ON THE EQUILIBRATION OF GEOTROPIC AND PHOTOTROPIC EXCITATIONS IN THE RAT.

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I.

Analysis of the phototropic movements of young rats (Crozier, 1926-27; Crozier and Pincus, 1926, 1926-27, b) has justified the assumption that in the absence of image formation, insured by employing animals with eyelids still unopened, these mammals behave as phototropic machines, with no detectable intervention of a central nervous factor. The young rat, in a field of light, orients until the excitations on its two sides are equal; over the range of intensities used, excitation is proportional to the logarithm of the intensity of the light. Geotropic orientation of these animals, also, is proportional to the logarithm of the active gravitational pull, although the reason for this particular relationship (Crozier and Pincus, 1926, 1926-27, a; Pincus, 1926-27) is probably not the same as in the case of phototropic excitation.

These investigations began with the double objective of discovering the limits of tropistic analysis as it might be applied to the conduct of mammals, and of utilizing the results for the study of central functions (Crozier, 1926-27). With reference to the latter purpose it may be pointed out that there are at least two general methods possible to pursue. One of these consists in the opposition of tropistic modes of response in such ways as to permit quantitative evaluation of the resolution or equilibration of the imposed conflicts in behavior (Crozier, 1926-27; Crozier and Pincus, 1926). The conduct of the young rats in a compound field of excitation involving opposed phototropic and geotropic responses provides an elementary situation amenable to precisely this sort of treatment.

1 Aside from that involved in photokinetic movements of the head, which is itself amenable to quantitative treatment in the same terms (Crozier, 1926-27).
The simplicity of the actual result gives the best possible proof of the adequacy of the initial assumptions with regard to the mathematical representation of the phototropic and the geotropic excitations. It also constitutes a second-order proof that in the resolution of such conflicts the rat is behaving as a machine. There are several ways in which phototropic stimulation might be conceived to modify the effectiveness of simultaneous geotropic excitation: (a) the constants in the equation for the geotropic effect might be modified, or its threshold altered; or (b) the whole form of the equation might be changed, either at once or as a function of the time of exposure to the light. The possibility first mentioned (a) could be dealt with very simply, and obviously could give a means for the quantitative expression such as we seek for a "central factor." The second possibility might be expected if complex psychic processes are implicated, but change with time cannot be simply tested for, because of photic adaptation. The net result of these considerations is, that if from the respective known expressions for the phototropic and the geotropic effects it is possible to predict the mathematical form of the balance between phototropic and geotropic excitations there will remain no need nor indeed any room for a psyche in this particular case. Since this is the actual result, it will be noticed that the initial assumptions of the tropism doctrine are doubly confirmed. So far as we are aware this is the first case in which just this sort of analysis has been possible, and the fact that it has been carried out with a mammal makes it all the more interesting.

II.

The rats used in previous analysis of phototropism and of geotropism were of the same genetic history as those employed for the present experiments, and in this respect the results are strictly comparable. The phototropic conduct has been treated as depending upon the fact that the excitation is proportional to \( \log I \). The geotropic response upon an inclined plane is such that the angle of upward orientation on this plane is proportional to \( \log \sin \alpha \), where \( \alpha \) is the inclination of the creeping plane to the horizontal. If the arrangement be made such that the intensity of light is found at each of a number of
values of \( \alpha \) which is just sufficient to suppress geotropic orientation, we should expect that

\[
\log I = K \log \sin \alpha + C,
\]

where \( K \) and \( C \) are constants. This could be the result only if the presence of the light failed to affect the form of the connection between geotropic excitation and response. The actual result should therefore afford a criterion for the evaluation of the kind of central nervous adjustment eventuating from the competition of the two forms of stimulation. The significance of the constant \( C \) cannot be directly determined, for we do not yet know the magnitude of the corresponding quantity in the equation for phototropic effect; but, as we shall point out subsequently, it may be estimated indirectly.

