PHOTOTROPISM IN YOUNG RATS.

By W. J. CROZIER and G. PINCUS.

(*From the Laboratory of General Physiology, Harvard University, Cambridge.*)

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I.

A good deal has been written as to the limits of tropistic interpretation, particularly with regard to the behavior of higher animals such as hymenopterans and mammals. It seems to us that for any one who has seriously concerned himself with the analysis of animal conduct these discussions are for the most part extremely unsatisfactory. The study of the behavior of vertebrates has probably suffered a good deal from historically derived preoccupation with psychological questions. Perhaps the chief difficulty has been the absence of experiments likely to produce clear-cut and fruitful ideas. We are aware that to many the mere mention of "clear-cut ideas" in such connection is unpleasant. What we propose, however, is a system of analysis deliberately based upon a notion which to some would unquestionably appear a pernicious simplification. We have sought to discover well defined instances of tropistic conduct in mammals. These are of intrinsic interest. But their ultimate utility for our purpose consists in the fact that these tropisms, if found, may be brought into conflict, and the resolution of such conflicts studied under varied conditions (*cf.* Crozier, 1923–24, *a*, *b;* Crozier and Federighi, 1924–25, *a;* Crozier and Stier, 1926–27). It seems to us that the procedure of which this outline is a very bald statement should make possible a method of approach for the investigation of central nervous states otherwise inaccessible to measurement. It is a method, moreover, which frankly recognizes moment-to-moment variability in conduct, but which seeks to obtain quantitative evidence as to the nature of this variability and its physical basis.

It is necessary to find organisms capable of providing experimental results of the type required. For several reasons we have employed young rats and mice. Suitable tests have shown that they exhibit modes of behavior adapted for our purpose. And enough is known about them genetically to encourage the hope that it may be possible to utilize hereditary genes for the production of desired modifications of structural and other features.

The stereotropic behavior of these mammals has been described in a previous paper (Crozier and Pincus, 1926–27, *a*). We propose now to present proof of truly heliotropic conduct in young rats. It happens that the experiments seem not without significance for certain aspects of the general theory of phototropism. Beyond this, the occurrence of positive stereotropism and of negative phototropism during creeping makes it possible to bring these individually definite and predictable modes of response into conflict, in such a way that the animal must be guided by one form of response to the exclusion of the other, and to observe the manner in which the resolution of such conflicts may be modified. The nature of the results under these conditions will be discussed on another occasion.

II.

Conceived as a forced movement of the organism as a whole, tropistic conduct requires the presence of a preexisting mechanism, sometimes referred to as a "behavior pattern" (Child, 1924)—although this phrase may not in itself be particularly illuminating—so that the mode of response is a direct expression of the way in which the organism is constructed; and indeed there exist types of phototropic response, for example, which need not be interpreted in terms of adaptive requirements (Crozier and Arey, 1919–20). When the behavior of higher animals, such as man, is examined, attempts have been made to refer to the category of tropisms such phenomena as the guidance of movement by ideas (Royce, 1903) or by "memory images" (Loeb, 1918). Before analysis can make more than figurative headway in this direction it is necessary to discover if any simple and recognizable tropistic movements occur in mammals. The case of stereotropism has recently been discussed (Crozier and Pincus, 1926–27, *a*). The proof of geotropism is even more illuminating (Crozier and Pincus, 1926–27, *b*). To test for the presence of phototropism certain difficulties must be obviated. Complex image-forming or eidoscopic eyes, with pronounced central nervous connections, obscure potential tropistic response (Rádl, 1903; Parker, 1903; Parker, 1922, *b*). Thus the seeming positive phototropism of the young loggerhead turtle moving toward the sea (Hooker, 1911) is apparently the result merely of the retinal image of an unbroken horizon (Parker, 1922, *a*). Corresponding phenomena complicate the phototropism of imaginal insects (Rádl, 1906; Parker, 1903; Crozier and Federighi, 1924–25, *b*).

The eyes of nestling rats of the strain used do not open until the 14th day after birth. For some days before the eyelids open these animals respond to light. But during this time the eye must be regarded as a "direction eye" (euthyoscopic), not as an image-forming organ. Thus the opportunity is given to study the reactions induced by illumination, apart from the rôle of images, and apart from the effects of memory traces. The experiments may at once be controlled by opening the eyelids to discover the influence of retinal images of illuminated fields. The result shows that the closed lids provide a natural screen which precludes the formation of definite images, but which permits photic excitation.

