ANALYSIS OF THE GEOTROPIC ORIENTATION OF YOUNG RATS. IV

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(Accepted for publication, September 3, 1931)

I

Observations utilized in providing material for the interpretation of orientation during the upward geotropic progression of young rats have been secured from three inbred lines of *R. norvegicus*, hybrid descendents from two of these, and one line of *R. rattus*. It has been desirable to obtain comparable data upon certain other lines. Experiments were undertaken with individuals of a line labelled *P*, started some years ago by inbreeding from the original stock which had also been the source of lines *A* and *B* of our previous accounts. It was expected that certain resemblances, and possibly some differences, would characterize lines *A*, *B*, and *P* and serve to differentiate them as a group from rats of line *K*. Evidence of this sort would amplify the proof that differences and similarities in the properties of geotropic behavior are correlated with hereditary differences and similarities among the tested individuals.

Race *P* was derived from the same original source as our *B* and *A*, namely, a miscellaneous group of rats arising from certain studies of linkage in rats made at the Bussey Institution of Harvard University and subsequently bred brother to sister. They differ from lines *B* and *A* in being pink-eyed, agouti, hooded. The former are (except for line *B') red-eyed, non-agouti, hooded.

Line *K* of our previous accounts originated from a quite different source. It is totally unrelated to lines *A*, *B*, and *P*, deriving from a pair of rats obtained from Miss Helen D. King in 1924.

1 Crozier and Pincus, 1926–27, a, b, c, d. 1927–28; Pincus, 1926–27.
2 Crozier and Pincus, 1929–30, a, b.
3 Crozier and Pincus, 1931–32 (III).
We accordingly look for rather definite similarities in the results to be obtained with $A$, $B$, and $P$ individuals, which will collectively differentiate them from $K$ rats. We may further expect, on the basis of earlier findings demonstrating genetic stability of geotropic performance within inbred lines, that these resemblances will not only include the relationship of orientation-angle $\theta$ to angle of slope of surface ($\alpha$), but will extend to the variability of the orientation-angle. These expectations are in fact met by the measurements. The findings are also of interest because they can be interpreted to show that certain of the effects distinguished in cross-bred individuals (e.g., $K \times A$; Crozier and Pincus, 1929-30) may be simulated in a "pure line" of rats. The result of this, in line $P$, is a disturbance of the approximate rectilinearity of the $\cos \theta$ vs. $\sin \alpha$ plot. By chance the races with which we first worked did not exhibit this peculiarity, $\Delta \cos \theta/\Delta \sin \alpha$ being very nearly constant; though in hybrids of $A$ and $K$, and in the back-cross offspring of that experiment, it is quite apparent and has been interpreted. The condition revealed in $P$ might of course be due perhaps, or in part, to a different disposition of the relative masses of the parts of the body, as compared, let us say, with race $A$; there are other possibilities, but the explanation apparently turns upon specific differences in the "number of receptors" in one of the three main groups distinguished in the analysis of the $\theta$-log $\sin \alpha$ curve.

II

Measurements with three litters of line $P$ are summarized in Table I, and the respective mean orientation-angles are plotted in Fig. 1.

It is noteworthy here, as with the data from tests with race $A$, that in the $\theta$ vs. log $\sin \alpha$ plot (Fig. 1) the mean $\theta$'s tend very definitely to exhibit a strictly limited scatter; marginal lines fairly including the plotted points are very closely constant in their separation in the abscissa direction. This means that the ratio of the lowest $\sin \alpha$ required to evoke a given mean $\theta$ to the highest $\sin \alpha$ ordinarily evoking that $\theta$-response, is constant. Consequently, to obtain a definite increase of mean $\theta$, one must increase mean $\sin \alpha$ giving that $\theta$ by a constant fraction; the total range of $\sin \alpha$'s evoking a given average $\theta$ is, for the $P$ line, about 10 percent of the lowest $\sin \alpha$ giving mean $\theta$ of that magnitude for a sample of the sizes ($n$) used. It is to be noted, however, that the "definite increase of $\theta$" thus evoked is not constant, but is a function of $\sin \alpha$. 

