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FIFTH REPORT ON THE PROGRESS OF PHYSIOLOGY.

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VASO-MOTOR NERVES.

ONE of the most important recent advances in our knowledge of the physiology of the circulation is the distinct recognition of the existence of a class of nerve-fibres whose function is to *dilate* the vessels to whose muscular walls they are distributed. That vascular dilatation may follow the stimulation of a nerve supplying the vessels under observation is not a recent discovery. The fact that irritation of the chorda tympani produces vascular dilatation and increased secretion in the submaxillary gland was observed by Bernard as long ago as 1858, but it is only within a few years that the cause of this dilatation has been shown not to lie in the increased glandular activity. This point may be regarded as having been settled by the experiments of Heidenhain,¹ who found that on a dog under the influence of atropine, irritation of the chorda tympani caused no increased salivary secretion, though the vascular dilatation took place as usual.

For a long time the fibres of the chorda tympani in the submaxillary gland and the nervi erigentes distributed to the corpora cavernosa penis, as described by Eckhard² and Lovén,³ were regarded as the only nerves possessing the power of producing vascular dilatation in the parts supplied by them, the observations of Bernard which led him to attribute to the pneumogastric nerve a similar power over the vessels of the kidney having lacked confirmation. Quite recently, however, Vulpian⁴ has shown that irritation of the lingual nerve causes a vascular dilatation in the corresponding side of the tongue. That this effect is due to the fibres of the chorda tympani, which are mingled with the lingual nerve, is proved by the fact that the dilatation does not take place when the former nerve has been divided, fifteen days previously, in the tympanum, and its fibres thus caused to degenerate throughout their course. Vulpian's observation, therefore, simply shows that the dilating power of the chorda tympani is not confined to those fibres which are distributed to the submaxillary gland.

¹ Pflüger's Archiv, v., page 309.

² Beiträge, iii., page 125.

³ Ludwig's Arbeiten, 1866, page 1.

⁴ Leçons sur l'appareil vaso-moteur: Paris, 1875, page 154.

Although the power of the nerves to dilate the blood-vessels has not been distinctly demonstrated, except in the regions alluded to, Vulpian is of the opinion that "vaso-dilator" nerves exist throughout the body, mingled with "vaso-constrictors" in such a way as to prevent their functions from being readily investigated. A similar view has also been adopted by Goltz,¹ who has invoked the power of the "vaso-dilator" nerves to explain phenomena which are usually regarded as caused by a paralysis of the "vaso-constrictors." The well-known fact that section of the sciatic nerve in an animal is followed by a rise of temperature in the corresponding limb, and that this increased temperature is only a temporary phenomenon, is explained by Goltz on the hypothesis that "vaso-dilator" nerve-fibres in the sciatic nerve are irritated by the section, causing a dilatation of the blood-vessels of the limb, and that after the effect of this irritation has passed away, the vessels resume their normal dimensions. In support of this view, Goltz presents the following observations:—

1. After the rise of temperature caused by section of the sciatic nerve has disappeared, it may be again produced by a second section of the nerve nearer the extremity.

2. If the rise of temperature which follows section of the sciatic nerve is really a phenomenon of irritation, a similar effect ought to be produced by other sorts of irritation; for example, by electrical stimulation of the nerve. Goltz finds that this is actually the case, electrical or chemical irritation of the lumbar cord or of the sciatic nerve, either in its continuity or at its peripheric end, causing a decided increase of temperature in the lower limbs. A slight and transient fall of temperature which generally precedes the rise is referred by Goltz to a displacement of the thermometer at the beginning of the irritation by the tetanic contraction of the muscles of the leg.

Goltz therefore concludes that the section of the nerve of a limb irritates the vaso-dilator fibres contained in it, and that this condition of irritation may last days or even weeks. It is to be noticed that this theory affords no explanation of the fact that irritation of the sympathetic nerve of the neck always causes, under normal conditions, a contraction of the vessels of the head, while its section with equal certainty produces vascular dilatation.

Quite recently Putzeys and Tarchanoff,² working under the direction of Goltz, have subjected the whole question to a renewed investigation. They find that section of the sciatic nerve on dogs, ducks, and frogs causes an immediate dilatation of the vessels of the foot, made evident both by the appearance of the vessels where they can be seen, and by the fact that blood flows more abundantly from a wound in the foot on

¹ Pflüger's Archiv, ix., page 174.

