STEREOTROPISM IN RATS AND MICE.

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I.

With diplopods (Crozier and Moore, 1922–23) and with larvæ of *Tenebrio* (Crozier, 1923–24, *a*, *b*) it has been 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 contact. Contact with two lateral surfaces of equal extent prevents stereotropic bending, and the animal proceeds in a straight path. It was also found, especially with *Tenebrio* larvæ, that stereotropic orientation due to unilateral contact, particularly at the anterior end, persists briefly after cessation of the contact; and that unequal bilateral contacts lead to orientation through an angle roughly proportional to the difference in areas of contact.

These observations can be repeated with a variety of forms, land isopods among others, and show the purely tropistic character of such orientations during creeping. The present experiments are concerned with rats and mice. In all essential details the results duplicate those obtained with arthropods. Their special interest lies in the fact that they demonstrate the occurrence of simple tropistic behavior in mammals. The effects of memory images (Loeb, 1918), and of the great enrichment of sensory fields and their central projections (Parker, 1922), enormously increase the number of possible responses which higher vertebrates may exhibit, and prediction of the course of movements is correspondingly restricted. In order to observe tropistic conduct in a mammal, it is necessary to deal with a type of response which dominates the animal's conduct so strongly as to exclude the influence of stimulations not directly connected with this particular aspect of behavior. The stereotropism of young rats and mice fulfills this condition.

The behavior of the young opossum at birth appears to give an instance of geotropism. After being licked free of blood and embryonic membranes, they climb "hand over hand" from the genital opening to the pouch (a distance of about three inches), and attach themselves to the teats (Hartman, 1920). "If the skin be tilted, the embryos can be made to travel upward and even *away* from the pouch for they are negatively geotropic." The postural reflexes of the decerebrated rabbit (Magnus, 1915–16) include responses which may be taken to have a basis in stereotropism. If placed on the ground with the body in an asymmetric position, the head moves to the normal symmetrical orientation even in the absence of otic labyrinths. This is prevented if a board is placed upon the animal lying in an asymmetrical position; when asymmetric contact-stimulation is equalized, the animal retains an abnormal position.

Accounts of the behavior of rats and mice (*e.g.* Vincent, 1911–12) contain a number of observations suggesting stereotropic guidance.[1] We desired to see if tropistic conduct could not be demonstrated more clearly. This is best accomplished by determining if, as in the case of invertebrates, stereotropic orientation during creeping might not obey the law of the composition of forces. In this event equal bilateral contacts should obliterate turning toward a source of contact. To rule out effects of vision and of the tactile rôle of vibrissæ, we have used animals lacking eyes or vibrissæ. It is neater, in so doing, to avoid experimental mutilation by employing individuals "operated upon" through the agency of a genetic factor, such as results in blindness. This we have been able to do.

II.

The animals used were young rats (*Rattus norvegicus*) and mice (*Mus musculus*) aged 9 to 20 days. The rats were albinos and dark-eyed young from a backcross of the King inbred albinos to hooded rats sired by King inbred males. The mice were all dark-eyed.

[1] Watson (1914, p. 424) seems to express a view generally held, that "the so-called 'stereotropism' which such animals exhibit is probably no more a case of stereotropism than is the action of a blind man in keeping near a wall or the edge of the side walk." On the preceding page, moreover, he considers it "strange" that when vibrissæ are removed from the *right* side, the rat keeps close to the *left* side of the path in a maze. *Cf.* also Przibram (1913, p. 99).

The eyes of young mice and rats are opened 10 to 14 days after birth. At first, only animals with unopened eyes were used; but it was soon found that young animals with opened eyes gave substantially the same results. Tests with rats were for the most part made in a dark room, under red light of low intensity, at 23–25°C. Experiments with mice were made at about the same temperature, but not in a dark room. Temperatures as low as 15° greatly reduce activity.

