

bears the name of superficial cardiac plexus. They are closely connected with each other and give off:

1. The right or posterior coronary plexus, accompanying the right coronary artery.
2. The left or anterior coronary plexus, accompanying the left coronary artery.

Filaments of these latter plexuses ramify under the pericardium.

Microscopical ganglia, which might perhaps be classed among the peripheral plexuses (homologues of Auerbach's and Meissner's plexuses in the wall of the intestine) (see the second foot-note on p. 581), occur in the nerves of the auricles and in the course of the coronary plexuses. The ramifications of the latter give rise also to the terminal plexuses which Gerlach has described as the "Grundplexus," and which, according to the recent investigations of von Openchowski, give off terminal fibres to the muscular fibres. Van Gehuchten has observed, by employment of the method of Golgi in the nerves of the heart of new-born white mice, a very abundant interlacing network between the nerve fibres of the muscle cells of the ventricle walls, but he has not been able to follow fibres of the peripheral ganglia. This same richness of fibres in every portion of the myocardium has been observed by Hymann and Demoor. The myocardial nerve filaments have also been beautifully demonstrated in the frog's heart by Strong.

II. SOLAR OR EPIGASTRIC PLEXUS.—This plexus lies in front of the aorta and of the pillars of the diaphragm, between the right and left suprarenal bodies, and surrounding the origin of the celiac and superior mesenteric arteries. It is the largest one of the three prevertebral plexuses, being supplied by the large and small splanchnic nerves and some branches of the pneumogastric. From the solar plexus smaller plexuses branch off, accompanying the principal visceral arteries of the abdomen, and thus forming the diaphragmatic, celiac, mesenteric, and other plexuses.

1. *Semilunar Ganglia (Solar Ganglia, Celiac Ganglia, Abdominal Brain).*—The two principal ganglionic masses of the solar plexus are the left and right semilunar ganglia, which are situated in the interstice between the suprarenal bodies, being connected with each other by a ganglionic and fibre lacework twining around the origin of the celiac and superior mesenteric arteries.

The lower part of these ganglia, usually detached from the remainder, is known as the aortico-renal ganglion, in which the small splanchnic nerve terminates, and which supplies the greater part of the renal plexus. Another part, lying below and to the right of the origin of the superior mesenteric artery, is named the superior mesenteric ganglion. The formation of the following plexuses is contributed to by the solar and other plexuses and by branches of the cerebro-spinal nerves.

2. *Diaphragmatic or Phrenic Plexus.*—This is situated along the arteries at the lower surface of the diaphragm and is derived from the upper part of the semilunar ganglion. It is also supplied by the phrenic nerves. On the right side this plexus contains a ganglion which marks the junction of the phrenic (cerebro-spinal) and the sympathetic fibres. It gives filaments to the diaphragm, to the vena cava, to the suprarenal body, and to the hepatic plexus.

3. *Suprarenal Plexus.*—The nerves to this plexus emanate from the solar plexus, chiefly from the outer part of the semilunar ganglion, but the plexus also receives some filaments from the diaphragmatic plexus and from one of the splanchnic nerves. It is beset with minute ganglia.

4. *Renal Plexus.*—The chief supply of this plexus is from the aortico-renal ganglion, but the solar and aortic plexuses, the smallest splanchnic nerve, and sometimes the small splanchnic nerve, as well as the first lumbar ganglion, furnish also filaments. Ganglia of different sizes (renal ganglia) are met here. The plexuses of both sides give off twigs to the spermatic plexus and a filament to the urethra. The plexus of the right side supplies some filaments to the vena cava.

5. *Spermatic Plexus.*—This is derived for the most part from the renal plexus, and receives in addition some filaments from the aortic plexus. In the male it follows the spermatic artery and supplies the testis, a small spermatic ganglion being frequently found in its course. In the female it accompanies the ovarian artery and is distributed to the ovary and uterus.

6. *Celiac Plexus.*—This large plexus, derived from the solar and situated in a kind of fenestrated sheath, surrounds the celiac artery. It subdivides with the artery into stomachic, hepatic, and splenic plexuses, which, following the respective blood-vessels, supply the stomach (coronary and pyloric plexuses), the liver (hepatic plexus), the gall bladder (cystic plexus, derived from the hepatic), the pancreas and duodenum (pancreatico-duodenal plexus, also chiefly from the hepatic), and the spleen (plexus splenicus, or lienalis). These plexuses anastomose with each other, with the mesenteric nerves, and with the suprarenal plexus. All of them receive additional supply from the pneumogastric nerve.

7. *Superior Mesenteric Plexus.*—This plexus is derived chiefly from the lower part of the solar plexus and from the superior mesenteric ganglion, receiving also fibres from the right pneumogastric at its junction with the celiac plexus. Following the course and distribution of the superior mesenteric artery, this plexus divides into subplexuses named after the respective vessels, which subplexuses finally pass upon the intestine along the line of attachment of the mesentery. A large number of the filaments terminate between the two layers of the mesentery in so-called Pacinian corpuscles. These are cerebrospinal fibres. In the wall of the intestine the peripheral plexuses (Auerbach's and Meissner's) are formed.