² Centralblatt für die medicinischen Wissenschaften, 1874, page 641.

the side where the nerve has been divided than on the opposite side. Electrical irritation of the peripheric end of the divided nerve causes, on the other hand, a decided contraction of the vessels, which, when the irritation lasts several minutes, gives place to a dilatation caused by exhaustion. Section of the sciatic nerve of a dog causes, as Goltz also found, a decided rise of temperature in the foot of the same side, while irritation of the peripheric end of the nerve causes, when the dog is curarized to paralyze the voluntary muscles, not a rise, but a fall, of temperature. The rise of temperature observed by Goltz as the result of irritation of the sciatic nerve is regarded, therefore, by Putzeys and Tarchanoff as the effect of over-irritation or exhaustion. The existence of "vaso-dilator" fibres in the sciatic nerve cannot therefore be considered as demonstrated.

In consideration of all these observations, the most probable view which we can take of the relations between the vaso-motor nerves and the vessels to which they are distributed seems to be the following:—

The smooth muscles of the blood-vessels are kept in a state of moderate tonic contraction under the influence of a plexus of nerve-fibres and ganglion cells closely surrounding and imbedded in the vascular walls.¹ This tonic contraction is increased by an impulse coming from the central nervous system through the "vaso-constrictor" nerves.

That these "vaso-constrictor" nerves are in a state of constant activity is evident from the fact that vascular dilatation follows their section (for example, in the cervical sympathetic or sciatic nerves). This vascular dilatation is, however, not permanent. After ten days or a fortnight, the vessels assume their original dimensions. To explain this, we must assume that after separation from the central nervous system the nervous plexus surrounding the vessels gradually acquires a higher degree of activity than it possessed before. A justification of this hypothesis is found in the analogous observation that the reflex centres in the spinal cord acquire a greater irritability after their separation from the brain by a section in the cervical region.

The "vaso-dilator" nerves act by inhibiting the activity of the ganglion cells in the nervous plexus around the vessels, thus causing a diminution of the vascular tonicity. These nerves are not in a state of continual activity, as is proved by the failure of the vessels to contract when the nerves are divided.² They are to be regarded, therefore, not as constant but as occasional antagonists of the "vaso-constrictor" nerves.

According to this theory, there is an evident analogy between the muscular walls of the blood-vessels and the heart. In both, the conditions of activity are contained in the organs themselves; and in both, influences derived from the central nervous system may either increase

¹ See Vulpian, *op. cit.*, page 36.

² Vulpian, *Archives de Physiologie*, vi., page 175.

or diminish this activity, the vagus nerve being analogous to the vasodilators and the "accelerator" nerve to the vaso-constrictors.

It will be noticed that this theory affords no explanation of the observation of Goltz, above alluded to, on the effect of a second section of the sciatic nerve on the temperature of the limb. Should this observation be confirmed, some modification of the above theory will be necessary.

VASO-MOTOR CENTRES.

From the fact that nervous centres presiding over the movements of the different voluntary muscles of the body are distributed through the length of the spinal cord, it is natural to suppose that the vaso-motor nerves arise from similarly situated centres. This, however, is not the opinion of the majority of physiologists at the present day. The experiments of Owsjannikow¹ on rabbits seemed conclusive on this point. This observer found that a section through the medulla oblongata one or two m. m. below the tubercula quadrigemina did not produce vascular paralysis, as indicated by a manometer registering the arterial blood-tension. Any lower section, however, did produce vascular paralysis, and the lower the section the more complete was the paralysis, until a point four or five m. m. above the calamus scriptorius was reached. After the medulla had been divided at this point, not only did lower sections fail to produce additional paralysis, but the irritation of sensitive nerves did not cause a reflex contraction of the blood-vessels and consequent rise of blood-tension. Owsjannikow concluded, therefore, that the vaso-motor centre lies in a portion of the medulla oblongata whose upper and lower limits are those above indicated, and whose extent from above downward is in rabbits about four m. m. These observations have been confirmed by Dittmar,² who, by improved methods of making the sections, has been able to determine the limits of the vaso-motor centre with great accuracy, and by partial sections of the cervical cord has proved that both the centripetal and the centrifugal fibres, which are concerned in the reflex contraction of blood-vessels, run in the lateral columns of the spinal cord.

On the other hand, Vulpian³ reports many observations which seem to prove that certain of the vaso-motor nerves do not have their origin exclusively in the medulla oblongata. He finds, for instance, that after section of the cervical cord the temperature of the posterior limbs rises, and that a subsequent section of one of the sciatic nerves causes a still further rise in the corresponding limb, indicating the presence of tonic vaso-motor centres in the cord below the cervical region. He also finds that, when the brain and upper part of the cord of a frog have been

¹ Ludwig's Arbeiten, 1871, page 21.

