THE GEOTROPIC CONDUCT OF YOUNG RATS.

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I.

If tropistic behavior is to be utilized for ultimate analysis of the inner processes controlling conduct it is quite necessary that the most complete possible mathematical expressions be found for at least several different modes of response. Only in the case of phototropism has any considerable progress in this direction been achieved. We have reference, not so much to the theory of sensory activation, as to the reasonably complete formulation of relationships between the magnitude of the excitatory intensity and the speed and extent of the induced orientation. In this respect the knowledge of geotropism, by contrast, is singularly defective.

For plants, it is found that geotropic excitation is proportional to the sine of the angle of the stimulated part with the horizontal (Fitting, 1905; Pekelharing, 1910). From the relationship between mass of attached leaf and rate of geotropic curvature in horizontal stems of Bryophyllum, Loeb (1918, 1924) inferred that the curvature was dependent upon the amount of (gravitationally directed) substance sent into the stem by the leaf. This is obviously consistent with the finding that the “presentation time” for geotropic response is directly proportional to the effective gravitational component (Pekelharing, 1910).

Quite recently the question of geotropic orientation in animals has been reexamined by Cole (1925-26), from the standpoint of the rôle taken by direct action of gravity as leading to tensions produced in muscles which support the organism’s weight. With Helix Cole was able to show that the speed of upward creeping, after orientation is accomplished, increases with the sine of the angle of inclination of the creeping surface, and thus as the active component of gravity. This leads to the view, substantiated by the effects of forcing such an
animal to carry additional loads (Crozier and Federighi, 1924–25; Cole, 1925–26), that orientation is controlled not by some statocyst function but by the differential gravitational pull upon the two sides of the body (Loeb, 1897),—a view earlier advocated for Chitons (Arey and Crozier, 1919), which lack the statocyst of gasteropods.

The information we desired to obtain for the analytical account of geotropism required data upon the amount of upward orientation in a negatively geotropic animal, and the precision of this orientation, as related to the inclination of the creeping surface. For reasons indicated in earlier papers (Crozier and Pincus, 1926–27, a, b; 1926) we have employed for these experiments young rats of known genetic history, studied during the period of about 2 days which intervenes between the 12th day after birth and the time when the eyelids opened. It happens that with these animals certain new or hitherto ignored features of the geotropic response become apparent and greatly improve the opportunities for investigation. The result seems to indicate quite clearly a direct dependence of orientation upon the distribution of the animal's weight upon the legs of the two sides of the body. Formulae are derivable describing the orientation with considerable exactness.

We regard it as an interesting fact that, for the first time, a detailed account of a tropism is possible which is based upon experiments with a mammal. This amounts to a sort of reversal of anthropomorphism, and constitutes a decided obstacle for those who would emphasize the greater "simplicity" of lower animals. The simplicity of conduct which permits the mathematical formulation of a mode of behavior is not so much a matter of zoological affinity as it is of dynamical symmetry in the organism and of the choice of experimental conditions which permit the animal to display its potentialities as a machine.

II.

In order to record trails of geotropic orientation each rat was placed upon a fine-meshed wire grid, which permitted a good foothold for creeping. When placed on the creeping plane the axis of the body was at first horizontal, or, occasionally, with the head pointing downward. The tilt of the wire surface was measured on a protractor.
The angle θ was measured when the animal had oriented and was creeping steadily. The correspondence of the wire grid to coordinate paper made it possible to copy the path upon record sheets. The path was indicated either by marking with chalk the position of the rat’s axis on the wire, or by placing a straight-edge parallel to the axis. The central stripe due to the hooding factor facilitated such procedure. The path of orientation is a straight line, as shown diagrammatically in Fig. 1, unless, after “hesitation,” the rat veers to the opposite side—in which case the angle θ is found to be the same.

Fig. 1. Diagram showing terms used in description of orientation of rats creeping upon a wire grid inclined at α to the horizontal. The position of orientation is defined by the angle θ, the active component of gravity being G sin α. As described in the text, the path A may be steadily pursued, or the animal may swing to one (B) equally inclined but in the opposite direction.

To obtain data which might be legitimately averaged it is necessary to employ rats as closely comparable as possible. Two albino rats, aged 13 to 14 days, were used in obtaining the records in Fig. 7. Those employed for the other measurements (Fig. 2, etc.) were of different stock, but litter mates. They were brothers of the seventh backcross generation of King inbred albinos with a dark-eyed stock, and were therefore practically homozygous.
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III.