8. *Aortic Plexus.*—The aortic or intermesenteric plexus (plexus aorticus abdominalis) is arranged along the abdominal aorta between the origin of the superior and that of the inferior mesenteric artery, mostly in the form of two lateral cords, which are connected above with the semilunar ganglia and renal plexuses, and in front with each other by communicating branches passing in front of the aorta. The plexus is also supplied from some of the lumbar ganglia. It continues on the inferior mesenteric artery to form the inferior mesenteric plexus. The latter is connected with the inferior mesenteric ganglion, placed below the origin of the artery. The aortic plexus furnishes also part of the spermatic plexus. It gives some filaments to the inferior vena cava, and ends below in the hypogastric plexus.

9. *Inferior Mesenteric Plexus.*—This plexus, springing mainly from the left lateral part of the aortic plexus, clusters around the inferior mesenteric artery. It supplies the left or descending and the sigmoid colon, and the rectum. Its colonic branches anastomose with the middle colonic branches of the superior mesenteric plexus. Other branches connect in the pelvis with the pelvic plexus.

III. HYPOGASTRIC PLEXUS.—The hypogastric plexus, destined for the supply of the viscera of the pelvis, is a flat plexiform mass situated in front of the lowest lumbar vertebra, between the two common iliac arteries. It is the downward continuation of the two cords which form the aortic plexus, and it receives a considerable supply of branches from the lumbar ganglia. Below, it bifurcates to form the pelvic or inferior hypogastric plexuses.

The inferior hypogastric or pelvic plexuses, one on each side, are derived from the hypogastric plexus. They lie by the side of the rectum, and of the vagina in the female. After descending a short distance, they receive branches from spinal nerves, namely, the third and fourth and sometimes the second sacral, and from the sacral ganglion of the sympathetic.

The plexus ramifies with and along the branches of the internal iliac artery, forming the hemorrhoidal and vesical nerves which are common to both sexes, and other nerves or plexuses special to each, viz., in the male, for the prostate, vesiculae seminales, and vas deferens; in the female, for the vagina, uterus, ovaries, and Fallopian

tubes. Accordingly, the following plexuses can be distinguished:

1. *Hemorrhoidal Plexus.*—Originating from the upper part of the pelvic plexus, this plexus anastomoses with the nerves (superior hemorrhoidal) which descend with the inferior mesenteric artery and penetrate the coats of the rectum.

2. *Vesical Plexus.*—The nerve plexuses of the bladder are continued from the lower part of the pelvic plexus and are placed chiefly on the lower surface of the bladder. Besides supplying the latter, they furnish nerves to the vas deferens and to the seminal vesicle.

3. *Prostatic Plexus.*—Situated between the prostate gland and the levator ani, this plexus supplies the prostate and the seminal vesicle in the form of the nervi cavernosi or erigentes. It is then continued forward to supply the erectile substance of the penis.

4. *Vaginal Nerves.*—These nerves, derived from the lower part of the pelvic plexus, proceed directly to the vagina.

5. *Nerves of the Uterus.*—According to Foote and Chapman, from whom the description here following is taken,* the uterus has a double nerve supply, namely, from the uterine and from the ovarian plexus. The uterine plexus, they find, is formed by the union of the hypogastric plexus with the sacral sympathetic cord. At this point of union there is a cluster of small ganglia called the ganglion cervicale of Frankenhäuser, situated upon either side of the cervix just at its junction with the vaginal wall. From this point the plexus spreads out fan-like, following and encircling the branches of the internal iliac artery. It distributes its branches to the uterus, vagina, rectum, bladder, ureter, broad ligaments, and pelvic fascia. The branches to the uterus are few in number and supply the lower uterine segments, being composed mainly of fibres from the third sacral nerves. Thus far no fibres from the uterine plexus have been found to enter the uterus above the internal os, unless some of its branches, passing to the broad ligaments, enter the uterus after uniting with the branches of the ovarian plexus. As yet this is undetermined.

The uterine plexus receives its connections with the spinal cord from the third sacral nerve, with some branches from the fourth, and at times from the second. The hypogastric portion of the plexus also has spinal connections through the rami communicantes of the first and second lumbar ganglia of the sympathetic.

The ovarian plexus is derived from the renal plexus and the upper aortic. These plexuses derive their fibres from the solar plexus upon the left side, and from the solar and hepatic plexuses on the right. The connections passing from the plexus to the central nervous system are along the following paths: 1. Through the rami communicantes of the lower dorsal nerves. 2. The greater and lesser splanchnics. 3. The pneumogastric.

The ovarian plexus receives its filaments from the

vagus through the renal plexus, from which it is probably derived. The uterine plexus has merely a spinal connection.

Chapman and Foote conclude that of the two plexuses described the ovarian is the controlling nerve supply to the ovary, tube, and uterus, and the path along which are conveyed the most important stimuli passing to these organs.