Young rats of dark-eyed, black hooded stock were principally used in these experiments. The hooding factor produces a narrow band of dark hairs along the mid-dorsal line, which greatly facilitates the taking of graphical records of individual movements. While the eyelids are still closed the rats invariably move away from a source of light, with a promptness and precision rivalling that of a blow-fly larva. This is best seen between the ages 8 and 14 days; before the 8th day creeping is too uncertain to permit very definite orientation.

III.

One means of testing the phototropic nature of this response is to determine the character of the reaction when the animal is influenced by two sources of light. The lights used in these experiments were opposed at 180°. Young rats which start creeping on a line midway between two lights of equal intensity orient themselves in a direction perpendicular to the line joining the two lights (*cf.* Loeb, 1905; Patten, 1914). If the lights are of unequal intensity the path of oriented creeping is deflected toward the weaker light.

A black cloth, fastened to the observation table, permitted the animals to obtain a firm creeping grip. A system of circular and radial coordinates was marked in white upon the cloth, and allowed the changing position of the animal to be charted upon similarly marked record sheets. Creeping was begun near the center of the observation table, and the path was recorded until the outer marked circle had been reached. Only such complete trails were studied, the few instances being ignored in which, after very brief creeping, the animal squatted down on the cloth and refused to move. Each rat was "run" repeatedly, first with one side toward the stronger light, then the other. The intensities of the two lights were measured directly in the zone of creeping. Nitrogen-filled bulbs served as sources. The angle of orientation was measured from the charted record of each orientation test.

TABLE I.

Angles of orientation toward the weaker light, I_1 and I_2 opposed at 180°; H is the calculated effective inclination of the photoreceptive surfaces (see text).

I_1	I_2	θ	H/2
foot candles	*foot candles*		
8.0	8.0	0.19° ± 0.01	
8.0	7.0	5.98° ± 1.2	24.4°
8.6	7.0	15.8° ± 1.4	19.9°
8.6	5.7	22.4° ± 1.1	28.0°
8.6	4.6	27.9° ± 1.8	29.5°
8.6	3.9	32.2° ± 2.0	35.2°
8.2	3.4	31.1° ± 2.5	38.7°
9.5	3.1	41.0° ± 3.0	30.3°
10.3	2.9	44.3° ± 2.0	30.5°
12.0	2.67	47.4° ± 2.1	30.3°
14.0	2.65	52.0° ± 3.3	25.9°

The results of different series of experiments are collected in Table I. The consistency of the measurements of the angles of orientation, especially as seen in the small probable errors of the means, is surprisingly good.

Orientation by lights opposed at 180° should be definable (Crozier, 1926–27) by the equation

$$\tan \theta = \left(\frac{I_1 + I_2}{I_1 - I_2}\right)\left(\cot \frac{H}{2}\right) \tag{1}$$

where θ is the angle between the line of orientation and the normal to the path of the light beams, I_1 and I_2 are the intensities of the lights ($I_1 > I_2$), and H is the average angle between the photoreceptive surfaces. It has been pointed out (Crozier, 1926–27) that this angle, H, should increase if orientation becomes more precise with increasing total acting light intensity; or, on the other hand, decrease if predominantly influenced by photokinetic movements; in either case H should be very nearly proportional to log $I_1 I_2$. In this way the variation of $H/2$ with log $I_1 I_2$ gives a test of the formula,—especially since cases are available in which H does not appreciably vary at all, and for which equation (1) holds with all desirable precision. For the rats, H decreases almost linearly as log $I_1 I_2$ increases (Crozier, 1926-27). An approximate graphical illustration of the relations between θ, I_1, and I_2 may be given (Fig. 1) by using the empirical relation

