MUSCLE TENSION AND REFLEXES IN THE EARTHWORM.

By A. R. MOORE.

(*From the Physiological Laboratory of Rutgers College, New Brunswick.*)

(Received for publication, November 20, 1922.)

I.

It was first shown by Friedländer[1] that a decapitated piece of earthworm would perform normal peristalsis, with perfect coordination between the segments, if it were pulled forward over a rough surface. This experiment proved that the brain was not necessary to locomotion but did not clearly decide the question as to whether the impulse to movement was given by sensory stimulation of the integument in contact with the surface or by tension of the muscles themselves as the result of pulling.

The first possibility, namely, contact stimulation of the integument, has been shown to be sufficient cause to initiate peristalsis in a suspended preparation of the worm.[2] On the other hand, if sensory stimulation of the dermal layer could be avoided it would be possible to test the value of muscle tension alone as a cause of peristalsis. For this purpose it is only necessary to put the worm into an M/8 solution of $MgCl_2$, allowing it to remain until there is no response to the stroke of a moist camel's hair brush. If a piece of suitable length be cut from the median portion of the worm and arranged in the usual fashion for making a kymographic record, the effect of tension in initiating peristalsis can be demonstrated. It should be noted at the outset that no spontaneous contractions occur and that stroking the preparation with a brush does not initiate peristalsis. Next, let a weight be attached to the lower end of the piece so as to exert a tension of 1 or 2 gm. The extension resulting from the force of the weight is immediately followed by further active extension of the worm for a

[1] Friedländer, B., *Arch. ges. Physiol.*, 1894, lviii, 168.

[2] Garrey, W. E., and Moore, A. R., *Am. J. Physiol.*, 1915–16, xxxix, 140.

few millimeters, the result of contraction of the circular musculature.[3] This movement is succeeded by strong contraction of the longitudinal musculature (Fig. 1). Alternate extension and retraction of the preparation take place as long as the weight remains or until the muscles are fatigued. It should be noted that when tension is the

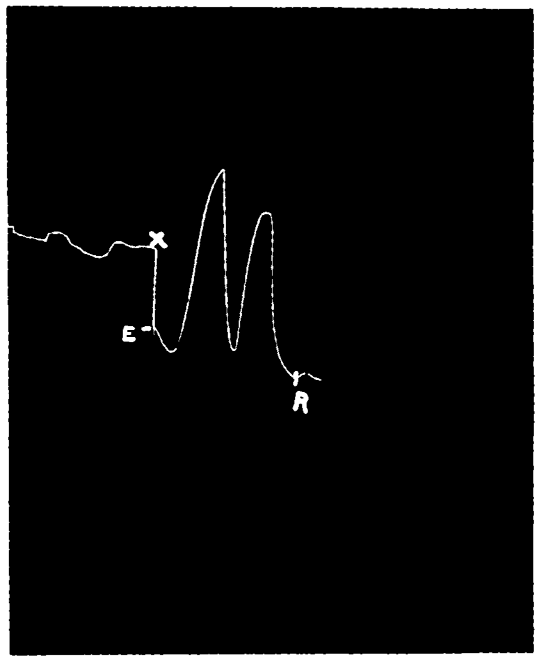

Fig. 1. The effect of tension in producing peristalsis in a piece of earthworm, the cutaneous sensory cells of which had been anesthetized by $MgCl_2$. *X* indicates the point at which the weight of 1 gm. was applied; *E* shows the beginning of the phase of active extension; *R* shows the point at which the weight was removed. Contraction is shown by upstroke; relaxation by downstroke.

exciting cause of peristalsis the first phase of the wave is extension; but if dermal stimulation is the exciting cause, extension is the first phase of peristalsis only in case stimulation is applied at the anterior end of the preparation. If the sensory stimulation be applied at the posterior end, the first phase of peristalsis is a shortening.[4]

[3] See also Biedermann, W., *Arch. ges. Physiol.*, 1904, cii, 487.

[4] Garrey, W. E., and Moore, A. R., *Am. J. Physiol.*, 1915, xxxix, 140.

