

HOMOSTROPHIC REFLEX AND STEREOTROPISM IN DIPLOPODS.

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I.

In former papers (1, 2) by one of us, it has been shown in annelids that reflex orientation of the head segments in response to bending of the posterior part (3) is a reaction mediated by a definite neuromuscular mechanism. This reaction has been called the homostrophic reflex (1). The receptors of this reflex lie in the muscle sheath and are distributed throughout the length of the animal; the efferent nerves, on the other hand, have their origin in a limited number of the anterior ganglia, 15 to 20 in *Lumbricus*, 2 to 3 in *Nereis*. The afferent impulses travel forward by way of the ventral nerve cord. Since bending of the head has no effect on the course of backward locomotion, the reaction shows definite polarity. Attention has been called to the fact that certain vertebrates, namely fishes and rabbits, show a muscle tension reflex similar to the homostrophic reflex of annelids. Consequently, it is of interest to find how widespread is the occurrence of this type of regulatory reaction among the invertebrate phyla.

Among the arthropods, most hexapods and crustaceans present the difficulty that the body is incapable of extensive lateral movement. With the larvæ of *Tenebrio molitor* it is possible to obtain some evidence of the homostrophic reflex, but the results are not clear because of the variable tension of the abdominal musculature. Material suitable for the demonstration of the reflex is available among the diplopods, *Julus venustus*, *Parajulus pennsylvanicus*, and *Polydesmus*.

The locomotion of these animals has been studied by Clementi (4), who also considers the "spiral reflex" characteristic of them.

The "spiral reflex" involves chiefly curvature in the dorsoventral plane. He and other observers seem not to have noticed the effects of lateral tension.

II.

It can easily be shown that the effects of unilateral tension on the position of the head and the direction of locomotion in diplopods correspond perfectly with those already described for annelids. The experiments are best made in the dark room under red light, and with animals from which the antennæ have been removed. The latter operation is not necessary, but seems to increase the precision of the reaction by removing a source of tactile excitation.

If the animal is put down with the body curved in the shape of a crescent, when locomotion starts the head end moves so as to direct the course in a line very nearly parallel with the position of the tail. Records were obtained by allowing the animal to walk over smoked paper (Fig. 1, *a* and *b*). When a specimen is creeping actively, gentle bending of the tail to one side results in accurate orientation of the head region in a line parallel to that made by the tail (Figs. 2 and 3). This reflex orientation of the head also may be induced in quiescent animals by passive unilateral tension of the posterior region of the body. The zone of the body in which tension must be applied to be effective lies between the fourth or fifth segment from the anterior end and the fourth segment from the posterior end. The experiment cannot be made at the extreme limits of the body because the few segments at either end cannot be bent. It is probable, therefore, that the receptors are distributed throughout the body as in annelids.

If the ventral nerve cord is cut at any level, by means of ventral incision with a sharp needle, then the position of the head of the diplopod is not affected by bending the animal posterior to the cut. This proves that the afferent impulse is propagated over the ventral nerve cord.

Removal of the head leaves a preparation which may remain alive in a moist atmosphere for a week and which exhibits characteristic movements, even of locomotion, but no trace of homostrophic orientation is elicitable. The brain, therefore, plays the same necessary part in the homostrophic reflex of the diplopods as do the brain and

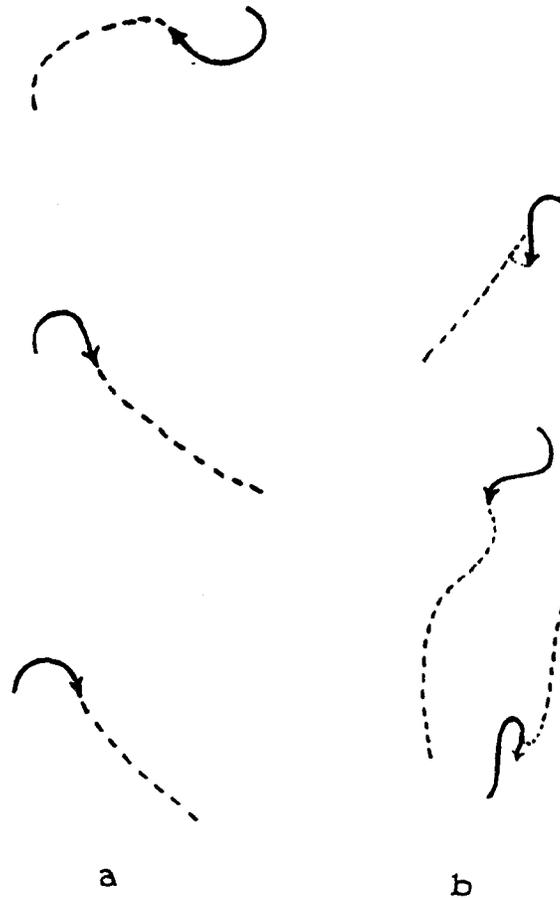


FIG. 1. *a.* Showing how the direction of progress is influenced by unilateral tension, when *Julus* is put down on a surface with the body curved. In these three cases the homostrophic bending is not so great as in some instances.