HISTOLOGY.

In discussing the histology of the sympathetic nervous system, it has been found convenient to divide the structures of the same into two groups, namely, first, the components of the sympathetic chain; second, the components of the nerve plexuses of the sympathetic and of the terminal mononuclear ganglia.

Histology of the Cords and Ganglia.—The nerves of the sympathetic nervous system are of variable appearance, white, gray, or grayish. The white contain proportionately a large amount of fine, white, medullated fibres; the gray a comparatively slight amount. In some parts of the sympathetic nerves the white and gray fibres run along for a considerable distance without blending, but usually after the white fasciculi have passed through one or more ganglia, the two sets of fibres become thoroughly mixed. The white fibres are about one-half the size of the gray, and measure from 2.5 μ to 3.3 μ in diameter. Most of them belong to the



FIG. 4583.—Section of Stellate Ganglion of a Normal Young Cat. Double stain (carma., Pal.); cps, pericellular capsula with nuclei; med, medullated fibres; non, non-medullated fibres.

cerebro-spinal, but part of them to the sympathetic system; at least the investigations of Huber and Dögiel speak in favor of fibres of the latter kind. Besides the fine medullated fibres, coarse ones are met with in smaller number. These Roux has proved to be for the most part, if not all, cerebro-spinal sensory fibres.

The type of cells entering into the constitution of the sympathetic ganglia forms a very important distinction between mammalia and fishes and other vertebrates; it also furnishes a point of distinction between the sympathetic and spinal ganglia in each class. In the mammalia the cells are multipolar; in the fishes and amphibia they are unipolar and bipolar. Retzius has used this fact to great advantage in allotting certain ganglia of the cephalic extremity, previously regarded as belonging to the cerebro-spinal nerves, to their proper class.

The ganglia themselves are surrounded by a thin, firm, adherent covering of connective tissue, which sends prolongations through the ganglion and divides it into compartments of different sizes and shapes. The individuality of these compartments is obscured by the fibre constituents of the ganglion. The nerve cells of the ganglion are surrounded by a pericellular capsule (Fig. 4583, cps), a membrane in which nuclei are embedded at definite intervals. It is taught by some histologists (Schultze) that this transparent capsule is continuous with the primitive sheaths of the nerve fibres. On careful examination it is seen to consist of flat epithelial-like cells, and contains a certain amount of connective tissue, probably the same as that entering into the formation of the compartments of the ganglion. In Fig. 4583, which

*The writer is indebted to these authors for a private communication of their results, part of which has not been published yet, while in part they have appeared in the form of a preliminary communication in the Brooklyn Medical Journal, December, 1901.

illustrates a piece of the stellate ganglion of a young cat (double stain: carmine, Pal.), the medullated fibres (*med*) appear as heavy black strands; the non-medullated (*non*) as reddish-brown fibres. The bundles of medullated fibres go predominantly toward the middle of the ganglion, where they undergo brush-like division. In the centre of the ganglion are seen bundles of medullated and non-medullated fibres, while toward the periphery the fibres are almost exclusively of the latter variety (fibres of Remak). Delicate bundles of these non-medullated fibres are seen passing between the constituent cells of the ganglia, particularly toward the periphery.

Fig. 4584 represents part of a sympathetic ganglion, showing the cells as they are brought out with Nissl's method of staining (methylene blue). The cells have usually one nucleus, but Huber and Bruckner observed

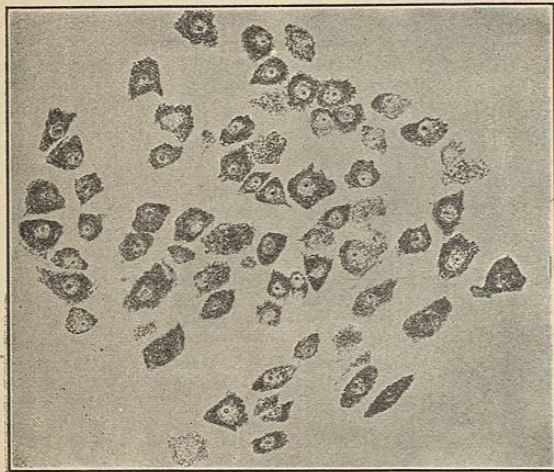


Fig. 4584.—Cells from a Part of a Sympathetic Ganglion.

cells with two nuclei, and Bruckner quotes Professor Obregia as having seen numerous cells with two nuclei make their appearance after electrical excitation. Some cells then also showed partial and others complete division. An endocellular network, apparently of the same nature as Golgi found it in the cells of the intervertebral ganglia, was observed by Veratti in the cells of the cervical ganglia of the sympathetic.

Besides nerve cells, Stilling has discovered in the sympathetic ganglia large polygonal cells, staining deeply in chromic acid and found also in the suprarenal capsules.

Each nerve cell has many protoplasmic processes of longer or shorter course that terminate not far distant from the cells of their origin, and a nervous process (axone) which goes to form a constituent of a peripheral ramus, of a ramus intermedius, or of a ramus communicans.