Published November 20, 1931
Litter I, five individuals (3♂, 2♀) was of the fourteenth brother × sister inbred generation (P₁₄); litter II, four individuals (2♂, 2♀), resulted from a mating of a P₁₄ female with a male derived from litter mates of P₁₃; litter III, three individuals (2♂, 1♀), was produced in another mating similar to that giving II. All were used 13 days after birth. In each case twenty observations of θ were secured with each individual at each slope (α). The differing number of individuals in the three instances facilitated certain checks upon the "variability number" subsequently computed. For Series I, II, III the respective temperatures were: 20.4° ± 0.3°; 22.5° ± 0.5°; 22.1° ± 0.4°, the limits here indicating the extreme ranges. The methods of recording oriented paths are given in a preceding paper (Crozier and Pincus,

TABLE I

Orientation-angles (θ) at various inclinations of surface (α), young rats of race P. Three litters: No. I, five individuals; No. II, four individuals; No. III, three individuals; n = 20 with each individual at each slope.

<table>
<thead>
<tr>
<th>α degrees</th>
<th>θ, degrees</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>P₁₄ I</td>
</tr>
<tr>
<td>15</td>
<td>47.9 ±1.18</td>
</tr>
<tr>
<td>20</td>
<td>55.0 ±1.17</td>
</tr>
<tr>
<td>25</td>
<td>57.8 ±0.990</td>
</tr>
<tr>
<td>30</td>
<td>61.7 ±0.895</td>
</tr>
<tr>
<td>35</td>
<td>68.4 ±0.795</td>
</tr>
<tr>
<td>40</td>
<td></td>
</tr>
<tr>
<td>45</td>
<td>73.1 ±0.746</td>
</tr>
<tr>
<td>55</td>
<td>77.7 ±0.494</td>
</tr>
<tr>
<td>62.5</td>
<td></td>
</tr>
<tr>
<td>70</td>
<td>80.2 ±0.586</td>
</tr>
</tbody>
</table>
The three series are satisfactorily concordant; one of them, as with line $B$, tends to be *slightly* higher throughout.

The form of the curve connecting orientation-angle $\theta$ with $\log \sin \alpha$ is that previously found with other lines. It resembles those for lines $A$ and $B$, and with them differs distinctly from that for line $K$. The $P$ curve most closely approaches that for the $A$ rats, but $\theta$ is consistently higher than with $A$ except above $\alpha = 55^\circ$. Whereas with $A$ no consistent orientation has been obtainable at $\alpha = 15^\circ$, it is regularly secured at that inclination of surface with $P$ and with $B$. $A$ rats require a higher threshold slope ($20^\circ$) for orientation, and show a lower orientation-angle at that inclination of surface, than do $B$ or $P$.

These two facts cannot be directly related, however, because $K$ rats, with still lower $\theta$'s at low slopes, respond clearly and definitely at $\alpha =
When lines $A$ and $B$ are crossed, as described in a later paper, the $F_1$ individuals show the threshold of slope and the threshold $\theta$ of the $B$ parents. Although the curve for $P$ is superficially closer to that for $A$ than for $B$, it will be shown in the analysis of the graph that its fundamental similarities are with the $B$ curve rather than with the $A$. In view of the fact that on the basis of mere tabulation of the data and their standard deviations it might be suggested that $A$ and $P$ curves are not really distinct, cases of this type again illustrate the necessity of considering response or performance as a function of measured variables (cf. Crozier and Pincus, 1929-30, a). Testing the response of $A$ and $P$ individuals by estimations of $\theta$ at one value of $\alpha$ would leave one no choice but to decide them so similar as to be

![Graph showing the relationship between $\sin \alpha$ and $P_\theta$.](image)

Fig. 2. The $\sigma$ of mean $\theta$ declines rectilinearly as $\sin \alpha$ is increased. Series I (cf. Table I, and Fig. 3).

practically indistinguishable, although this error would result from a rather different cause than that which could easily lead to similar confusion if $K$ rats were incompletely compared with either $A$ or $P$.