b. Instances of homostrophic orientation of the head of *Julus*, more precise than in *a.* Here the phenomenon is not obscured by the retrograde wave of body straightening.

The full line indicates initial position of the body; the dotted line shows subsequent course.

(In Figs. 1, 2, and 3 the paths indicated have been traced from records made by the diplopods upon smoked paper.)

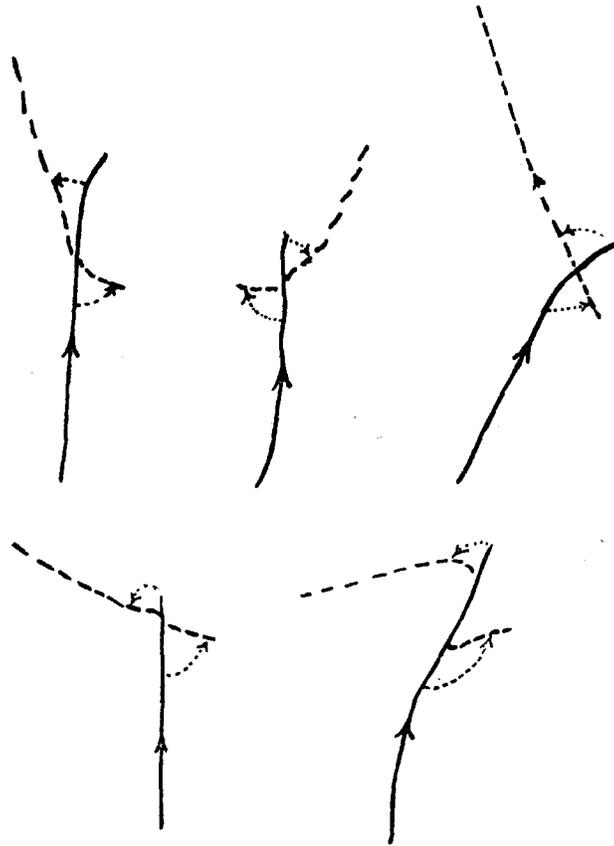


FIG. 2. The change in path of progression induced by lateral displacement of the tail. The dotted line shows the path after sideward bending of the tail.



FIG. 3. The homostrophic orientation of the head following lateral contact with an obstacle (x). The fact that the reflex may be somewhat delayed increases the appearance of "intelligent" pursuit of a straight path.

adjacent ventral ganglia in *Nereis*, and as do the anterior 15 to 20 ganglia in *Lumbricus*. It is of interest that in diplopods the first three segments behind the head which homologize with the thoracic region of the insects (4), morphologically and physiologically, do not contain the origin of the motor neurons of the homostrophic reflex.

In order to determine whether the receptors of the reflex lie in the muscles of the legs or in the body wall, the legs were clipped from the median region for about one-fourth the length of the animal. In a second experiment all the legs were removed. In the latter case, of course, no locomotion was possible, only bending of the body. In either case the homostrophic reflex follows appropriate displacement of the tail. Hence the receptors for the reflex are in the body wall.

In backward locomotion, whether of normal or decapitated specimens, enforced displacement of the anterior end does not affect the direction of locomotion. This is identical with the corresponding phenomenon in annelids, and proves the existence of similar polarity in the mechanism.

III.

There are two types of reflex response which may modify or even mask the homostrophic reflex in diplopods. First, it is frequently seen, especially when the animal is moving rapidly, that the tail may be brought into alignment with the anterior part by a sort of retrograde wave of straightening.

In the second place, stereotropism is effective in masking the homostrophic reflex, since during the time a part of the animal's body remains in unilateral contact with a surface, the head will turn in the direction of the region of contact. This may be shown in the following way. The diplopod is allowed to crawl along in contact with the edge of a triangular glass plate. Upon reaching the corner, the head deflects toward the side which is still partially in contact with the glass (Fig. 4, *a*, *b*). If, now, the glass be removed while the body of the animal is still bent, the existing curvature will cause homostrophic bending of the head (Fig. 4, *c*), although previously it was unable to do so. The case of stereotropism just described is of especial interest for two reasons.

