glion gives off from its dorsal ramus another nerve which runs parallel to the posterior dissepiment and gives off branches to it.

According to my reconstructions the fourth segment is a typical one. In the third segment the middle and posterior nerve leave the cord as a single nerve but soon divide into the typical middle and posterior nerves. In the second segment the same thing is found as in the third segment, although the middle and posterior nerves travel a much longer distance as a single nerve, before they break up into the the typical nerves in the second segment. In the first segment, two of the nerves take their origin from the sub-oesophageal ganglion, and one from the commissure; these nerves passing into the first segment form an anastomosis between the circular and longitudinal muscles very similar to the condition found in the other segments.

The prostomium is innervated by a large double nerve from each side of the brain. These nerves divide into numerous branches as they approach the anterior end of the prostomium.

From either side of the commissure two nerves are given off which form a network around the oesophagus and pharynx. This is very similar to the arrangement which Dr. Bristol found in *Nephelis*.

A COMPARATIVE STUDY OF THE FUNCTIONS OF THE CENTRAL
NERVOUS SYSTEM OF ARTHROPODS. A BRIEF SUMMARY
OF THE RESULTS, BY ALBRECHT BETHE.¹

Translated from the German

By W. W. NORMAN.

The brain (supraoesophageal ganglion) of the Arthropods is to be regarded first as an inhibitory organ; in addition to this it exercises a tone upon the musculature of the whole body. It is also of course a central organ for the parts of the body innervated by it. It is not however the seat of co-

¹ *Pflüger's Archiv.*, Bd. 68, p. 449.

ordination of motions (Burmeister, Lemôine and others), of direction (Fauvre), or of a general center of motions (Steiner). The animals experimented upon by me include the most distantly related forms,—species in which in reference to segmentation, and body-proportions the greatest differences prevail. In all of these forms section of the oesophageal commissures (or removal of the brain, in which naturally the organs innervated by the brain no longer came into consideration) was in no case followed by paralysis in a single movable organ. Likewise all of the more complicated reflex actions, which can be observed in the normal animal (with the exception of such as are to be regarded as having connection with both brain and ventral cord) remain after isolation of the brain, as compensatory movements of the eyes, walking and swimming movements, flying movements, turning over when placed on the back, eating, copulation, cleaning legs and body, etc. [With *Carcinus* the possibility of forward motion is lost. This is, however, a special case, which will be more fully explained in a later paper]. All motions are changed in so far as the tone of the muscles is changed from that existing in the normal animals. I am of the opinion that to this alone are due all the irregularities which appear in walking, swimming and flying. The essential point, it seems to me, is that all the reflexes are still possible (auslösbar).

The changed tone which appears on removal of the brain, is due to a general lowering of the muscular force, which may be readily observed (especially if one of the commissures be cut), in the case of *Carcinus*, *Astacus*, *Squilla*, and *Dytiscus* by the difference in pressure exerted by the muscles of the two sides against the hand of the observer. (In the case of *Carcinus* this difference was actually measured.) The changed tone may also be observed in the stronger tension of certain muscle groups over others, chiefly the flexors over the extensors. This is shown by the position of the extremities, which after the operation remain more strongly flexed than normally, especially in the coxal joints, thus causing the body to be held higher than usual and in case of section of *one* of the oesophageal commissures, or of removal of one half of the brain the

body is turned to one side (*Carcinus*, *Astacus*, *Pachytylus*, *Apis*, *Dytiscus*). The lowering of the muscular tone is, however, perhaps plainest to be seen in the case of those animals, in which the body-segments are movable against each other. Here is always to be seen a curvature of the body toward the uninjured side, when the operation is made on one side only (*Astacus*, *Squilla*, *Apis*). From this and from the fact that only the extremities of the operated side of the body are held abnormally after section of an oesophageal commissure, it follows that each half of the brain exercises a tone only or chiefly upon the same side of the body.