The variation in form and extent of the dendritic processes of the multipolar cells of the sympathetic ganglia, as seen with Golgi's method, is considerable. In some dendrites the terminal ramifications are very numerous and cluster in the shape of a basket, forming a pericellular network around other cells. This network, however, does not come in contact with the cell bodies, but lies around the capsule of the cells (Huber). Ramon y Cajal is inclined to the belief that these clusters are of great significance in explaining the functional interrelationship of the cells, a belief which is not shared by von Kölliker and van Gehuchten. Others terminate very simply and free, each one of the dendrites having a number of nodes or varicosities developed upon it. When the protoplasmic processes terminate freely among the cells of the ganglion, their ulterior ramifications are very fine and it is difficult to distinguish them from the termination in the ganglion of the nerve fibres that enter and end there.

Dogiel assumes that all cells of a ganglion are associated by means of a network formed by the dendritic processes. Some of these processes reach even into the next ganglion.

Nerve Fibres of the Ganglia of the Sympathetic Chain and Their Connections.—The nerve fibres in a sympathetic ganglion may be enumerated as:

1. Fibres of passage.
2. Fibres originating from cells of the ganglion.
3. Terminal fibres from other sources.

The ganglion may also contain collaterals from communicating rami or commissural fibres, and probably from peripheral rami, if we assume that fibres arise from cells of the peripheral sympathetic ganglia.

Most nerve fibres in passing through a sympathetic ganglion give off collateral branches, which terminate by free ramifications between and around the cells which enter into the constitution of the ganglion. In every ganglion of the sympathetic chain there are found a number of fibres that terminate there. These may be longitudinal fibres belonging to the sympathetic chain, or peripheral (centripetal) fibres arising from nerve cells of peripheral ganglia and cerebro-spinal fibres conducted by the communicans ramus (see Fig. 4576). Many of those fibres which are continued as pale fibres lose their medullary sheaths on joining with the cells of the ganglia; others pass through the proximate ganglion without relationship to the nerve cells (*fibres de passage*, see Fig. 4576), and are continued toward the peripheral distribution as fine medullated fibres; but even these lose their sheaths in passing through the distal ganglia of the sympathetic system. All these terminal and lateral ramifications produce in the substance of each ganglion a most intricate interlacement of nerve fibrillae enveloping the protoplasmic prolongations and the bodies of the cells which make up the real ganglionic mass.

Fibres that come from the roots of the spinal nerves end in arborizations within the sympathetic ganglia. According to Ramon y Cajal, they form definite pericellular networks (not confirmed by Lenhossek), which Huber finds to be always intracapsular, *i.e.*, situated within the capsule of the cell. Directly before reaching the cell around which they terminate, many of these fibres describe a number of spiral turns around the neuraxon of such cell (Huber). These fibres that pass in from the spinal roots are some of them unquestionably motor (see Fig. 4576), and take their origin, according to Kölliker, from cells of the spinal cord (denied by Dogiel).

Sala describes two types of fibres in a ganglion: (1) The varicose fibres, so called because of the tortuosity in parts of their course; and (2) the dividing fibres, found chiefly in the periphery of the ganglion. The varicose fibres are probably identical with Remak's fibres. They remain undivided. Many of them take their origin from the cells of the ganglion within which they are seen, while others take their origin in adjoining ganglia (fibres of passage), without entering into any connection with it, as they do not give off collaterals. The dividing fibres send off collaterals, the ramifications of which constitute the diffuse network of the ganglion. Sala believed that the varicose, undivided fibres are the real sympathetic fibres, *i.e.*, that they originate from cells of the sympathetic ganglia, while the dividing fibres are in reality from the cerebro-spinal system.

Langley's conclusions: According to Langley, who based his conclusions upon the nicotine experiments (quoted in the foot-note on p. 587), all the cerebro-spinal motor fibres that enter into the sympathetic nervous system terminate in one or another sympathetic ganglion by establishing connection with the constituent cells of the ganglion. The axis-cylinder prolongations of the centrifugal sympathetic fibres terminate in the muscular walls of the blood-vessels, in the viscera, or in the glands. The sympathetic ganglia are in reality the ending-place of one set of neurones and the place of origin of a second set. Each ganglion of the sympathetic trunk is to be regarded as a primary centre apart from any connections with the spinal cord. The fibres which

it sends off run in the main to the corresponding spinal nerve and follow the course of this nerve. These fibres, emerging from the ganglion as a primary centre, are connected with all the peripheral structures with which sympathetic fibres can be connected and which lie in their course, so that the function of the nerve fibres is determined by the structures in which they terminate and not by the nature of the nerve fibres. A nerve fibre proceeding from a sympathetic cell has no other sympathetic cell in its course (the cells of Meissner and Auerbach's plexuses are not considered by Langley to be types of sympathetic nerve cells). The fibres from the spinal cord to the sympathetic ganglion connect certain cells of the spinal cord with the cells of the spinal ganglia in the same way as the fibres of the pyramidal tract connect certain cells of the brain with the cells of the spinal cord. These spinal fibres become pilo-motor, vaso-motor, secretory, according as the fibres from the sympathetic with which they are connected end within the erector muscles of the hair, the muscles of the blood-vessels, or within the glands.