As in the earlier experiments, $P. E_\theta$ declines rectilinearly with $\sin \alpha$ (Crozier and Pincus, 1931-32), and $P. E_{\theta/\theta}$ with $\log \sin \alpha$ — the $\theta$ vs. $\log \sin \alpha$ plot being again nearly enough rectilinear for the purpose of this test (which otherwise would be made by plotting $P. E_{\theta/\theta}$ against $\theta$). [Cf. Figs. 2, 3; 4, 5.] The “variability numbers” computed from the slopes of the lines in Figs. 4, 5 are collected in Table II. This quantity is obtained (Crozier and Pincus, 1929-30; 1931-32; Crozier, 1929) as $\Delta (100 \ P. E_{\theta/\theta})/\Delta (\log \sin \alpha)$, multiplied
by $\sqrt{n/N}$, where $n =$ number of observations upon each individual, $N =$ number of individuals in the group (litter); it signifies the mean

![Graph 1](image1)

**Fig. 3.** $P.E_\theta$ vs. $\sin \alpha$ for Series II, III (cf. Fig. 2; data in Table I)

![Graph 2](image2)

**Fig. 4.** The relative variability of the geotropic orientation ($P.E_\theta/\theta$) declines rectilinearly as $\log \sin \alpha$ is increased. Series I (cf. Fig. 5).

percentage change of the mean root mean square deviation from the general mean $\theta$, per individual, per unit change of the independent variable ($\log \sin \alpha$). The three series in Table I agree remarkably
well, and permit comparisons with the corresponding indices already computed for the other races (Table II). Of the three series, I is the most reliable, partly because observations were taken at a larger number of slopes (α). In Series III one individual gave particularly low θ's; this rat, θ, was much below the weight of the others, al-

though its mean θ's showed no differences from those of the other individuals; it weighed 14.2 gm., its litter mates 20 gm. The rats of litters I and II weighed 15–16 gm. Careful inspection of individual records has demonstrated for the P race, as with earlier data for A, K, B, that there are no correlations of geotropic responsiveness (θ)

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**TABLE II**

Variability numbers for geotropic response in four races of *R. norvegicus*. Mean values for K, A, B, taken from a previous paper.  

<table>
<thead>
<tr>
<th>Line</th>
<th>V.N. from Δ (P.E./θ)/(Δ log sin α = 0.4)</th>
</tr>
</thead>
<tbody>
<tr>
<td>K</td>
<td>5.78</td>
</tr>
<tr>
<td>A</td>
<td>2.84</td>
</tr>
<tr>
<td>B</td>
<td>3.32</td>
</tr>
<tr>
<td>P</td>
<td>2.86</td>
</tr>
</tbody>
</table>

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**Fig. 5.** P.E./θ as function of log sin α, Series II, III (cf. Fig. 4)
with individual weight, or with sex. In Series II the observations at two slopes ($\alpha = 40^\circ, 45^\circ$) were taken in the evening, when variability of performance is greater, but the distortion is not serious (Fig. 3, 5) although definitely detectable. (We shall later consider this aspect of the measurement of variability in greater detail.) The variability numbers 2.76, 3.02, 2.84 are in unusually good agreement, and the weighted mean is plainly of the same order of magnitude as in lines $A$ and $B$ (Table II)—$P$ and $A$ are indeed not really distinguishable in this respect. The correspondence of this fact with the known common derivation of the three lines is consistent with the different magnitude for line $K$, and with the behavior of the variability number in breeding tests.$^{2,3}$ V.N. cannot be very directly connected, it is clear, with the threshold for response, and attempts to characterize the relative geotropic sensitivities of the several lines on these bases would be in conflict.$^5$