It is evident that receptors for tension exist in the musculature of the worm, since, in the foregoing experiments cuticular sense cells have been eliminated by magnesium anesthesia. Tension on the nerve cord itself has no effect.[5] Since contraction of the circular muscles is the first response to passive extension, it is clear that the receptors which are stimulated by tension of the longitudinal musculature are connected by nervous paths with the circular muscles. Such an arrangement may well be the basis of the reciprocal innervation phenomena noted by Garrey and Moore[6] and by Knowlton and Moore.[7] The anatomical basis of this receptor system has been demonstrated by Dawson.[8] He has proven the existence of nerve cells of sensory type, imbedded for the most part in the ventral musculature of the earthworm. Presumably these are the neurons which act as receptors for the tension reflex just described. The results obtained by Straub,[9] Budington,[10] and Bovard[11] lend support to this hypothesis. Straub removed the ventral nerve cord from thirty segments of a worm and after 8 days tested the preparation for the tension reflex. He obtained positive results and supposed this to be the reaction of the muscle cells to their own stretching, since he afterward found no evidence of regenerated ventral ganglia. Nevertheless, Budington's work shows that the pieces of worm used by Straub must have contained some nervous tissue outside the region of the ventral cord, and that therefore Straub's results must have been the result of neuron reflexes. Budington found, on the contrary, that if the precaution be taken to remove the underlying strip of the myodermal wall with the nerve cord, it becomes impossible to elicit a reflex to stretching in such a piece. Therefore, it is evident that Straub was able to observe the tension reflex because he left the intermyal neurons intact, while Budington obtained a negative result because he took care to remove them.

[5] Garrey, W. E., and Moore, A. R., *Am. J. Physiol.*, 1915, xxxix, 139.

[6] Garrey, W. E., and Moore, A. R., *Am. J. Physiol.*, 1915, xxxix, 146.

[7] Knowlton, F. P., and Moore, A. R., *Am. J. Physiol.*, 1917, xliv, 490.

[8] Dawson, A. B., *J. Comp. Neur.*, 1920–21, xxxii, 155.

[9] Straub, W., *Arch. ges. Physiol.*, 1900, lxxix, 379.

[10] Budington, R. A., *Am. J. Physiol.*, 1902, vii, 155.

[11] Bovard, J. F., *Univ. California Pub. Zool.*, 1918, xviii, 135.

It turns out then that the peristaltic waves in Friedländer's experiment are initiated both by sensory stimulation of the integument and by stimulation of the proprioceptors of the muscle layer as the result of passive tension of the myodermal sheath. Each mechanism furnishes a reinforcement of the other and makes the essential peristalsis doubly sure.

II.

Since the musculature of the earthworm contains receptors adequate to initiate reflexes, the possibility arises that such neurons play a part in the coordination of bodily movements. Morgulis[12] has described experiments by means of which he proved that passive deflection of the posterior part of an earthworm results, when locomotion is resumed, in a turning of the anterior segments in a direction parallel to the enforced orientation of the posterior part. The reaction was demonstrated by arranging a worm so that the anterior half rested on a table and the posterior half on a movable piece of slate. Movement of the slate to the right or left caused corresponding alterations in the orientation of the anterior segments of the worm. The result in all cases was a movement of the head segments in such fashion that the line of progress was parallel to the orientation of the posterior segments. Morgulis did not attempt to analyze this phenomenon as to receptors, effectors, and neural paths.

That the effect described is the result of reflexes arising from unequal tension of the musculature rather than from cuticular stimulation is proven by the fact that specimens in which the sensory cells of the epidermis have been anesthetized with $MgCl_2$ give the characteristic response of the head segments when the posterior half of the worm is bent. This is true when the anterior half of the worm is anesthetized, or the posterior half, or the entire worm. In such cases the response is more sluggish than in the normal animal but is none the less definite. The receptors for the reaction therefore lie within the muscular wall. We are thus dealing with proprioceptors similar in function to those discussed in the first part of this paper; it is difficult to escape the conclusion that the receptors in the two cases are the same.

[12] Morgulis, S., *J. Comp. Neur. and Psych.*, 1910, xx, 616.

Furthermore, it can be shown in this experiment that the path of transmission of the impulse forward is through the ventral nerve cord, since section of the cord anterior to the zone of flexion prevents the response from taking place. The reaction can be described by the statement that passive tension of the musculature on one side of the body induces active contraction of the musculature of the same side, forward of the point under tension.[13] Since the result of the reflex is to bring the course of progress into conformity with the new position assumed by the tail, we may refer to it as a *homostrophic* reflex and the innervation concerned as *homostrophic* innervation.[14]