The above conclusion is hinted at from the changes of tone in the organs which are innervated by the brain. For example there is observed a change in the position of the eyes of *Carcinus*, *Astacus*, and *Squilla*; of the first pair of antennæ in *Carcinus*, of the second pair of antennæ in *Astacus* and *Squilla* and the antennæ in *Hydrophilus*. This change in tone is particularly well shown through the asymmetry which arises after section of one of the oesophageal commissures and extends here chiefly to the organs innervated by that half of the brain situated on the same side. Is it to be concluded from this, that the ventral cord exercises a tone upon the parts of the body situated in front in the same way as the brain does on the parts of the body situated more posteriorly? At most, only the suboesophageal ganglia could be considered since after section of the commissures behind this ganglionic mass a change in the tone of the organs of the head no longer takes place, and, further, changes of the front part of the animal (in front of the section of the ventral cord) after cross-section of the ventral cord can under no conditions be confirmed.

It has been claimed that Arthropods after removal of the brain cease to make spontaneous movements. If we are to understand by spontaneous motions that an external stimulus is not evident for the origin of the motion or for the change of one form of motion to another, then spontaneity is present in all of the Arthropods observed by me after removal of the brain. It was best demonstrated in the case of *Astacus*, where

the animal resting quietly suddenly begins the walking-movements without changing position, then stops these and begins to rub itself, etc.

The assertion that the brain of Arthropods is an inhibitory organ is supported by the following facts :

1. It was observed in almost all of the animals experimented upon, that reflex actions of an animal deprived of its brain are called forth by such stimuli as under normal conditions fail to cause a reaction.

2. The animals operated upon are in almost continual motion and rarely make a pause, while the same animals under normal conditions often remain quiet for a long time and execute movements only when there is cause. *Astacus* and *Carcinus* work the mouth organs almost unceasingly even when they have no food ; also even without the application of any stimulus. *Carcini*, *Astaci*, *Squillæ*, *Apes* and *Dystici* deprived of their brain, rub themselves by the hour, or make, even when lying on their backs, powerless walking movements. The only animal in which this was not clearly the case was the grasshopper (*Pachytylus*). Through lack of inhibitory impulses the motions of the animals are purposeless. The inhibition arising from each half of the brain extends only to the corresponding side of the body, since only upon that side of the body on which the oesophageal commissure is cut, or the half of the brain is removed appear the continued actions of the extremities. This increase in motion upon the operated side is very plainly present in all of the animals upon which I operated, indeed even in *Pachytylus* it is decidedly expressed, where extirpation of the whole brain gave no definite result. The strongest proof for the inhibition theory is the circular motion to the side of the uninjured half of the brain, which appears *always* in the case of some animals (*Pachytylus*, *Apus*), frequently in the case of others (*Astacus*, *Squilla*, *Dytiscus*), after removal of one half of the brain, and which I believe must be referred solely to the freedom from inhibition on the operated side of the body.

It is not a forced movement as Fauvre and Steiner suppose; does not depend upon a center of direction (Fauvre) situated in the brain; nor is it a general center of motion (Steiner), since after removal of the inhibition of the uninjured side through applied stimuli forward motion and even *circus* motion to the injured side may be called forth in any of the animals experimented upon except the *Brachyura* (*Carcinus*), in which here the *circus* motion to the right or left (toward the uninjured side) is a forced one. This rests on the fact that upon the operated side the lateral motion becomes impossible, and forward motion appears in its stead, while the legs of the uninjured side continue to go sideways.

3. In the case of animals with negative phototropism it was established that this property is lost after longitudinal splitting of the brain (*Carcinus*, *Astacus*, *Hydrophilus*). As for *Carcinus* the same effect could be produced by removal of the globuli.

