ON STEREOTROPISM IN TENEBRIO LARVÆ.

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I.

Proof of the tropistic character of orientation induced through lateral contact with a surface, in a creeping animal of suitable sensitivity, has been described for *Parajulus* and other diplopods (1). In view of the scant attention heretofore given to stereotropism, it is worth while to extend and to develop the proof in relation to other organisms. The conditions under which stereotropism suffers reversal of sign also deserve careful scrutiny for the sake of comparison with the known reversals of behavior in other tropistic responses.

With the diplopods it was shown that posterior unilateral contact of the creeping animal with the edge of a thick glass plate forces the head to turn in the direction of the contact. The response persists only so long as the contact is maintained. It may at any moment be brought to an end by removing the glass plate; the homostrophic response (1) due to the previously established bending of the body, immediately supervenes. Moreover, if equal areas of contact obtain on the two sides of the animal stereotropic bending fails to appear.

Precisely similar phenomena are observed with the meal worm larvæ of *Tenebrio*. Earlier attempts (1) to study homostrophy in these insects were not very successful, owing to the general increase in tone of the abdominal musculature which results from local mechanical stimulation in attempts to bend the tail of the larva to one side. Homostrophic response is easily obtained, however, by allowing the animal to creep past the corner of a thick glass plate with whose edge the larva has been in lateral contact. The observations are made in a dark room, under red light of low intensity. Fig. 1 shows the result of such an experiment.

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II.

We are concerned here merely with the facts (*a*) that a true stereotropic orientation results from lateral contact of the moving organism with a surface; and (*b*) that the orientation is dependent upon the continuous generation of stimuli derived from such contact.

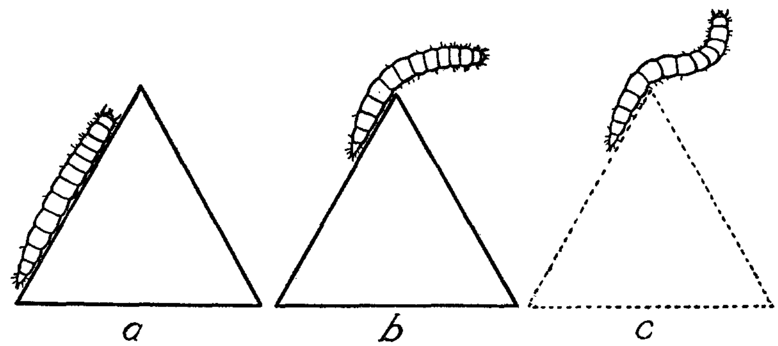

FIG. 1. Stereotropic orientation of larval *Tenebrio* (*a*, *b*, successive positions) and reflex homostrophic orientation released (at *c*) when source of contacts is removed.

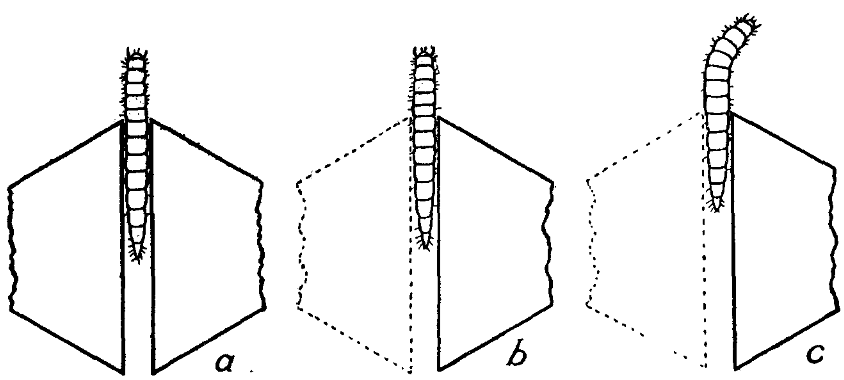

FIG. 2. Balanced action of equal bilateral contact zones shown in pursuit of a straight course (*a*). Removal of contact plate on one side (*b*) is immediately followed by stereotropic bending (*c*).

Where a *Tenebrio* larva creeps between two glass plates so arranged as to give equal contacts on the two sides of the animal, the larva on emergence from the zone of contacts pursues a perfectly straight course. The experimental manipulation is not quite so easy as with *Parajulus*, since the posterior region of the body of the *Tenebrio* larva tapers, whereas that of *Parajulus* is nearly constant in diameter. But the result, pictured in Fig. 2, *a*, is not especially difficult to observe.

The orienting influence of contact appears also in the tendency of a *Tenebrio* larva to creep over an object with which it is in lateral apposition. This it does by lifting the head and bending it sharply toward the side tactually stimulated, as shown in Fig. 3.

The responses to temporary localized contacts of sufficient area are of some special interest. If the anterior end be momentarily

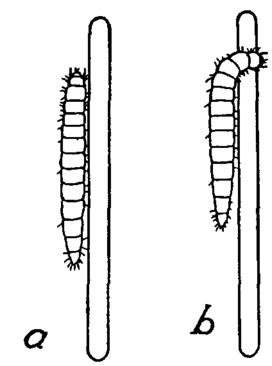

FIG. 3.