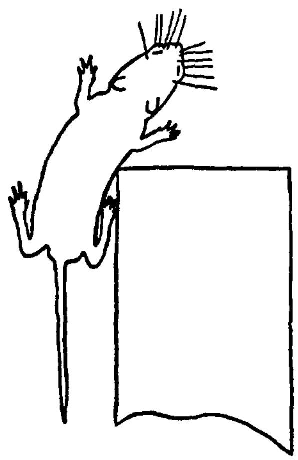


FIG. 1.

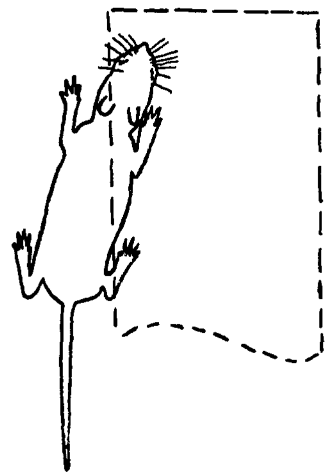


FIG. 2.

FIG. 1. Stereotropic orientation of young rat or mouse at the corner of a box along one side of which it has been creeping.

FIG. 2. A young rat or mouse has been creeping in contact with the side of a box (dashed outline); the removal of the box results in partial orientation toward that side.

Typical stereotropic behavior is observed in animals creeping or walking at a fairly rapid rate. During slow progression there is more opportunity for the lurching gait to induce movements which, while in the main of stereotropic origin, nevertheless interfere with diagrammatic orientation.

Contact with a vertical surface during creeping results in its being followed closely, and at the end of the surface bending is invariably seen toward the contact side. Depending upon the rate of creeping, the animal either proceeds at an angle with the path while in contact, or if the progression has been slow, it may turn and continue to maintain contact. Fig. 1 shows the path taken after contact with the side of a box, and at its corner. If the box is suddenly removed while the animal is creeping, there is always a swerving toward the side where the box was located (Fig. 2). Stroking one side causes turning in that direction. These results are exactly similar to those gotten with arthropods.

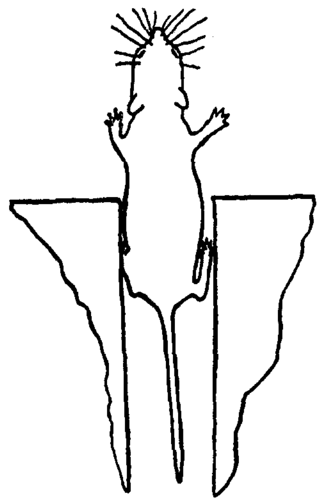
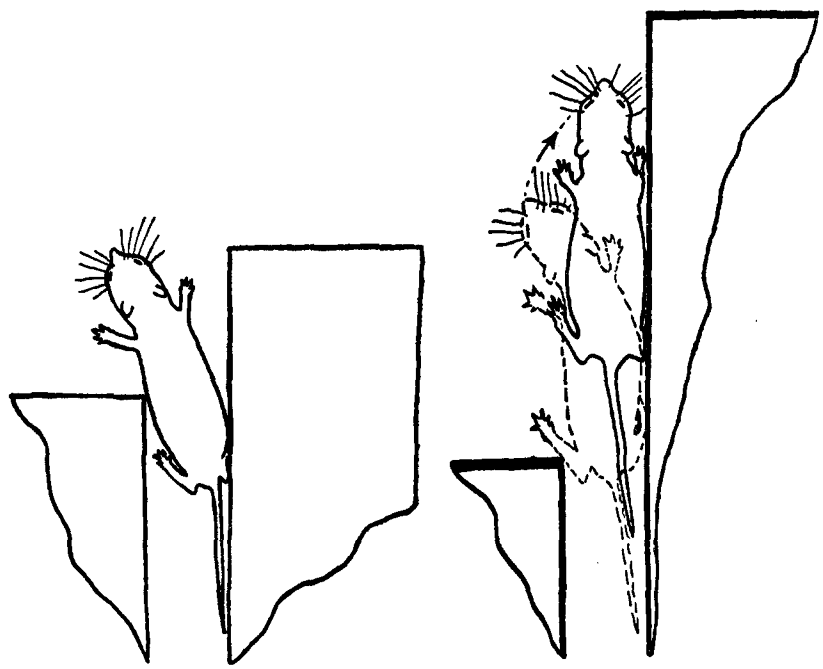


FIG. 3. A young rat or mouse creeping in a passage-way between two boxes, just wide enough to permit gentle contact on either side during the animal's swaying progression, is found to emerge from the passage-way without orientation. Equivalent bilateral stimulations prevent stereotropic turning.

