wished to examine, and then stimulated the peripheral end of the cut cervical sympathetic. The contraction which resulted and which was abolished by cutting the remaining nerve could only be due to fibres from the superior cervical ganglion running to this nerve. The second method used was the excision of the ganglion stellatum and the stimulation of the ear nerves after allowing time for degeneration.

To see which nerves obtain fibres from the ganglion stellatum we removed the superior cervical ganglion and waited the time necessary for degeneration. The constriction now obtained on stimulating the ear nerves was due to fibres from the ganglion stellatum, since, after having removed both ganglia, stimulation of the ear nerves never gave the slightest vaso-constriction. The results in the special nerves were the following:

Facialis posterior. This nerve receives all its vaso-constrictor fibres from the superior cervical ganglion, because, after having removed this ganglion and waited the time necessary for degeneration, stimulation of this nerve did not cause a constriction. On the other hand, after having removed the ganglion stellatum the vaso-constriction on stimulating this nerve was not diminished.

Auricularis ventralis. This nerve receives fibres from both ganglia, as is shown by the following results:

(1) Stimulation of the peripheral end of the cervical sympathetic (the dorsal cervical and all branches of the facialis posterior being cut previously) caused a constriction, chiefly for about 2 cm. in the middle of the central artery of the ear. The remaining upper half of the artery was only slightly contracted but many of the smaller vessels had disappeared. After cutting the ventral auricular as well, the stimulation of the cervical sympathetic did not cause a constriction.

(2) After the excision of the ganglion stellatum (three experiments) stimulation of the ventral auricular nerve still caused a constriction. The central artery showed the best constriction in the middle of the ear. The part corresponded well with that on stimulating the cervical sympathetic under the condition in para. 1 (*supra*). In comparison with the contraction obtained on the normal side the effect was always smaller; in particular the tip and the posterior border remained more or less dilated (see Fig. 2).

This agrees with our observation on cutting the cervical sympathetic. In some experiments the posterior border remained contracted and the tip was little dilated, in the other cases the whole ear dilated equally (see also Tigerstedt(10)).

These two series of experiments showed that the ventral auricular receives some fibres from the superior cervical ganglion.

(3) After having removed the superior cervical ganglion and having waited the time for degeneration, stimulation of the ventral auricular with strong currents always caused a constriction (Schiff, Fletcher). Weak currents often produced vaso-dilatation. This will be discussed in the section on the vaso-dilator nerves.

The contraction was mostly stronger than that after the ganglion stellatum had been removed, so that it seemed that the ventral auricular receives more fibres from the ganglion stellatum than from the superior cervical ganglion.

(4) After having removed both the ganglia, stimulation of the ventral auricular did not cause any contraction even with the strongest currents.

Auricularis dorsalis. The dorsal auricular obtains most of its fibres from the superior cervical ganglion. We found, however, that after removing this ganglion we were able to cause a small constriction on the upper part of the anterior border in all experiments. This constriction concerned only a very small region in comparison with that obtained on the normal side (see Fig. 4). As it was abolished after excision of both the ganglia it indicates the origin of some fibres from the ganglion stellatum. Stimulation of the dorsal auricular after the excision of the ganglion stellatum did not show a distinct diminution of the constriction. We may conclude, therefore, that this nerve receives most of its fibres from the superior cervical ganglion and only some from the ganglion stellatum. These latter explain the non-degenerate fibres on the anterior border of the ear, which Eugling found constantly after having removed the superior cervical ganglion and cut the ventral auricular previously.

In the dog and in the cat the vessels of the ear are not provided with any post-ganglionic fibres from the ganglion stellatum. Fletcher, since he found only fibres from the ganglion stellatum in the auricularis ventralis, legitimately assumed the reason to be that this nerve is more anterior in the cat than in the rabbit. We, however, have found fibres from the ganglion stellatum in both cervical nerves and our explanation is that even the pre-ganglionic fibres for the ear vessels are more anterior in origin in the cat than in the rabbit. As Langley(11) showed, the pre-ganglionic fibres for the ear vessels run in the cat in the I–IV thoracic nerves and in the rabbit in the II–VIII thoracic nerves.

We must furthermore assume that the ramus vertebralis in the rabbit sends vaso-constrictor fibres not only to the third but even to the second cervical nerve.

The figures show diagrammatically the vaso-constrictor distribution in the external ear of the rabbit. The shaded sections are the parts in which contracted vaso-constriction occurs on stimulation of the nerves.