The medullary fibres of the ciliary ganglion have been traced by Kölliker immediately into the eyeball through the ciliary nerve into the sphincter of the iris, ending in the ciliary body.

THE MORPHOLOGICAL ORGANIZATION OF THE VARIOUS RAMI.—I. Rami internodiales.

II. Rami communicantes.

III. Rami peripherales.

I. *The Rami Internodiales* (see Fig. 4576, ramus internodialis).—The fibres that are to be seen passing longitudinally from a ganglion into a ramus internodialis are the axis-cylinder prolongations of nerve cells situated in the same ganglion or in an adjacent ganglion. In other words, these rami internodiales or interganglionic longitudinal strands of the sympathetic are made up of vertical commissural fibres, coursing longitudinally through superimposed ganglia.

II. *The Rami Communicantes.*—The rami communicantes are connected with the so-called anterior division or ramus ventralis of the cerebro-spinal nerves to which they are joined. In a ramus communicans two classes of fibres, namely, fibres conducting toward the ganglion and fibres conducting away from the ganglion, are found. (See Fig. 4576, ramus communicans.)

Of those conducting toward the ganglion, part is of centrifugal* function, being derived from cells of the spinal cord, through either the anterior or the posterior† roots; another part are possibly fibres of afferent or centripetal (sensory) function, running from a peripheral nerve through the ramus communicans into the ganglion; at least the existence of such fibres is theoretically required. Of the second class of fibres of the ramus communicans—namely, of those conducting away from the ganglion—some are centrifugal or efferent (although not necessarily strictly motor), originating from cells of that or an adjoining ganglion, and, after having joined the cerebro-spinal nerve with which the ramus communicans of centrifugal function is connected, pass within the nerve toward the periphery, reaching the latter by way either of the anterior or of the posterior division of the nerve (see Fig. 4576, ramus communicans). Others of those fibres which conduct away from the ganglion also originate from cells of the latter or of an adjoining ganglion, but on reaching the cerebro-spinal nerve do not pass toward the periphery, but into the spinal ganglion of said nerve, terminating, according to Cajal, in free ramifications around the cells of that spinal ganglion, thus transmitting the sensory or, more generally speaking, afferent impulses from the sympathetic to the cerebro-spinal system. According to Dogiel, who distinguishes two types of cells in the spinal ganglion, the said fibres terminate around cells

* *I.e.*, efferent function, usually motor but not necessarily so, as inhibitory fibres, too, may be of efferent function.

† That motor fibres are contained in the posterior roots has been demonstrated directly histologically by Lenhossek, who in the chick saw fibres which originated in the spinal cord enter into the posterior root, and indirectly, that is, by physiological experiment, by Morat, who proved the presence of vaso-dilator fibres in these roots.

of the "second" type, and the latter cells again transfer to the typical spinal ganglion cells the impulses derived from the sympathetic system.

Grossly, a ramus communicans can usually be separated into two parts, a gray ramus and a white ramus. The white ramus contains fibres passing into it from both roots of the corresponding spinal nerve, principally from the anterior root; the gray ramus contains mostly fibres destined for the periphery, although some of them are distributed to the vessels of the spinal cord and the nerve roots.

The Peripheral Rami (see Fig. 4576, ramus periphericus).—The peripheral nerves of the sympathetic nervous system are made up of nerve fibres of two kinds, medullated and non-medullated (fibres of Remak). The non-medullated or fibres of Remak form the chief constituent of the sympathetic nerves. These nerves pass into the walls of the vessels of the viscera, or into the glands of the intestinal and urogenital system. The peripheral sympathetic nerves may be classified functionally into three kinds—motor, sensory, and secretory; and probably a group of inhibitory fibres corresponds to each of these three groups.

The motor are destined to innervate the muscles of the vessels and the viscera. The motor fibres innervate also a certain number of striated muscles, such as the heart (Huber), the upper part of the oesophagus, and the pharynx. The secretory fibres go to the glands of the intestine and urogenital system, to the sweat glands, the mucous glands, etc.

The sensory fibres terminate by free ramifications between the epithelial cells of the mucous membranes or in the depths of the walls of the viscera and the vessels, or between the formative elements of the glands (Dogiel, Schematkin, Huber). When they terminate between the two layers of the mesentery, they constitute the Pacinian corpuscles.

Kölliker thinks that all the sensory fibres of the sympathetic system belong in reality to the cerebro-spinal system. Dogiel, on the contrary, it seems to us, has shown, and is confirmed in this by Huber, that in the peripheral organs which are dependent on the sympathetic there exist special nerve cells of sensory nature, whose protoplasmic prolongations terminate between the epithelial or endothelial cells, and whose axis cylinders terminate centripetally in a sympathetic ganglion in order to make connection with the cells of origin of a motor fibre, and constitute with this last a reflex nerve arc, as in the cerebro-spinal system.