The behavior of a rat creeping upon an inclined plane shows one striking peculiarity. It is well known that during the upward locomotion of at least certain negatively geotropic animals the path of progression, especially at inclinations less than 90°, may not be exactly normal to the intersection of the creeping plane with the horizontal. As the inclination is made less, the deviation from the normal increases. This is very obvious in the rats. But there is to be added the further and very important fact that when a rat, at first placed head downward, or with body axis horizontal, orients upward it does so until a certain quite definite angle has been reached, and then progresses in a straight line. If creeping becomes interrupted, the rat may show "nervous" random movements of the head. In case these are directed downward, the rat continues creeping along the previous oriented path. But should they be directed upward, locomotion may be pursued at an angle which is exactly the converse of that at first followed. Thus if the angle of orientation was at first 72° to the left, brief creeping may be seen which is more or less irregular but which becomes definite again either at 72° ± to the left, or at 72° ± to the right (cf. Fig. 1). This clearly points to the limitation of geotropic orientation by a certain threshold determined through the distribution of the gravitational effect upon the two sides of the body. We shall have occasion to return to this point subsequently.

The results summarized in Table I are derived from twenty tests at each inclination, upon each of two rats from the same litter. Individual quantitative differences undoubtedly exist between diverse genetic strains, but since we are not concerned at the moment with this aspect of the matter we have restricted our account to illustrative material free from this source of confusion. The interpretation of data upon other individuals is entirely consistent with that here detailed. The entries in Table I concern (1) the angle of inclination (α) of the creeping plane to the horizontal; (2) the mean angle of orientation in the creeping plane (θ); and (3) the measure of the variability of θ, employing for this purpose the probable error \(0.8534 \Sigma \sqrt{n} / n - 1\) expressed as a percentage of the mean.

It is apparent from Table I that the degree of upward orientation
(θ) increases steadily as the inclination of the creeping plane (α) is made greater; and also that the degree of scatter of the individual readings proportionately decreases—that is, the precision of the orientation is enhanced. The minimum inclination leading to a measurable effect lies between α = 10° and α = 15°. At 15° the variability of the measurements of θ is disproportionately high, due presumably to the fact that the threshold effect is intrinsically variable from moment to moment. At values of α > 70°, orientation is precisely upward (θ = 90°).

**TABLE I.**

The mean angles of upward orientation (θ) of young rats during creeping upon a surface inclined at angles (α) with the horizontal, and the precision of the respective mean values of θ. The precision is expressed by the probable error as a percentage of the mean (which is equivalent to the coefficient of variation).

<table>
<thead>
<tr>
<th>α°</th>
<th>θ</th>
<th>Variability of θ (per cent)</th>
</tr>
</thead>
<tbody>
<tr>
<td>15</td>
<td>32.6°</td>
<td>8.18</td>
</tr>
<tr>
<td>20</td>
<td>44.5°</td>
<td>2.27</td>
</tr>
<tr>
<td>25</td>
<td>52.9°</td>
<td>1.87</td>
</tr>
<tr>
<td>30</td>
<td>67.4°</td>
<td>1.70</td>
</tr>
<tr>
<td>35</td>
<td>64.0°</td>
<td>1.41</td>
</tr>
<tr>
<td>40</td>
<td>69.8°</td>
<td>1.18</td>
</tr>
<tr>
<td>50</td>
<td>77.9°</td>
<td>1.04</td>
</tr>
<tr>
<td>60</td>
<td>84.7°</td>
<td>0.529</td>
</tr>
<tr>
<td>70</td>
<td>88.3°</td>
<td>0.351</td>
</tr>
</tbody>
</table>

The extent of orientation (θ) is not directly proportional to the gravitational component in the creeping plane, but to its logarithm. The graph in Fig. 2 shows that the equation

\[ \theta = K \log (\sin \alpha) \]  

(1)

gives a satisfactory account of the observations; the goodness of fit is probably due to the fact that the individuals used were very closely comparable.

The extent of orientation as a function of α has been measured in certain molluscs by Davenport and Perkins (1897-98) and by Kanda (1916). In the former paper figures are given for the amount of orientation (θ), corrected for random movement, which is visible in *Limax maximus* after 45 seconds exposure upon an
inclined plane. Essentially this method was also followed by Kanda (1916), who tabulated the percentage of *Littorina* individuals oriented upward after 1 minute exposure. At best, that is with full correction for movements not directed by geotropism, this procedure can give no quantitative expression for the geotropic excitation; for we should need to have, rather, measurements of the times required to produce a given amount of orientation, expressed either as a constant angle (θ) or as a certain percentage of individuals. For this reason little can be gotten from these data. But it is perhaps significant that the amount of orientation, when expressed in this way, increases more rapidly than log sin α (Fig. 3).