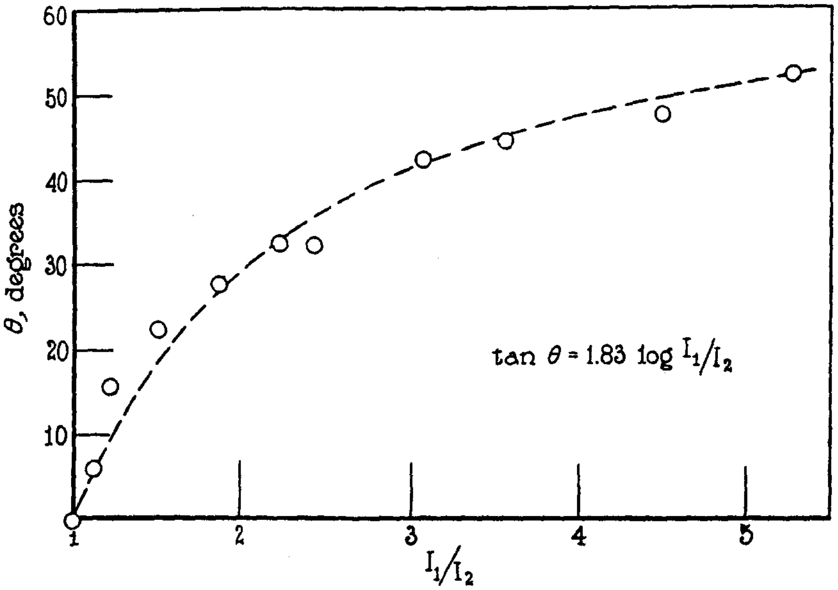

FIG. 1. The empirical formula tan $\theta = K$ log I_1/I_2 gives an approximate description of the variation in angle of orientation as dependent upon I_1 and I_2, and may be used in order to obtain a graphical representation of the results.

$$\tan\theta = K \log I_1/I_2 \qquad (2)$$

obtained by M. M. Moore (1923–24) for such cases. It has been shown (Crozier, 1926–27) why, for ordinary ranges of intensities, this may give a very fair expression of the facts.

When I_1 and I_2 are equal, the path of orientation should be normal to the line joining the sources of illumination. The experimental finding of a mean deviation of only $-0.2° \pm 0.01$ is probably within the error of the method of recording. Beyond this, the way in which θ increases as the ratio I_1/I_2 is altered shows that the orientation fully obeys the primary requirement of phototropism, for the equation (1) connecting θ, I_1, and I_2 is based simply on the theory that orientation ceases when the illumination of bilaterally disposed photoreceptors is equal.

IV.

It has sometimes been held that the results of experiments with opposed sources of light mean merely that the organism "seeks the dark". With the rat there is a rather neat way of removing this opinion, although it is obvious that the results contained in Table I should be sufficient demolition of it.

When the eyes open, a different situation results. In general, the young rats then seek the darkest region in the field of view, usually the shadows on either side of the lamp house. Older animals face the light, and creep toward the darkness at one side of it. If a young rat is placed facing the light, and at a point midway between two symmetrical zones of shade, it moves *away* from the light, in a straight line. If, however, it be placed nearer one shadow than the other it moves at once to the nearer, even moving almost directly *toward* the light to do so. If put at some distance from a lamp (say, 6 feet from a 100 watt bulb), it usually turns away from the light toward the recesses of the dark room. There seems to be a zone in which the tendency to turn away from the light and the stimulus leading to creeping toward the dark corners at the sides of the lamp house are about equalized. Thus even with the eyes opened there is still some evidence of negative phototropism, but it is clear that there is superimposed upon its simpler manifestation the positively orienting influence of darkened areas contrasting with a brighter one in the visual field (*cf.* also the results of learning tests with rats; Yerkes, 1907; Watson, 1914).

The type of response determined by the visual effect of darkness is obtained in rats kept in the ordinary illumination of the laboratory, or in those continually maintained in darkness until after the eyes have opened. It is secured at once if the eyelids are opened by operation before their normal time. This makes it possible to show directly that if the animal were "seeking the dark", in the sense in which this expression may be used with reference to vision, it would scarcely move in the way recorded in Table I.

V.

Another way of testing the occurrence of phototropism has to do with the examination of circus movements. With the young rats there are three possible ways of doing this. (*a*) One eye may be opened, at the age of, say, 12 days, the other eye remaining closed; or (*b*) one of the two unopened eyes may be covered by an opaque screen; or (*c*) one eye may be extracted.

In the first case, (*a*), care must be taken to prevent the possibility of image formation in the opened eye, by presenting a uniform visual field. When this is done it appears that the primitive phototropic effect, already noted as persisting in connection with the recently opened eye, brings it about that the rat circles slightly *toward the unopened eye.* This would result if stimulation of the opened eye were merely more intense, which is pretty certainly the case. These tests were made by illuminating prepared rats by a ring of electric bulbs suspended from a large circular metal frame, within which the rat crept. The lamps were brought within 3 feet of the creeping surface. This method is necessary to avoid shading of one eye by the rat's head, as when a single point source is used. With *high* total intensities of light (1000 m.c.) no definite circling to either side is obtainable.

The second method, (*b*), has disadvantages, because it is difficult to attach an adequate screen which the animal will ignore and which is small enough not to interfere with the vibrissæ.