The peripheral nerves of the sympathetic nervous system present a mode of distribution which is characteristic and which distinguishes them from the cerebro-spinal nerves proper. They have a remarkable tendency to unite, to interlace one with another, and to form plexuses. The nodes of these plexuses, which are frequently of considerable size, constitute the peripheral ganglia. The nerve cells themselves are of the multipolar type, and they have innumerable protoplasmic prolongations and one axis-cylinder prolongation (van Gehuchten's researches on adult cat and dog).

Histology of the Plexuses and the Monocellular Ganglia.—The ganglia of the celiac and hypogastric plexuses, the ophthalmic and sphenopalatine ganglia, and probably the ganglia of the heart are of a similar constitution to the ganglia of the great sympathetic chain. According to Ramon y Cajal, the cells have a fibre of Remak, or an axis-cylinder prolongation, which leaves the ganglion to join a ramus communicans or to form a peripheral branch passing to the organ which it supplies; and, in addition, there are the protoplasmic prolongations which end near the cells of their origin within the ganglion itself.

The peripheral ganglia (visceral ganglia of Cajal), *i.e.*, the ganglia of the intestines, the bladder, the oesophagus, etc., are composed of small multipolar cells, the expansions of which, after extensive ramifications, pass into the plexuses which terminate either in non-striated muscular fibres or in glandular cells. In addition to these they

contain, according to Cajal, fibres of passage* which are possibly the continuation of fibres from the grand sympathetic chain and collaterals which end between the nerve cells. He believes that there are no anastomoses between the visceral ganglia, the fibres of passage, or the collaterals of the visceral ganglia. Cajal describes small monocular ganglia which are found in the interstices of the glandular tissue or in the intestines within the villi; such are the interstitial nerve cells of the glands of Lieberkühn, the nerve cells of the pancreas, and those of the salivary glands. He calls these cells interstitial ganglia, in contrast with the ganglia of the order of Auerbach's and Meissner's plexuses, which he refers to as visceral ganglia, properly called.

Each gland, and perhaps each group of non-striated muscular fibres, no matter how small it may be, contains interstitial nerve cells, the expansions of which help to build up the plexus formed by the visceral ganglia and the fibres of the great sympathetic nerve.

Arnstein observed the neuraxon of a sympathetic neurone ending in smooth muscle tissue. Huber traced small branches of non-medullated fibres from some of the small ganglia found in the cat's auricle to their ending in heart muscle, and also the neuraxes of sympathetic neurones of the sublingual ganglion (Langley) to the epilamellar plexus surrounding alveoli of the gland of the same name.

In the pia mater of the brain Huber found two kinds of nerve fibres, medullated and non-medullated ones. The former he considers to be sensory and to end for the most part with their varicose, non-medullated, terminal branches in fibrous tissue—i.e., adventitia of vessels—or in the pia. The non-medullated fibres he considers to be vaso-motor nerves, forming primary plexuses in the adventitia. Through frequent branching of the fibres of the latter an interlacing network is formed. Within this plexus is formed a second one, not so well defined, lying evidently internal to the muscular coat and giving off terminal fibrils to the muscular tissue of the vessels. In the dura cerebri Huber found sympathetic nerves forming perivascular plexuses and medullated sensory nerves, terminating in the dura. It would seem that the termination of the sensory fibres at one end must spread over a relatively large area, thus precluding a finer localization of sensory impressions.

PHYSIOLOGY.

GENERAL FACTS AND FUNCTIONAL CLASSIFICATION.—It may safely be said that the sympathetic system has, to a great extent, a controlling influence over the secretion of most of the glands, the lachrymal, the salivary, the sweat glands, the glands of the stomach and intestines, the liver, the kidney, etc.; that it presides over the circulation by regulating the calibre of the blood-vessels and the action of the heart; that it influences respiration; and, finally, that all involuntary muscles, those of the digestive apparatus, of the genito-urinary system, of the hair follicles (pilomotor nerves), are under its control to such extent that, for instance, in certain mammals the bladder still continues to fulfil its function for weeks after all the cerebro-spinal motor nerves leading to it have been severed. In short, we find that all vegetative life of the organism is, to a greater or less extent, under the control of the sympathetic system. Therefore it may properly be called the vegetative nerve system *par excellence*.

In discussing the processes which are said to be under the influence of the sympathetic system, we shall subdivide the subject as follows:

- I. Secretory influence:
 - (a) Lachrymal glands.
 - (b) Sweat glands.
 - (c) Mammary glands.
 - (d) Glands of the digestive apparatus.
- 1. Salivary glands.

* Meaning fibres which only pass through the ganglion without in any way becoming connected with the cells of the latter.