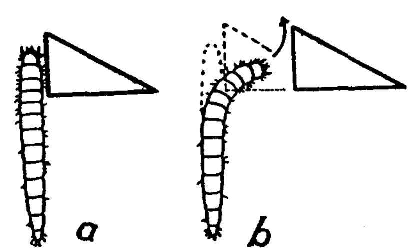

FIG. 4.

FIG. 3. A creeping larva in lateral contact with a glass rod (*a*) elevates the head and swings anterior end of the body toward the source of contacts (*b*).

FIG. 4. Stereotropic response is exhibited (*b*) after the source of contact (*a*) is removed.

touched at one side with the flat edge of a piece of glass and the glass quickly withdrawn, the head bends toward the previously existing contact. This response, illustrated in Fig. 4, is quickly followed by resumption of the originally straight path of creeping.

This particular observation shows how under certain conditions a tropistic orientation may be initiated and continued after the external inciting cause has ceased to act. In this respect the experiment gives a simple model of the phototropic orientation described for the firefly by Mast (2). As Loeb has already pointed out (3), it is of course no contradiction of phototropism doctrine, that orientation should occur after the stimulating agency has ceased to act. It is sufficient to suppose that either the peripheral sensory disturbance initiated by activation continues for an interval after the outer stimulus is withdrawn; or else, that a central nervous state is induced, in this case by unilateral contact of the head with a solid object, which persists for a detectable interval. The probable correctness of the latter interpretation is suggested by the fact that if the organism be already in a state of stereotropic activity, as in the case where posterior lateral contact is being maintained on one side only (Fig. 5, *a*), the response to a new contact surface on the opposite side of the body (see Fig. 5, *b*) is exhibited without sensible delay, resulting in an immediate readjustment of the position of the head appropriate to bilateral stimulation. From this standpoint the various stereotropic reactions seem perhaps capable of giving information as to the persistence of central nervous conditions ("physiological states") which may result from peripheral excitation.

Removal of the head of the *Tenebrio* larva leaves a preparation which fails to show either homostrophy or stereotropism. The independence of the nervous mechanisms for stereotropism or homostrophic reflex is well shown, however, by the behavior of normal larvæ creeping backward. Reversed creeping is easily obtained by breathing upon a quiescent individual; it may also be induced by illumination of a larva in lateral contact with a glass plate. In reversed creeping stereotropism is shown by the positive curvature of the posterior end of the body as it protrudes beyond a contact plate. Homostrophy is not evidenced in backward creeping.

III.

The stereotropic orientation of *Tenebrio* larvæ readily undergoes reversal of sign. The responses already described are those most usually obtained. But if a larva is creeping very rapidly, as a result of previous handling or repeated mechanical stimulation, it orients away from the edge of the glass plate instead of toward it. This is also true with the diplopods. Negative stereotropism inhibits homostrophy. Temperatures below 14°C. and starvation for several days are also conditions in which negative stereotropism tends to be exhibited.

Such reversal might be due either to a central nervous state connected primarily with the speed of creeping at the moment, or to the altered character of the peripheral stimulation. The tactile excitations responsible for the stereotropism of *Tenebrio* and *Parajulus* are due to the effect of gentle contact upon the body surface and its "hairs." Sufficiently vigorous contacts evoke negative stereotropism. In a slowly creeping larva, not in lateral contact with foreign surfaces, a gentle stroking of the body "hairs" (without touching the body surface directly) results in positive orientation of the head; more vigorous stroking leads to the bending of the head away from the side stimulated.

Reversal of response as determined by relative intensity of stimulation does not necessarily imply duplicity of sensory organs. The contact stimulation of the foot of *Chiton* (4) supplies an instance in point. Contact with a surface area of less than about 25 sq. mm. leads to local retraction of the foot, although, as shown by experiments with the part of the foot temporarily involved in a locomotor wave, positive attachment is physically possible to even smaller areas of contact; contact with a surface greater than 25 sq. mm. leads to positive attachment of the foot. The positive response to contacts sufficiently large is reversed by strychnine (5). It is sufficient, therefore, to conceive that reversal of response is due solely to central phenomena, and that a single type of peripheral receptor is involved in both positive and negative stereotropism (6). Vigorous "self-stimulation" of body hairs during rapid creeping is responsible for negative stereotropism in the arthropods studied, but the same effect may be produced by suitably stimulating the body hairs of a slowly creeping larva with a moving object; hence there is no need to suppose a special central nervous state determined merely by the fact of rapid progression.

IV.

It should be important to quantitate the stereotropic orientation in terms of the relative amounts of excitation on the two sides of the body. Experiments with this end in view have not as yet given precise results. This is due chiefly to the fact that the amount of stereotropic bending due to a unilateral contact depends a good deal upon the rate of creeping. Qualitatively, however, it is easily shown that while equal amounts of contact on the two sides obliterate the tendency to bend, unequal amounts of contact do so only partially and in proportion to the difference between the areas of contact on the two sides.