The third procedure, (*c*), results in very clear-cut exhibitions of maintained circling toward the blind side. The amount of turning depends, as in *Limax* (Crozier and Federighi, 1924, *a*) upon the speed of creeping. With high intensities of illumination the rat squats more or less at one point and pivots about the strongly flexed hind limb of

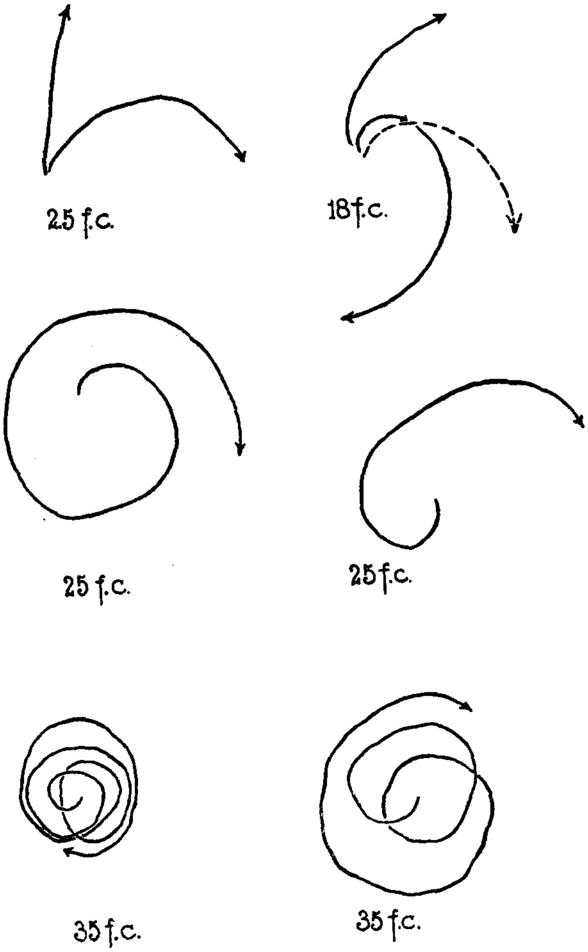

FIG. 2. Circus movement trails of young rats with one eye (the right) removed, the eyelids of the other not yet parted. Illumination from a single source, vertically above the center of the creeping stage. Intensities of the lights (foot candles) measured photometrically at the creeping stage. Scale 1:10. These trails are typical. The amplitude of the orientation movement increases with the intensity of the light. This is in part due to the fact that the animal creeps little but turns constantly. The records were obtained by following the positions of a marked spot at shoulder level on the animal's back, as seen against a system of coordinates in white lines upon a black cloth covering the creeping stage.

the blind side. More creeping movement is evident with lower intensities of light. Several typical trails of circling progression are given in Fig. 2, and fairly illustrate the type of behavior constantly observed. The postures of the legs are strikingly influenced by the light. Extensor tonus is enhanced on the photoreceptive side, and most markedly in the anterior limb; the legs of the other, blind, side are flexed, the hind leg much more so. The turning movement is brought about through the pushing effect of the extended legs, coupled with protraction by those of the blind side. The tonic effect of the light (Fig. 3) is as definite here as with insects (Garrey, 1918–19; Crozier and Federighi, 1924–25, *a*). Under continuous exposure the circle of turning broadens into a spiral, due to light adaptation. We may point out that this gives promise of providing a method for the quantitative treatment of light adaptation.

FIG. 3. The orienting posture of a rat, left eye functional but as yet unopened, right eye removed, illuminated from above.

VI.

The result of these tests is to show that the quantitative criteria supplied (1) by the action of opposed illuminations and (2) by the requirement of circus movements, agree in demonstrating the elementary tropistic nature of the movements of the rat as influenced by light. Upon this basic phototropism the image-forming capacity of the opened eye imposes certain modifications and restrictions. If one desires to employ quantitatively predictable behavior as an index instrument for analysis of conduct, it is necessary to choose experimental conditions such as permit the organism to display its capacities as a machine. The phototropism of the rat may thus be studied if the effect of visual images is avoided; and if young rats are employed, before the opening of the eyelids, there is not even a possibility of the memory of such images.

VII.

SUMMARY.

Before the eyelids have opened young rats are negatively heliotropic. They behave very much as does the larva of the blow-fly. The angle of orientation by lights opposed at 180° may be calculated by an equation based upon the elementary requirement of phototropism, namely that orientation is attained when the illumination of bilaterally disposed photoreceptors is equal. The precision of orientation decreases very nearly in proportion to the sum of the logarithms of the acting light intensities, due to photokinetic head movements. When the eyelids are opened, the rats move toward a darkened place in the field of vision, usually toward the shaded region immediately to one side of the lamp house. Therefore, when heliotropic, the rat is not "seeking the dark". The phototropism of these animals may be brought into conflict with their pronounced stereotropism, and the resolution of such conflicts may perhaps be utilized for the investigation of central nervous states.

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