- 2. Glands of the stomach and intestine.
- 3. Liver.
- 4. Pancreas.
- (e) Kidney.
- (f) Glycosuria.*
- II. Vascular functions.
- III. Cardiac functions.
- IV. Respiratory functions.
- V. Influence upon involuntary automatic motions.
 - (a) Stomach and intestines.
 - (b) Bladder.
 - (c) Uterus, etc.
 - (d) Pilomotor nerves.
 - (e) Pupil.
- VI. Tropic and tonic functions.
- VII. Reflex action of the sympathetic.
- VIII. Functional interrelation of cerebro-spinal and sympathetic systems.

I. SECRETORY FUNCTIONS.—The sympathetic system has been proven to exert its influence on the secretion of the lachrymal glands, of the glands of the stomach and intestine (including the pancreas), of the salivary glands, of the sweat glands, and on the secretion of bile and urine. We shall mention here for convenience' sake, although not really coming under this heading, the relation of certain lesions of the sympathetic to the production of glycosuria.

Matthews (1897) has recently given the mechanism of secretion a careful experimental study, and his conclusions are of such vital interest that no one can afford to neglect them in discussing the physiology of secretion. We give these conclusions in his own wording:

"There is no single mechanism of secretion. In some glands the stored metabolic products are driven out of the cells by the action of muscle, as in amphibian skin glands and sudoriferous glands; in others they are removed by currents of lymph, which are probably the result of osmosis, as in the pancreas, stomach, salivary glands; in some cases the cells imbibe water until they burst and their contents rush into the gland lumen, as in the intestinal cells of ptychoptera larvæ; in others the inner end of the cell crumbles to pieces, as in the mammalian milk glands. Two or more of these mechanisms may coexist in one gland, and it is this which has rendered the physiology of such glands as the salivary so confusing. Whether secretory nerves exist or whether secretion is ever a function of the gland cell must be considered at present an open question."

(a) *Lachrymal Secretion*.—According to Demtschenko and Wolferz, excitation of the sympathetic nerve of the neck (in cats) causes lachrymal secretion. The sympathetic lachrymal secretion differs physically from the trigeminal secretion; for the former is cloudy, and the latter clear and transparent. Bechterew and Mislawski confirm this statement of the influence of the cervical sympathetic nerve upon lachrymal secretion. They find, moreover, that both the cerebral cortex (internal parts of the anterior and posterior portions of the sigmoid convolutions) and the thalamus (circumscribed spot in the depth of its internal part at the level of the anterior portion of the gray commissure) preside over lachrymal secretion by way of the fifth nerve, partly also by way of the cervical sympathetic.

G. Fischer excited the cervical sympathetic nerve with the faradic current in the heads of two decapitated men, and found as a result considerable lachrymal secretion besides the oculo-pupillary effects mentioned on page 587. Jonnesco also found the presence of secretory fibres for the lachrymal glands in the cervical sympathetic of man, his conclusions being derived from a study of epileptics in whom therapeutically the cervical sympathetic had been cut or removed.

(b) *Sweat Secretion*.—Although it stands unquestioned that sweat secretion is under the control of the nervous system, the manner of this influence is still a matter of debate. While it seemed to have been proven by Luch-

* Taken under this heading for convenience' sake.

singer that this influence was a direct one, and not one acting indirectly, through vascular effect, his results have again been made doubtful by the recent researches of Matthews, who concludes that the sweat glands, like the salivary glands, receive a double nerve supply and probably possess a double mechanism of secretion, i.e., a muscular and an osmotic, as explained on page 582.

Vulpian distinguishes for the salivary glands secretion-exciting nerve fibres (fibres excito-sudorales), and, antagonistic to these, sweat-moderating fibres. The subject has not been followed up, however, and the physiological facts, which have thus far come to the writer's knowledge, concern only sweat-exciting fibres.

The pathway pursued by the sweat-secretory fibres in their course from the spinal cord to the sweat glands is not fully known in its whole extent. They leave the spinal cord by the anterior roots. Whether the posterior roots conduct some of these fibres has never been debated. The statements as to their further course are very diverse. All authors admit, it seems, that part of the fibres pass through the great ganglionic cords before joining the peripheral nerves, and some writers (Nawrocki and Luchsinger, and Langley) go so far as to say that all sweat fibres destined for the limbs are derived *indirectly*, i.e., through intermediation of the sympathetic nerve, from the spinal cord, a view opposed by Vulpian and later modified again even by Luchsinger as far as the hind paws of the cat were concerned.

Regarding the sweat fibres for the fore paws, views have been equally divided; Vulpian claiming on the one hand that part of the sweat fibres go directly from the spinal cord to the brachial plexus; Luchsinger, and lately Langley, contending on the other hand that all sweat fibres for the forepaw enter the thoracic sympathetic and pass through the stellate ganglion before joining the nerves of the brachial plexus.