**Fig. 2.** The angle of upward orientation (θ) is directly proportional to log sin α, where α is the inclination of the creeping surface. With the exception of one point, the mean values of θ do not depart from the line drawn by more than their probable errors. (The points are averages of 40 measurements.)

This could be understood if the speed of orientation, so measured, should depend upon two things, namely speed of creeping and speed of turning, and if each of these separate elements of the act of orientation (Arey and Crozier, 1921; Crozier and Cole, 1923) should be proportional to log sin α. For the data of Davenport and Perkins this is very nearly true for values of α above 15°, and for Kanda's figures below α = 67° ±, but not very much weight can be given to the result.

The speed of upward creeping is frequently governed by the intensity of geotropic excitation, and in certain instances can be measured as an index of the effect
of gravity. Cole (1925–26) has done this with Helix, and concluded that the speed of movement, after orientation is attained, varies as \( \sin \alpha \). For the rat, as we shall show presently, the velocity of upward movement decreases as \( \log \sin \alpha \) increases. Question arises as to the existence of any real difference between the two cases. We believe that there is no real difference, because Cole's data show considerable deviation from \( (K) (\sin \alpha) \) at low values of \( \alpha \), and especially for the reason that the speed measured was that of the vertical ascension. The significance of the latter point lies in the fact that the extent of the average orientation \( \langle \theta \rangle \), in the

![Figure 3](image.png)

**Fig. 3.** Curve A. Angle of upward gravitational orientation \( \langle \theta \rangle \) (corrected) for Limax, after 45 seconds; (data from Davenport and Perkins, 1897–98). Ordinate scale at the left.

Curve B. One series of measurements ("C") of percentages of oriented individuals after 1 minute (Littorina); ordinate scale at the right. (Data from Kanda, 1916.)

terms previously given), increases with \( \alpha \). Therefore the apparent speed of movement, measured as described, would probably be increased to an illegitimate extent. The data as given show that for Helix the "speed of vertical travel" increases faster than \( \log \sin \alpha \) (Fig. 4).

We have somewhat regretted the form of the relation \( \theta = K \log \sin \alpha \), although there are numerous instances of its applicability to other types of response (cf. Hecht, 1919–20; and many further cases), partly
because of its distressing generality, and partly because of its common association with the Weber-Fechner law. The latter interpretation is frequently misleading (cf., especially, Hecht, 1923–24, 1924–25, and, for the case of phototropism under balanced illumination, Crozier, 1926–27). But until more is known of this particular phenomenon we may accept the formula as a convenient empirical expression.

There is additional evidence of its applicability. If our conception of the orientation is correct, then as the gravitational effect is made greater the precision of the upwardly directed movement should be-

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**Fig. 4.** The speed of ascension of *Helix* as related to the inclination (α) of the creeping surface. (Data from Cole, 1925–26.)

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**Fig. 5.** The decrease in the coefficient of variability (p.e. as per cent of the mean), of the measured values of θ (= angle of upward orientation) is proportional to log sin α.
come correspondingly enhanced. This may be investigated by comparing the numerical expressions for variability of $\theta$ as measured at each value of $\alpha$. If the reduction of variability ($V$) is proportional to the gravitational stimulus, then

$$-V = K \log \sin \alpha$$

Fig. 5 shows that this relationship is well satisfied, with the exception of the relatively very large variability at $\alpha = 15^\circ$; the deviation here is certainly due to the fact that this inclination is very close to the threshold value for any geotropic effect, as already stated. Thus not only the amplitude or extent, but also the precision of the orientation is determined by the logarithm of the component of gravity acting in the plane of creeping.

**IV.**

In searching for some clue as to the origin of the logarithmic relation between gravitational stimulus and geotropic response we have noted that if attention be paid to the process of creeping during orientation still another relationship emerges. Until a constant value of $\theta$ is attained upon a sloping surface the rat is chiefly pulled upward by the forward leg of one side of the body and pushed upward by the leg of the opposite side, which is less extended. When $\theta$ becomes constant the turning moment vanishes. We may consider, roughly and very crudely, that the orienting power is derived from the actions of levers on the opposite sides, and that the lever arm ($x$) on the "down" side is shorter than that ($y$) on the "up" side. Then the torque is responsible for turning upward. When the critical angle of orientation is exceeded, the locomotor action on the two sides of the body becomes equalized, so that if this value of $\theta$ is definitely exceeded (i.e., beyond a fluctuating zone, of increasing smallness as $\alpha$ is made larger), the rat is no more constrained than upon a horizontal surface, and is free to turn, should it chance to do so, until an equivalent $\theta$ is reached on the other side of the perpendicular. We have already described precisely this behavior. In the line of progression defined by $\theta$, the locomotor effectiveness of the opposed limbs is just barely identical. This means that if we assume the axes of the legs to have mean positions perpendicular to that of the body, then $(x \cos \theta - y \cos \theta)$ exactly
balances the total downward pull of the animal's weight, where \( x \) and \( y \) are the "lengths" of the legs as levers on the two sides. Hence,