When the vibrissæ have been recently cut away the creeping movements are slower and more uncertain, yet the stereotropic responses continue; several days later the uncertainty of the creeping is lost, but the animal continues to move with head held close to the floor. Removal of the tail has even less effect. Removal of both tail and vibrissæ does not materially interfere. The surface of the body and legs is thus sufficient to control stereotropism.

III.

A young rat or mouse creeping between two boxes so placed as to give equal contact on either side typically emerges from the alley-way in a perfectly straight course (Fig. 3). The bulging of the body at the level of the hind legs, coupled with the lurching gait, sometimes causes quite unequal contacts on the two sides, and this results in modification of the path on emergence. If one box is advanced beyond the other, the animal frequently emerges at an angle toward the extended



a *b*

FIG. 4. *a*. Contact at one side with the corner of a box may lead to orientation toward that side, apparently due, in part at least, to more intense tactile excitation than is provided by a continuous flat surface (or by smoothly rounded corners; see Fig. 5).

b. When such a corner is passed, orientation persists toward a continuing contact on the opposite side.

side. This angle decreases with increase of the excess contact zone on that side. If one surface extends more than the length of the body beyond the corner of the opposed box, the mouse or rat emerges at a very acute angle and then orients so as to round the corner against the surface of the more extended box (Fig. 4). This is not exactly the result obtained with arthropods and other forms, which emerge at an angle toward the side of more extensive contact. But further tests show that this at-first-sight anomalous result is due to the relatively excessive tactile stimulation provided by the sharp corners of the wooden boxes used in such experiments. The same outcome is generally observed if thick blocks of paraffin are used instead, provided they have

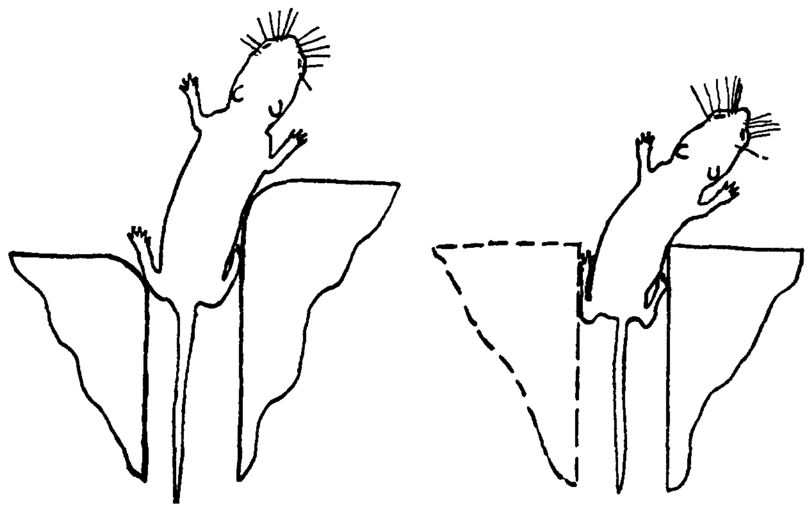


FIG. 5. FIG. 6.

FIG. 5. When blocks providing lateral contacts are of unequal extent, the young rat or mouse orients toward the side of more extensive contacts, but does not completely turn the corner unless the difference in extent of the two blocks is more than half the length of the animal. This, the expected result from a tropistic standpoint, is obtained when the corners of the contact blocks are smoothly rounded.