The next point to be determined is the distribution of the receptor system of the homostrophic reflex in the earthworm. To this end the region of passive tension was carried forward as far as practicable; namely, to the 5 to 7 segments, with the result that segments 1 to 3 showed the characteristic response. It is clear, therefore, that this receptor system extends throughout the length of the animal. The same is not, however, true of the corresponding effector mechanism. Removal of the cerebral ganglia or amputation of the anterior segments up to 15 does not interfere with the response, but removal of the anterior 20 segments destroys it for a period of about 2 weeks, after which the reflex returns. The effector system is consequently confined to the anterior 15 to 20 segments—the part of the animal which corresponds in a general way to the head and neck region of the vertebrates. It is not without interest in this connection that a limited number of anterior segments constitute a morphological head in the annelids, since it has been shown that only a certain number of head segments can regenerate. The number is characteristic for each species and varies in the phylum from 4 in *Allolobophora fœtida* to about 15 in *Criodrilus*.[15]

It has doubtless occurred to the reader that the tension reflex of the annelid described above bears a striking resemblance to similar

[13] In reversed locomotion passive unilateral tension of the head segments was without effect upon the direction of progress.

[14] From the Greek noun στροφή meaning a twist or turn as of the body in dancing or wrestling, and the Greek prefix ὁμο- signifying the same; hence *homostrophic* meaning twisting or turning which maintains progress in the same direction.

[15] Hyman, L. H., *J. Exp. Zool.*, 1916, xx, 125.

reflexes exhibited by the neck and body muscles of the vertebrates in their effect on the tension of the eye muscles. The reaction was first observed by Lyon[16] in the dogfish. He showed that if the head of *Mustelus* be held immovable while the tail is bent to the right, the result is a forward rotation of the right and a backward rotation of the left eyeball. In other words, the eyes move as if the animal were to run a course parallel to the position of the tail. This, it will be noted, is exactly analogous to the body positions assumed by the earthworm as the result of unilateral tension. Lyon further found that the reflex passed forward by way of the spinal cord, and that fin movements were not affected by passive tension of the body musculature. De Kleyn[17] has demonstrated the relation in rabbits between passive tension of the neck muscles and compensatory rotation of the eyes. He also has shown that the cervical nerves function as paths for the impulse and that the reflex occurs unvaryingly only in case the semicircular canals are removed. The fact that the eye muscles can be affected simultaneously by the homostrophic reflex resulting from bending the head, and stimulation of the semicircular canals by rotation of the animal on a turntable, has been demonstrated for rabbits by Maxwell, Burke, and Reston.[18] The experiments proved that the effect on eye movements was equal to the algebraic sum of the two forces—a clear case of the interaction of geotropism and the homostrophic reflex.

To summarize, it may be said that the homostrophic reflex plays a subordinate rôle in the orientation of the more highly differentiated forms, the greater part of the work of determining the position in space being taken over by the semicircular canals, statocysts, or light receptors. In earthworms, where geosensitive organs are absent, this form of muscular coordination must be a device of the first importance. As to the question of the relation of the homostrophic reflex to tropisms, it can be said that in general they are the complements of each other. The tropisms constitute a class of responses of the organism to external forces and the homostrophic

[16] Lyon, E. P., *Am. J. Physiol.*, 1900–01, iv, 77.

[17] de Kleyn, A., *Arch. néerl. physiol. homme et animaux*, 1917–18, ii, 644.

[18] Maxwell, S. S., Burke, U. L., and Reston, C., *Am. J. Physiol.*, 1921–22, lviii, 432.

reflex is the reaction of the animal to its own internal tensions. Consequently every turn of the body in response to a momentary external force carries with it its own correction, and the animal continues its course without great deviation. For this reason any permanent alteration of the path by reason of tropistic orientation of the earthworm can occur only when the exciting cause is a force constantly applied.

It also may be not without significance for psychology that in a comparatively simple form, such as an annelid, muscle tension profoundly affects the processes of the central nervous system, and that such tensions exert a determining effect upon a major activity of the animal—locomotion.

SUMMARY.

1. By the use of preparations of earthworm in which the cutaneous receptors have been anesthetized with a solution of M/8 $MgCl_2$, it is shown that peristalsis can be initiated by tension alone.

2. The receptors of the tension reflex are the intermyal sensory cells of the ventral region of the body wall.

3. It is concluded that Straub obtained the tension reflex because his preparations contained the intermyal receptors; Budington was unable to observe the tension reflex in any preparation from which the intermyal receptors had been removed.

4. Intermyal receptors are the receptors of the following reaction: Passive unilateral tension of the posterior part of an earthworm induces active homolateral tension of the musculature of the anterior segments, and results in the course of progress being brought into line with the enforced orientation of the tail. This reaction is termed the *homostrophic* reflex.

5. The receptors for the reaction are distributed throughout the entire length of the worm, the effectors are limited to the anterior 15 to 20 segments. The impulse is conducted by the ventral nerve cord.

6. The interaction of the homostrophic reflex and tropisms is considered.