\[
(x - y) \cos \theta = G \sin \alpha,
\]

and

\[
\frac{\cos \theta}{\sin \alpha} = \frac{G}{(x - y)}.
\]

Fig. 6. The cosine of the angle of upward orientation (\( \theta \)) decreases in direct proportion to the sine of the angle of inclination (\( \alpha \)) of the creeping plane.

It was pointed out previously that the legs on the upward side are of course more extended; hence, \( y > x \); and if \( x - y \) is constant for all magnitudes of \( \theta \), we have

\[
- \cos \theta = K \sin \alpha
\]
This relationship is in fact displayed, with unexpected exactness, as shown in Fig. 6, and gives an independent means of checking the significance of the data summarized in Table I. The constancy of the quantity labelled \((x - y)\), derived from the applicability of (3), at once suggests that the difference between the work done by the limbs of the two sides of the body in lifting the animal's weight must be reduced to constant fraction of the total before a stable orientation is attainable. This does not explain, of course, why the animal orients upward rather than downward, which may be determined by the inner ears; but it does explain why the amplitude of orientation attains its particular values as the inclination of the surface is varied, and in our opinion it gives an excellent illustration of the muscle-tension theory of orientation.

V.

From Fig. 6, by extrapolation to \(\cos \theta = 1\), it is found that the ideal threshold value of \(\alpha\) is at about 6.5°; at this point the component of gravity in the plane so slightly tilted is 0.113 \(G\). Experimentally, so far as can be determined, the threshold angle is higher than this (10-15°). Hence we may assume, very roughly, because the extrapolation is probably invalid, that when the ratio of the loads on the two sides of the body falls below 10:9, no further orientation occurs. From the derivation of equation (3),

\[
(x - y) \cos \theta = W G \sin \alpha,
\]

\[
\frac{\cos \theta}{\sin \alpha} = \frac{W G}{(x - y)},
\]

it follows that if the weight, \(W G\), be increased by attaching an additional load with thread to the animal's tail, then, at a given value of \(\alpha\) and of \(\theta\), the product \((x - y) \cos \theta\) must be larger. The effect of adding such loads is to increase the magnitude of \(\theta\); hence it would be expected, from the formula, that \((x - y)\) must increase. The fact is that the locomotion is more labored with added weights attached, and the limbs, especially on the upward side, do become more extended—hence there is good evidence for the occurrence of a change corresponding to an increase in the value of \((x - y)\). The velocity of creeping is decreased in proportion to the added load.
It is of greater interest to see the effect of additional weights upon the extent of the upward orientation ($\theta$). If the effect were a purely mechanical one we would expect to find $\theta$ increased in direct proportion to the added weight. But from equation (1),

$$\theta = K \log \sin \alpha,$$

we should expect the change to be such that

$$\theta = K (\log \sin \alpha + \log W \sin \alpha),$$

(4)

where $W$ is the added mass, and, when $\alpha$ is constant, $\theta$ should increase as $\log W$. Fig. 7 shows that it does. The addition of as little as 1.0 gm. increases the upward orientation somewhat. It is worth while to investigate more fully the relations between $\theta$, $\alpha$, added load, and rate of locomotion, and in a later paper it is proposed to do so.

VI.

SUMMARY.

Young rats, old enough to creep well but before the eyelids are open, orient and move upward upon an inclined surface. The angle of geotropic orientation on such a surface ($\theta$) is proportional to the logarithm of the component of gravity parallel to the inclined plane.
This result is compared with the scanty information available for other animals; there is indication that it may be generally valid. The precision of the orientation, measured by the percentage dispersion of the individual measurements, also increases in proportion to the logarithm of this component. The cosine of the angle of orientation decreases very nearly in proportion to the sine of the angle of inclination. A possible interpretation of this is given as involving the idea that upward orientation ceases when the differential pull of the body weight upon the opposed legs reaches a threshold value. Attaching weights (W) to the tail causes $\theta$ to increase, and in proportion to $\log W$.

CITATIONS.