Thus in Fig. 5, *a*, the slowly creeping *Tenebrio* larva showing positive curvature with reference to one zone of contact has brought into touch with its opposite side a surface of lesser extent. A new position

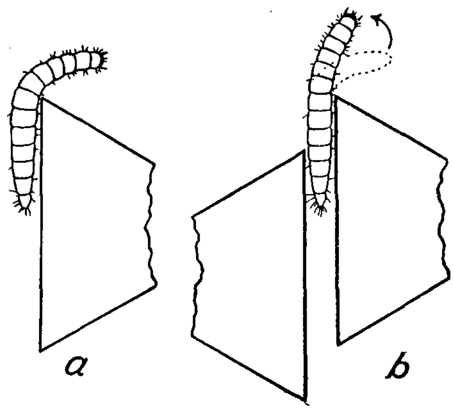

FIG. 5.

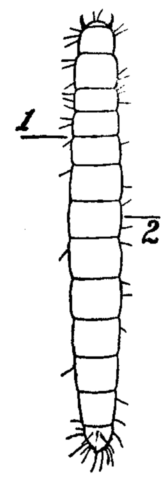

FIG. 6.

FIG. 5. A larva in stereotropic orientation toward unilateral contact (*a*) responds by lesser stereotropic curvature when a less extensive contact is introduced at the other side (*b*).

FIG. 6. Showing asymmetrical distribution of tactile " hairs." Positions of knife edges in experiments discussed in text are indicated at 1 and 2. ×2.4.

of orientation, showing lesser curvature toward the side originally stimulated, is immediately assumed (Fig. 5, *b*).

Interpretation of such experiments requires preliminary proof that the effective stimulation is not derived solely from the level of the body at which contact is no longer maintained. In the experiment illustrated in Fig. 5 it might be suggested that the animal bends most strongly toward that side on which the contact ceases nearer the head. This interpretation would presuppose that the effective stimulation is local, rather than general over the whole area of contact. But it could not then be understood why when the body is completely in contact along either side the animal should tend to come to rest, which with *Tenebrio* and especially with *Parajulus*, as with *Nereis* (7), is precisely the case. The outcome of tests in which two knife edges at different segmental levels are used to stimulate the body hairs (Fig. 6) is also unfavorable to this view. In general, a larva creeping between two knife edges placed as in Fig. 6, not too far apart, maintains a straight path. The sparse distribution of the "hairs" introduces irregularities of stimulation, however, and a better test is made with two zones of contacts beginning at the same level anteriorly but not of the same length. During ordinary creeping the result of such a test is always a bending of the head toward the side of more extensive contacts.

Experiments made to determine the orienting effect of unequal bilateral contacts were based upon the assumption that equal areas of surface would be equivalent in activating ability. Since the tactile hairs are often if not indeed usually asymmetrical (Fig. 6) in distribution, the assumption could be justified only in case this structural asymmetry is dynamically balanced. There has been in the actual trials every indication that the functional symmetry does not fluctuate with uneven distribution of the body hairs.

V.

The stereotropic response of *Tenebrio* and *Parajulus* is inhibited by light of sufficient intensity. Creeping under red light the animal persistently maintains contact with a vertical glass plate at one side. Horizontal white light of low intensity, coming through the vertical glass, does not influence the stereotropism, though adequately enforcing negative phototropism when no lateral contact is involved. At 16°C. light of about 132 meter candles intensity is required to inhibit stereotropism and to produce orientation away from a contact surface.

Bending of the anterior end toward the source of contact when the head has passed the solid surface (Fig. 1, 2) is also inhibited by light of about 132 m.c.

Photochemical inhibition of stereotropism in the tube feet of starfish was described by Moore (8). In this case an intensity of about 140 m.c., acting for 2 seconds, caused release of the terminal suckers from a glass plate.

It will be noticed that as result of this analysis it becomes possible not merely to "measure one tropism in terms of another" (9, 8), but to predict, or at least to understand, variations in the conduct of *Tenebrio* larva as determined under the simultaneous action of contact, light, temperature among external agencies, and of the homostrophic reflex of proprioceptive origin.

SUMMARY.

Larvæ of *Tenebrio* while creeping show homostrophic responses, and stereotropic orientation to lateral contacts. Homostrophic orientation is inhibited by stereotropism. Both depend upon the anterior portion of the central nervous system. Stereotropic orientation due to unilateral contact, particularly at the anterior end, persists briefly after the cessation of the contact.

Equal posterior bilateral contact of the body obliterates stereotropic bending. Unequal posterior bilateral contacts lead to orientation through an angle roughly proportional to the differences in contact areas. Functional symmetry in such responses is not disturbed by asymmetrical distribution of the body "hairs."

The stereotropic orientation undergoes reversal of direction, central in origin, when the stimulation is sufficiently intense.

Stereotropic response, leading to maintained lateral contact with a surface or to bending when the end of such a surface has been passed, is inhibited by a definite intensity of light.

These findings (1) round out the demonstration that stereotropism is truly of a tropistic character, and (2) make possible the understanding of conduct in a case involving the participation of contact stimulation, phototropism, temperature, and homostrophy.

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