$^5$ The variability of $\theta$ can be estimated in a slightly different way, by considering the data for each individual separately. Although this has been done for all our measurements, we prefer to keep together all the observations on each litter (with inbred lines). V.N. computed on the basis of mean P.E.$\alpha$ for a group, where $\theta_i$ is the individual mean $\theta$ at given $\alpha$, $n$ being constant, turns out a little higher or a little lower than the values given, though the general average is the same. The chief reason for this is that in addition to slight differences in the slope factor $\Delta$ P.E.$\alpha$/\Delta log sin $\alpha$, independent differences also occur in the ordinate intercept. In the $P$ series the individual V.N.'s range from 2.0 to 3.2.

### TABLE III

The percentage of the total observed relative variation of $\theta$ which is modifiable according to the magnitude of $\alpha$.

<table>
<thead>
<tr>
<th>Line</th>
<th>Proportionate relative variation</th>
</tr>
</thead>
<tbody>
<tr>
<td>$K$</td>
<td>85 ($\alpha = 15-70^\circ$)</td>
</tr>
<tr>
<td>$A$</td>
<td>56 ($\alpha = 20-70^\circ$)</td>
</tr>
<tr>
<td>$B$</td>
<td>74 ($\alpha = 15-70^\circ$)</td>
</tr>
<tr>
<td>$P$</td>
<td>59 ($\alpha = 15-70^\circ$)</td>
</tr>
</tbody>
</table>
III

The proportionate relative variation of orientation (Crozier and Pincus, 1931–32) is obtained by considering the percentage of the total area under graphs such as those in Figs. 2, 3, corrected for \( n \) and for \( N \), which is modifiable according to the slope \( a \). In the experiments with line \( P \) the result is given in Table III. The percentage of the total relative variation of the orientation angles which is governable by \( \sin a \) is 59.4 per cent, the weighted average of 62.5 (Series I); 58.9 (Series II — extrapolating to \( a = 15^\circ \)), 59 (Series III). This com-

![Graph](image)

**Fig. 6.** \( \cos \theta \) vs. \( \sin a \) for line \( P \), three series

...ares well, at first sight, with the value previously obtained with \( A \) rats (cf. Table III), but for \( A \) the range of \( a \) is only 20–70°. Comparing \( B \) and \( P \), the two having the same threshold slope, the total relative variation is greater with \( P \), while the proportion modifiable is definitely less.

IV

For the \( P \) race the graph of \( \cos \theta \) vs. \( \sin a \) is not simple (Fig. 6). It corresponds to that for \( B \) rats,\(^3\) except that the \( \theta \)'s are of course lower. The general form of the plot is somewhat like that for those segregates
produced in the back cross $F_1(A \times K) \times K$ in which receptor group $I$ is small, group $2$ large (Crozier and Pincus, 1929–30, b, p. 101). The change of slope indicated in Fig. 6 can be demonstrated real, and not merely statistically significant, by the behavior of $P.E_{\cos \theta}$, or of $P.E_{\theta}/\theta$ vs. $\sin \alpha$. In this respect it is analogous to the discontinuity in the corresponding curves established for guinea pigs (Upton, 1929–30; Crozier, 1929), although its nature is different. The identification of a discontinuity by such means is proof of its inherence in the data (cf. also: Hoagland and Crozier, 1931–32).

![Graph showing resolution into three sub-regions](image)

Fig. 7. $(\Delta \theta)/(\Delta \log \sin \alpha = 0.4)$ for line $P$, showing its resolution into three sub-regions analogous to those recognized with lines $K$, $A$, and $B$.