4. The mouth ganglia (suboesophageal ganglion) are in no arthropods (that I have investigated) the seat of all co-ordination of motion. In the case of *Astacus* and *Carcinus* they play the greatest rôle; here *progressive motion*, the possibility of holding the body on its legs, or of turning over when placed on its back are all lost. Paralysis, however, is not caused in a single segment of the posterior animal, and other complicated reflex actions as the motions of eating, of cleaning body and legs, etc., are still retained (*Astacus*, *Carcinus*). The effect of the removal of the mouth ganglia is not so marked in *Squilla*, *Pachytylus*, *Apis* and *Hydrophilus*. *Progressive motion* is still possible for *Squilla*, and in addition that of turning from the dorsal to the ventral position for the other three; the *wing movements for flying* in the case of the grasshopper and the bee; the reflex actions of swimming in the case of *Hydrophilus*, and of jumping in the case of *Pachytylus*; that is to say, all that the posterior animal is able to do is retained,—only there is in general a certain awkwardness and feebleness in the mentioned activities.

5. The degree of independence of the individual thor

acic ganglia, appears to vary for different animals. Only *Astacus* and *Hydrophilus* were more accurately studied as to this point. For *Hydrophilus* the three thoracic ganglia are equally coordinated centers, each being the center for the various reflex actions of the corresponding segment. On the other hand, in the case of *Astacus*, when the ventral cord is cut through between the first and second pair of walking legs there is a greater loss than when the section is made just behind the mouth ganglia; there is not only the loss of progressive motion, but also the movements of feeding. All other movements, particularly those of flexion and extension are localized in the ganglia of their respective segments.

6. Section of the transverse commissures between the halves of one or more ganglia produces no paralytic effects; for example, longitudinal section of the brain of *Carcinus*, *Astacus*, *Apis*, *Dytiscus*; similar sections of the thoracic ganglia of *Astacus* and *Carcinus*. It follows from this, that the motor elements for each half of the body lie in the corresponding halves of the ganglia, or at least that all the motor impulses to a muscle in no case make a total crossing in the ganglia.

7. The influence which the brain or any part of the central nervous system exercises upon the parts lying more posteriorly is conducted along one side only of the ventral cord, i. e., no crossing through the transverse commissures. (If a longitudinal commissure is cut through, the symptoms appear only along one side of the animal—*Astacus*, *Hydrophilus*).

8. A stimulus from the brain along the ventral cord is conducted with a local signal, i. e., so that a locally (or definitely) directed reaction follows, *only* through the oesophageal commissure of the stimulated side.

9. The transverse commissures of the brain can conduct impulses to the longitudinal commissure of the other side and thus to the ventral cord, but not in such a way as to bring about a definite reflex action; and even then the stimulus must be very strong.

10. It may be concluded from the experiments on the crayfish (*Astacus*), which have been in part confirmed upon

Carcinus and *Hydrophilus* that (a) an impulse can be conducted along the entire length of the ventral cord along one side only, i. e., through the longitudinal commissure of the side receiving the stimulus in such manner as to call forth a locally (definitely) directed reflex action. (b) The transverse commissures of each ganglion are the only paths along which an impulse calling forth a locally directed reflex action can be transmitted from the stimulated side to the other one.

THE FUNCTIONS OF THE OTOCYST. A REVIEW.

By E. P. LYON.

Up to the year 1887 it was generally believed that the otocyst as found in invertebrates was an organ of hearing. The resemblance of the capsule, with its sensitive hairs and otolith, to the ear of vertebrates was the main ground for this belief. Indeed "the otocyst was regarded as a reduction or rudimentary state of the membranous labyrinth." After the development of a definite theory of equilibrium and geotropic functions for the vertebrate ear, it was natural to expect that similar functions were subserved by the invertebrate otocyst. Some of the work which has been done in support of this view I shall briefly review.

I. The first paper, that of Delage, *Sur une Fonction nouvelle des Otocystes*, appeared in the *Archives de Zoologie Expérimentale et Générale* in 1887.

After trying mollusks of various kinds with little success, he turned his attention to crustaceans. A description of the behavior of two species will be sufficient to serve as a general index of Delage's work. The schizopod *Mysis* has its otocysts in the inner plates of the four-parted tail. The cysts could therefore be removed with ease. On account of their distance from the more delicate parts of the central nervous system the operation would seem likely to be free from severe shocks and