Two series of experiments were made according to the following procedure. The rats were dark-eyed, black hooded, 13 days after birth. In Series 1, three individuals were employed; in Series 2, 4, litter mates in each case. Tests were made upon a fine-meshed wire screen stretched upon a large square platform which could be inclined at known angles to the horizontal. This creeping stage was at one end of an extended arm carrying the light source, the latter adjustable as to distance from the stage. The dark-adapted rats were placed upon the stage, one at a time, and oriented upward toward the light until the light intensity became such that the animal was forced to creep in a horizontal path. It may be assumed that at this point the upward orienting tendency is exactly counteracted. The intensities were measured photometrically, not computed. The total exposure to the light was kept at 1 minute, with at least 10 minutes in darkness between successive tests. By repeated trials the exact distance was found at which horizontal creeping was enforced; the tests were repeated five times at each inclination, for each individual.

The results of the first series of tests, when \( \log I \) was plotted against \( \log \sin \alpha \), gave \( I \) proportional to \( (\sin \alpha)^K \), with \( K = 2.475 \). The second series of measurements, treated separately, gave \( K = 2.476 \).
This degree of concordance is probably fortuitous, but we would stress the point that the individuals concerned in the two sets of determinations were unusually similar from the standpoint of age and genetic uniformity. The two series of measurements are plotted together in Fig. 1, where it is obvious that they form a homogeneous whole.

Inasmuch as the variability of the response to the geotropic stimulus decreases in proportion to log sin α (Crozier and Pincus, 1926-27, a),

Fig. 1. The intensity of light required to inhibit geotropic orientation of young rats varies with the inclination of the creeping surface, in such a way that log I/log sin α is constant. For Series 1 each point is the mean of fifteen determinations; in Series 2, of twenty determinations.
and since the photokinetic sideward movements of the head increase in proportion to log I (Crozier, 1926–27; Crozier and Pincus, 1926–27, b), it is to be expected that the two recognizable sources of variation in the apparent equilibrating light intensity must probably tend to counterbalance. The variability of the intensity required to equal the geotropic stimulation should therefore be fairly small. To test this, the probable errors of I have been computed (Table I); expressed as percentages of the mean intensities, which give figures corresponding to the coefficient of variation, it is seen that in agreement with

<table>
<thead>
<tr>
<th>( \alpha )</th>
<th>Log sin ( \alpha )</th>
<th>( I, \text{mean} )</th>
<th>Log ( I )</th>
<th>( \text{P.E. of } I, \text{as per cent of mean} )</th>
</tr>
</thead>
<tbody>
<tr>
<td>15°</td>
<td>1.413</td>
<td>1.413</td>
<td>0.150</td>
<td>0.47</td>
</tr>
<tr>
<td>20°</td>
<td>1.534</td>
<td>2.353</td>
<td>0.372</td>
<td>0.38</td>
</tr>
<tr>
<td>30°</td>
<td>1.699</td>
<td>7.040</td>
<td>0.848</td>
<td>0.26</td>
</tr>
<tr>
<td>40°</td>
<td>1.808</td>
<td>11.22</td>
<td>1.050</td>
<td>0.26</td>
</tr>
<tr>
<td>50°</td>
<td>1.884</td>
<td>19.43</td>
<td>1.288</td>
<td>0.15</td>
</tr>
<tr>
<td>60°</td>
<td>1.938</td>
<td>31.19</td>
<td>1.493</td>
<td>0.77</td>
</tr>
<tr>
<td>70°</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
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this expectation the variability of \( I \) as measured is quite low. The quantity which inversely measures the photokinetic effect (Crozier, 1926–27) decreases linearly as log \( I \) increases, while the variability of geotropic orientation directly decreases as log sin \( \alpha \) increases (Crozier and Pincus, 1926–27, a). Thus it is to be expected that the coefficient of variation for \( I \) in the present experiments should pass through a minimum as \( \alpha \) increases from 10° to 70°. The differences among the probable errors in Table I are statistically significant. Fig. 2 shows that the variability of \( I \), as \( \alpha \) is increased, does pass through a minimum in the expected way.
Fig. 2. The variability of the intensity required to counterbalance geotropic excitation passes through a minimum as the angle of inclination of the creeping surface is increased (see text).

IV.

SUMMARY.

The intensity of light required to just counterbalance geotropic orientation of young rats, with eyelids unopened, is so related to the angle of inclination (α) of the creeping plane that the ratio log I/log sin α is constant. This relationship, and the statistical variability of I as measured at each value of α, may be deduced from the known phototropic and the geotropic conduct as studied separately, and affords proof that in the compounding of the two kinds of excitation the rat is behaving as a machine.

CITATIONS.