The ears are seen from behind so that the anterior border becomes the medial, the posterior the lateral border of the ear.

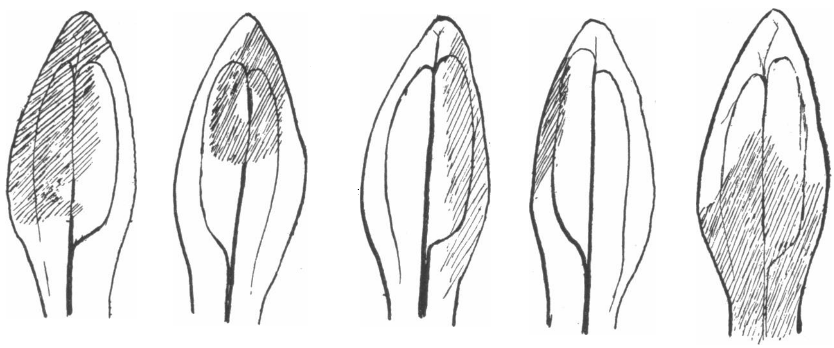

Fig. 1. Fig. 2. Fig. 3. Fig. 4. Fig. 5.

Fig. 1. Left ear. Contraction due to stimulation of the ventral auricular (p. 522).

Fig. 2. Right ear. The same as in Fig. 1, only the ganglion stell. removed three weeks previously. In the contracted area a small part of the central artery remained dilated (p. 523).

Fig. 3. Left ear. Contraction due to stimulation of the dorsal auricular (p. 522).

Fig. 4. Right ear. The same as in Fig. 3, only the sup. cerv. ganglion removed three weeks previously (p. 524).

Fig. 5. Left ear. Contraction due to stimulation of the periph. end of the cut cerv. sympathetic; the auriculo-cervical nerves are cut previously. The figure shows the distribution of the vaso-constrictors of the facialis posterior (p. 522).

The vaso-dilators of the external ear.

As to the origin of the vaso-dilators of the external ear of the rabbit, we find in the literature several statements which we can divide into three groups:

(1) The fibres in the cervical sympathetic.

Dziedzuhl(12) found that four days after the section of the cervical sympathetic stimulation of this nerve caused a vaso-dilatation of the ear vessels. It could be obtained till the eleventh day after the section. Dziedzuhl's explanation was, that the vaso-constrictor fibres of the cervical sympathetic degenerate more quickly than the vaso-dilator fibres, which under normal conditions are masked and which now appear. The experiments were recently repeated by Feldberg and Schilf(13), who could not confirm the results. References to earlier work on the subject are given in their paper.

(2) The vaso-dilatation of the auriculo temporalis (V).

Schiff(14) succeeded in obtaining a vaso-dilatation of the ear vessels in six out of 11 experiments, when he stimulated the intact auriculo-temporalis or its peripheral end. The vaso-dilatation began at once with the stimulation and ceased with it. Vulpian(15) could not confirm this; Claude Bernhard(16), however, sometimes observed on the ear of the dog a vaso-dilatation on stimulating this nerve.

(3) The "antidromic" vaso-dilatation and the dilatation of the cervical auricular nerves.

Krogh and Rehberg(17) tried vainly "to elicit any dilator response by electrical or mechanical stimulation of the peripheral ends of the sensory nerves to the rabbit's ear." But when they observed the vessels microscopically and stimulated them directly with a fine needle or a hair, they obtained a local vaso-dilatation which disappeared gradually with the proceeding degeneration of the cut cervical nerves. Nineteen days after the section it could no more be produced.

Winkler(18) observed a vaso-dilatation of the ear after section of the dorsal (and ventral) roots of the IV, V and VI cervical nerves. Whether this vaso-dilatation can be regarded as an antidromic vaso-dilatation, as Bayliss believed, or more properly as a reflex one, is not proved. The sensory cervical nerves which supply the ear come from the II and III cervical nerves, but the possibility of some kind of antidromic dilatation must be taken into account.

We made experiments on the auriculo-temporalis (V) and on the two cervical nerves.