² Ibid., 1873, page 103.

³ Op. cit., Lectures 7 and 8.

destroyed, a reflex vascular dilatation in the web of the foot may be produced by the application of an irritating substance to the web under observation. That this dilatation is due to a reflex action through the cord is evident from the fact that it does not occur after section of the sciatic nerve. He also shows that in a dog, curarized and kept alive by artificial respiration, a fall of temperature in the foot may be produced by irritation of the central end of the opposite sciatic nerve, the cord being divided in the dorsal region. On the strength of these observations, Vulpian concludes that, though the medulla oblongata exercises a powerful control over all the vaso-motor nerves of the body, it is not to be regarded as the exclusive seat of tonic and reflex vaso-motor centres. On the contrary, these centres, like those which preside over coördinated muscular movements, are distributed through the spinal cord.

A reconciliation of these different views is probably to be sought in the fact that Vulpian's conclusions are drawn from observations on the condition of the cutaneous blood-vessels as manifested by changes of temperature, while those of Owjsannikow and Dittmar are based upon determinations of the blood-tension which is affected by the condition of the blood-vessels generally, throughout the body.

In this connection the observations of Schlesinger¹ are of interest. This observer, experimenting on rabbits curarized and kept alive by artificial respiration, finds that section of the cervical cord does not prevent a reflex rise of blood-tension as the result of irritation of a sensitive nerve, provided that the animal is poisoned with strychnia, though without this poison the reflex phenomenon does not manifest itself. Now, the known action of strychnia being to increase the irritability of the centres of muscular movement lying in the spinal cord, the conclusion seems probable that vaso-motor centres also lie in this region, but that it is only when their irritability is increased by strychnia that these centres can, through stimulation of sensitive nerves, be brought into a sufficient degree of activity to produce any perceptible change in the blood-tension.

Budge, also, in his report of experiments showing that irritation of the crura cerebri causes a rise of blood-tension,² expresses the opinion that this effect is due to a reflex stimulation of vaso-motor centres in the spinal cord, through sensitive fibres lying in the crura cerebri.

With regard to the situation of the "vaso-dilator," as distinguished from "vaso-constrictor" centres, there is little that can be stated with positiveness. Only in the case of the *nervi erigentes* has a definite "vaso-dilator" centre been demonstrated. This is to be found, according to Goltz,³ in the lumbar region of the spinal cord, the proof being

¹ Wiener medicinische Jahrbücher, 1874, i., page 1.

² Pflüger's Archiv, vi., page 303.

³ Pflüger's Archiv, viii., page 460.

that in dogs, after division of the cord between the dorsal and lumbar regions, friction of the glans penis causes an erection, while after destruction of the lumbar cord no such reflex effect can be produced. A strong irritation of the sciatic nerve produces an inhibitory effect upon this "vaso-dilator" centre, so that during the continuance of the irritation, friction of the glans penis remains without effect. This centre can also be stimulated and inhibited by nerve-fibres coming to it from above, as is proved by the observations of Eckhard¹ that the irritation of certain parts of the brain will produce an erection, and by the fact that section of the dorsal cord favors the production of an erection by peripheric irritation, as, for example, by friction of the glans penis.

VASO-MOTOR NERVES OF LUNGS.

Recent observations of Badoud² seem to show that the blood-vessels of the lungs are kept in a state of very moderate tonic contraction under the influence of vaso-motor nerves. This observer, working under Fick's directions, measured the blood-tension in the right ventricle of dogs by means of a glass tube introduced through the jugular vein. The tension in the right ventricle during the systole is, of course, the maximum tension which can prevail in the pulmonary artery. The tension in the carotid artery was measured at the same time by a spring manometer. Section of the cervical cord was found to cause in the pulmonary circulation a considerable, and in the systemic circulation a much greater diminution of blood-tension. This shows that the normal tonicity of the pulmonary arteries is less than that which prevails in the systemic circulation. Irritation of the cord caused a rise of blood-tension in both the pulmonary and the systemic circulation, the rise in the former system of vessels being so great that it could not be regarded as a secondary effect of a contraction of the systemic arteries forcing the blood back upon the lungs, but indicating rather the existence of vaso-motor nerves in the pulmonary vessels themselves.

¹ Beiträge zur Anatomie und Physiologie, vii., page 69.

² Ueber den Einfluss des Hirns auf den Druck in der Lungenarterie. Würzburg. 1874.