In two cats in which Dr. Collins and myself had extirpated a stellate ganglion, sweat secretion could be produced in the fore paw of the operated side three and four and one-half months after the operation respectively, in one case by hypodermic injection of pilocarpine, in the other by instillation of the latter into the eye. In one of these two cats, when etherization was begun for the purpose of performing another operation, the struggles of the animal against being etherized produced considerable sweating of all paws except the forepaw of the side on which the stellate ganglion had been removed; this forepaw remained perfectly dry. These observations tend to throw some doubt on the contention of Langley and Luchsinger, mentioned at the end of the above paragraph, although their interpretation is by no means simple.*

For the sweat glands of the head, even Luchsinger admits both a sympathetic (fibres of the cervical sympathetic nerve) and a direct non-sympathetic nerve supply, the latter being furnished either by the spinal cord or by the oblongata. Luchsinger emphasizes the view, however, that the cervical sympathetic nerve is the principal sweat nerve for the head. (In pigs and cattle certain glands of the muzzle of cattle are the homologues of sweat glands.)

In man the presence in the cervical sympathetic nerve of sweat secretory fibres for the head was found by Jonnesco, who experimented on fifteen epileptics in whom the cervical sympathetic nerve was cut or resected for sake of treatment.

(c) *Lactal Secretion*.—Of the special influence of the nerves upon the mammary glands and upon the secretion of milk, we know only that while erection of the nipple is impossible when the spinal nerves which supply the breasts are divided, the secretion continues and is not arrested even when the sympathetic as well as the spinal nerves are severed (Foster).

(d) *Secretion of the Glands of the Digestive Apparatus*.—1. *Salivary Secretion*.† Secretion of the parotid gland

* For a detailed discussion of the question the reader is referred to the monograph by Dr. Collins and the writer. (See Bibliography.) † Claude Bernard's observations on the submaxillary gland and ganglion are referred to farther on, under the heading "Tonic Influence."

occurs not only by influence of cerebral nerve fibres, but also by that of the sympathetic nerve of the neck (von Wittich and Nawrocki). Secretory fibres for the salivary glands were also found by Jonnesco in the cervical sympathetic of man (experiments on fifteen epileptics who had the cervical sympathetic cut or removed). In their course toward the gland the secretory fibres of the cervical sympathetic become connected with the facial nerve (von Wittich).

The presence of real secretion-promoting or secretion-inhibiting fibres for the parotid gland in the cervical sympathetic nerve is denied by Jaenicke and doubted by Eckhard, the former explaining the "sympathetic" secretion of saliva purely by vaso-motor function.

Heidenhain finds (in rabbits and dogs) that parotid saliva secreted by excitation of the cervical sympathetic nerve differs from that obtained from excitation of the cerebral secretory fibres (nervus Jacobsoni) by its high percentage of organic, especially of albuminous, substances. To explain this effect—which, he says, takes place quite independently of the vaso-motor function of the sympathetic nerve—he assumes that the latter acts more through trophic than through secretory function upon the parotid.

Langley, who repeated Heidenhain's experiments, found that under the influence of excitation of the "trophic" fibres the number of granules seen in the protoplasm of the cells of the parotid gland increased considerably, while it diminished under the influence of the secretory fibres. He found, however, that in the cat the trophic fibres are not contained in the cervical sympathetic, but, on the contrary, in what is considered the cerebro-spinal secretory nerve, viz., in the chorda tympani.

In the light of Matthews' investigations Heidenhain's theories and the generally accepted trophic nerve mechanism of secretion are very questionable. Matthews concludes that the sympathetic nerve induces salivary secretion by acting on contractile tissue in the glands and thus causing a compression of ducts and alveoli; that, on the other hand, the chorda tympani or other dilator salivary secretory nerve probably causes secretion by its dilatory action on the blood-vessels, thus increasing osmosis.

2. *The Glands of the Stomach and Intestine*. The secretion of gastric juice in frogs continues for days (until death) after all connections of the stomach, except the mesentery deprived of its nerves, have been severed, showing that the centres presiding over the secretion of gastric juice are situated in the intragastric plexuses (Contejean). In these animals the pneumogastric and sympathetic nerves have a regulatory influence upon the secretion of the stomach glands.

Regarding the intestine, Moreau observed that after separation of a piece of intestine from the rest of the gut by two ligatures and severance of all nerves of the mesentery leading to it, this isolated piece of gut filled itself with an apparently abnormal secretion fluid.

The influence of special nerves upon the secretion of intestinal juice was studied by Dr. J. Collins and the writer with this result: Disturbance of digestion followed the removal of the stellate ganglion and of the lower thoracic portion of the sympathetic cord, and also the removal of a semilunar ganglion in the cat. The digestive disturbances following extirpation of the stellate ganglion were, however, more marked and more persistent than those noted after removal of the lower thoracic sympathetic. They consisted of diarrhoea and of putrefaction of the feces. The fecal matter was semicon-sistent, of yellow or dark grayish-brown color, and of exceedingly foul odor.

The putrefactive symptoms made their appearance sometimes as late as two and three months after the operations, and it was noted that the digestive disturbances had a tendency to increase, and, in two cases, persisted until the death of the animals, three and four and one-half months, respectively, after the operation. This

ganglion are referred to farther on, under the heading "Tonic Influence."