FIG. 6. An individual emerging from equal bilateral contacts with two boxes (*cf.* Fig. 3) proceeds in a straight path, without orientation; but if one of the boxes be removed (dashed outline), it promptly orients toward the remaining one.

sharp corners. But if the corners be smoothly rounded, the result of such tests is entirely consonant with the interpretation that stereotropic orientation during creeping varies in amplitude according to the difference in the excitations on the two sides (Fig. 5). If one of two opposed boxes providing bilateral contact at emergence be suddenly removed, the animal orients toward the remaining surface (Fig. 6).

These experiments were repeated many times, with particular effort to obviate any persistent tendency of single individuals to right- or left-hand turning.

During creeping in contact with a single vertical surface, the young rat or mouse, especially if moving very slowly, occasionally reverses direction. Observation shows that this occurs when the opposite side makes contact with the floor, as the animal falls into the "corner" between the floor and box; this is similar to the rotation of the body on its long axis observed with invertebrates creeping in the angle between a vertical and a horizontal surface. As a rule, the area of contact is then greater on the side toward the box, and orientation in this direction results in reversal of the path.

IV.

These responses have also been obtained with adult mice and rats, but visual and other sources of stimulation frequently make them much less precise.

Mice blind through hereditary defect characterized by absence of visual cells in the retina were very kindly loaned to us by Dr. Clyde Keeler of the Bussey Institution (*cf.* Keeler, 1926). The locomotion of these adult mice is much more direct than in the case of the very young individuals, and the typical stereotropic responses were obtainable with great certainty and clearness.

V.

The reactions we have described as typical are of course not exhibited with diagrammatic clearness at every trial. The more significant sorts of deviation, however, are themselves stereotropic in origin.

The stereotropism of rats and mice as observed in these experiments was always positive. Movement away from a contact surface is occasionally seen with the younger animals, but it is easily shown that this is an accidental consequence of the method of creeping. The leg muscles are not yet well developed, and the legs are disproportionately long; the body is kept fairly close to the ground and the legs are advanced in a way which cause the rather unsteady creeping act to be a succession of pronounced lurches. An occasional lunge removes the animal from a vertical contact surface, and if all contact has been lost it may creep away from it; usually, however, the residual effect of the contact surface is sufficient to cause reorientation toward it. In case complete separation from the vertical surface has not been followed by reorientation and return, test by contact with a new surface always shows that the animal is still positively stereotropic.

The swaying mode of progression may cause a young rat emerging from bilateral contacts to move toward one side. Thus in one series of trials, with five rats aged 20 days, each animal passed eight times between two vertical contact surfaces of equal extent; in another series eleven rats aged 12 to 14 days each passed five times through equal vertical contact zones; in thirty-one of the first forty tests, and in forty-four of the second lot of fifty-five tests, emergence was in a straight line; in the cases of deviation toward one side, it was seen that the divergence was due to a lunging in that direction rather than to an act of orientation.

When the animal moves at a fairly rapid rate the unilateral effects of lurching movements are more or less equalized. With older individuals the stronger legs make for a straighter course and the influence of lurching motion almost completely disappears. Thus animals about 25 days old show extremely regular reactions, as do the adult blind mice.

The chief sources of apparent irregularity in the stereotropic responses is found to lie in chance contacts of tail and especially of vibrissæ with the boxes employed to give contact surfaces. These variations are reduced by removal of vibrissæ and tail, but the slowness and uncertainty of progression subsequent to these operations introduce other complications and prevent precise measurement of the relation of unequal contact on the two sides to the angle of orientation.

VI.

SUMMARY.

Typical stereotropic orientation toward a lateral surface of contact is obtained in young rats and mice, and with adult mice congenitally blind. Removal of vibrissæ or tail or both does not essentially affect this response.

Equal contact on both sides of the body prevents orientation toward either source of contact. Unequal contact areas on the two sides leads to orientation toward the more extensive contact.

This behavior very exactly parallels the stereotropic conduct of arthropods, and thus provides a fairly complete instance of a tropism in mammals.

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