First, the response occurs only while the exciting force is acting; *i.e.*, while a part of the body is in contact with a surface. The reaction is therefore not the result of *change*, but rather of *constant action* of the physical force.

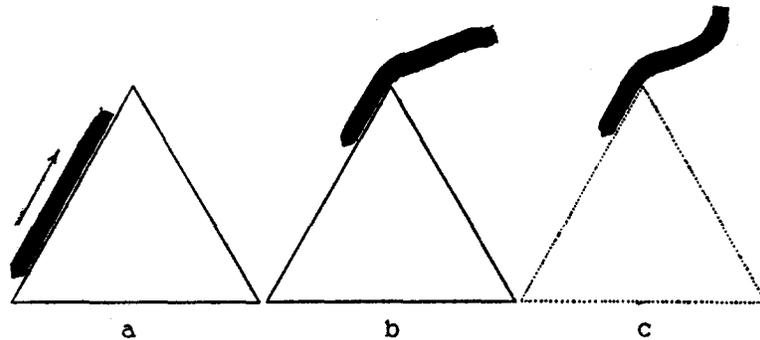


FIG. 4. Stereotropic orientation of the anterior end of *Julus*, induced by unilateral contact with a thick glass plate; *a* and *b* show successive positions. During stereotropic orientation the homostrophic reflex is inhibited, as is demonstrated by the immediate effect of removing the glass plate shown at *c*, where the head bends to a course parallel with the position of the tail.

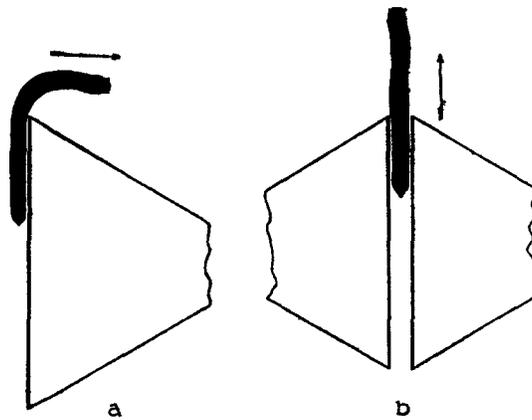


FIG. 5. Proof of the vector character of stereotropism. In *a* is shown the effect of unilateral contact upon the path of *Julus* creeping beyond the corner of the glass plate. In *b* is shown the path of *Julus* emerging from the zone of equal bilateral contact with two such plates. Balanced stimulation results in absence of bending.

Second, the response shows a vector character in that the direction of locomotion is determined by unilateral contact (Fig. 5, *a*). It should be possible, then, by producing equal contacts on the two sides, to cause the animal to creep in a straight line as it leaves the zone of contact. In fact this is precisely what happens. A diplopod is allowed to crawl between two parallel glass plates so placed that the edges just touch the animal on either side. When the animal crawls out into the open field it does not bend to either side but pursues a straight course (Fig. 5, *b*).

This phenomenon is analogous to the reaction of the tube feet of starfish to two points of contact (5). The tube feet between the two points bend at right angles to a line joining the points. This relationship of direction of movement to two sources of stimulation in tropisms was first worked out for heliotropism (6, 7). It has been proven by a number of workers that an animal which is heliotropic responds to two lights of equal intensity by moving along a path which bisects the angle formed by the lights with the organism. The reaction of a diplopod to contact stimulation of the two lateral surfaces of the body is strictly comparable to the reaction of a heliotropic organism exposed to two lights of equal intensity. In each case the organisms behave according to the law of the parallelogram of forces when the two forces are equal.

IV.

SUMMARY.

1. With suitable arthropods, such as the diplopods, it can be shown that body orientation following passive unilateral tension involves the homostrophic reflex. The phenomenon is exhibited when the animal is quiescent and during forward locomotion, but nothing of the sort appears in backward locomotion.
2. Receptors for the homostrophic reflex are in the body wall and are distributed throughout the length of the animal.
3. The effector nerves take their origin from the ganglia of the head alone.
4. The diplopods are stereotropic, the head turning toward the side in contact with a solid surface only as long as some part of the

body maintains contact. Under suitable conditions stereotropism may mask the homostrophic reflex.

5. When a diplopod is in contact with two lateral surfaces of equal extent the path upon emergence is a straight one, conforming to the law of the parallelogram of forces.

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