Auriculo-temporalis (V). Our experiments were made on ten rabbits. In two of the animals the superior cervical ganglion was removed previously. We stimulated mechanically and electrically, always beginning with weak currents, gradually increasing. In the first experiment we observed a vaso-dilatation of the central artery 5–25 sec. after the electrical stimulation of the nerve had ceased. This dilatation lasted some seconds only. In all the following nine experiments, however, we did not succeed in obtaining a distinct vaso-dilatation. During the first experiment we were probably less alive than later to the rhythmic variations first observed by Schiff and to central influences. We also believe, that the vaso-dilatation of the six experiments of Schiff during the stimulation of the nerve was due to central influences. Schiff stimulated in some experiments the intact nerve with central connections undisturbed. The form of the vaso-dilatation described by him (the lack of a latent period, the beginning and ceasing with the stimulation) differs considerably from that always observed on stimulating vaso-dilators in sensory nerves.

The auricularis ventralis and dorsalis. Before I began my experiments the late Prof. Langley wrote me, "that sometimes the cervical auricular nerves (chiefly the great auricular) under strong induction currents of low frequency or weak induction shocks of high frequency, caused a great dilatation of the vessels in the ear, gradually beginning in the capillary region." He advised me to take away the ganglion cervical superior or the ganglion stellatum to see if it would then be easier to obtain a vaso-dilatation on stimulating these nerves.

In four experiments, in which both the ganglia of one side were removed 11–25 days previously, mechanical and electrical stimulation with weak and strong currents of both the auriculo cervical nerves caused a marked dilatation. The dilatation of the ventral auricular concerned the whole ear except the anterior border. That of the dorsal auricular concerned the anterior border. The vaso-dilator distribution is the same as the sensory nerves distribution and nearly the same as that of the constrictor fibres.

The dilatation occurred on mechanical stimulation after a latent period of 10–25 sec. On electrical stimulation which lasted one minute it occurred during the stimulation with a weak current 25–30 sec., with a strong current 5–10 sec. after the beginning of the stimulation. The dilatation began in the smallest vessels and spread gradually to the great vessels, including also the central artery when the ventral auricularis was stimulated. During the first minute this vaso-dilatation increased, after 4 minutes it faded slowly away. Even with the strongest unbearable currents it was at no time possible to obtain the slightest vaso-constriction.

The section of these nerves also produced a constant vaso-dilatation. The ear showed a much redder tone (due to dilatation of the small vessels) than the ear of the normal side, where the cervical sympathetic was cut. The effect must be regarded as due to stimulation of the nerves by the section. While the dilatation due to the sympathetic section did not fade away for a long time, the dilatation after cutting the cervical nerves gradually diminished and after 10–15 min. all the small vessels had disappeared and the large vessels were no more dilated than before the beginning of the experiment (see Method). In the experiments on those rabbits on which only the ganglion stellatum *or* only the cervical ganglion had been removed, stimulation of the cervical nerves mechanically or with weak currents caused a dilatation. Stronger currents always gave a vaso-constriction, the details of which we have already described. In some cases, where the superior cervical ganglion had been removed, the current on stimulating the ventral auricular was just strong enough to show the effect on both dilator and (remaining) constrictor fibres: the central artery contracted partly, but the small vessels dilated and the ear tip remained very red. Weakening the current during the stimulation abolished the constrictor effect on the central artery, strengthening the current caused a contraction of the small vessels as well.

As the two cervical nerves of the ear are sensory nerves there can be no doubt that the vaso-dilatation is due to "antidromic" reaction. We think, however, that the sensory dorsal roots of cervicals II and III must be responsible for this and that the vaso-dilatation of the experiments of Winkler(18) (c. IV, V, VI) is a reflex effect.

Conclusion.

(1) A method of removing the ganglion stellatum above the first rib in the rabbit is described.

(2) It is found that the vaso-constrictor fibres for the external ear run in the facialis posterior, the auricularis ventralis and the auricularis dorsalis.

The origin of the post-ganglionic vaso-constrictor fibres of the facialis posterior lies in the superior cervical ganglion, of the auricularis ventralis and dorsalis in both the superior cervical ganglion and the ganglion stellatum. The dorsal auricular, however, obtains only very few fibres from the ganglion stellatum.

(3) Vaso-dilator fibres of the external ear could not be found in the auriculo-temporalis (V). They run in the auricularis ventralis and dorsalis. Each nerve supplies a special region similar to the sensory distribution of these auriculo-cervical nerves.

I should like to record my indebtedness to the late Prof. Langley for much useful advice at the commencement of this research, and my appreciation of the loss it sustained when his death deprived me of his criticism and encouragement.

Prof. Barcroft has generously helped me with the preparation of this paper; and I wish to thank him for his patience and kindness.

My wife has assisted me throughout the course of the experiments described above, and I owe much to her constant help.

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