We have utilized the relationship between $\cos \theta$ and $\sin \alpha$ largely as a matter of convenience, because for races $K$, $A$, $B$, and for our stock of mice (Crozier and Oxnard, 1926–27) and of Rattus rattus (Crozier and Pincus, 1926–27), it gives a sufficiently rectilinear plot. The deviations from a simple straight line, in such representations, are none the less definite and real (Pincus and Crozier, 1929). With cross-bred individuals this is very clear (Crozier and Pincus, 1930–31). For race $B$ we were inclined to ignore the indications of discontinuity at about $\alpha = 50^\circ$ (3), pending further data; but more recent measurements with $B$ rats show it to be definite, and the behavior of $P$ discloses an exactly similar state of affairs. If we were to take the $\cos \theta$ vs. $\sin \alpha$ plots as a basis for analysis, we could point to the pres-
ence in "pure line" P of components of reactiveness somewhat resembling those brought into single individuals by breeding experiments with lines K and A.  

V

It was shown previously\(^2,3\) that by taking into account the fact that the act of stepping provides the excitation which controls the geotropic orientation during progression, the slopes \(\Delta \theta / \Delta \log \sin \alpha\) of curves such as that given in Fig. 1 can be employed to obtain a picture of the distribution of effective thresholds for excitation in the array of receptors concerned. For race P this is given in Fig. 7. As with the lines of rats earlier used, the curve is obviously composite, and is resolvable into three distinct parts or regions. When we compare the graph with those for races A and B it is clear that the affinities of P are with the B line rather than with A. For B it was pointed out\(^3\) that the three "groups of sense organs" contributing to the composite distribution are "small" in B as contrasted with those for race K and more flattened than in A, but that 1 (see Fig. 7) was larger than in A, 2 and 3 smaller. The analysis in Fig. 7 indicates that a similar resolution of the curve is possible for P, which is much more like the result obtained with B than the findings for A. The areas under the three sub-curves are, in planimeter units on the same scales:

<table>
<thead>
<tr>
<th>Group</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>A</td>
<td>3.10</td>
<td>6.18</td>
<td>1.12</td>
<td>10.4</td>
</tr>
<tr>
<td>B</td>
<td>4.46</td>
<td>4.00</td>
<td>0.65</td>
<td>9.11</td>
</tr>
<tr>
<td>P</td>
<td>4.68</td>
<td>4.12</td>
<td>0.71</td>
<td>9.51</td>
</tr>
</tbody>
</table>

The form of the sub-curves is also slightly different in the three cases. The maxima occur at about the same values of \(\sin \alpha\), that for P 2 a little below that for B 2.

This material enables us to interpret tentatively the meaning of differences of threshold slope of substratum for orientation, and also of the relation of variation of \(\theta\) to total number of receptor units.

We may suppose that to be effective in determining orientation the
total excitation must exceed a certain value. In terms of the excitation-units presumed to be characterized by the frequency distributions in Fig. 7, we can as an approximation suppose that this means that a certain number of excitation-units must be brought into play. The fact that central thresholds and "resistances" perhaps vary from line to line of rats is probably to some extent taken care of by the nature of the units in which the elements of excitation ("receptor units") are defined (Crozier and Pincus, 1929-30, b). We might then look for threshold $\alpha$ to be that inclination at which $\sin \alpha$ is adequate to excite a certain number of receptor units. This number corresponds pictorially to the missing left-hand margin of the differential curves. The total excitation at threshold slope is, in our terms, measured by threshold $\theta$. The magnitude of $\sin \alpha$ able to produce this intensity of excitation will depend on the form of the frequency distribution of area 1. For $K$ rats this "group of receptors" is large, its outline is steep, and $\theta$ at threshold slope is relatively low. On this basis we expect threshold $\sin \alpha$ to be relatively low for the $K$ line; the threshold inclination is at about $\alpha = 15^\circ$. Curve 1 for $B$ and for $P$ definitely encloses a larger area than in the case of $A$, and we look for a higher threshold slope in $A$, which was found; the form of Curve 1 in $P$ (as deduced from the analysis) is such that it is steeper, less spread than in $B$; we expect then with $P$ a lower $\theta$ at $\alpha = 15^\circ$ than with $B$, which again accords with the findings. The attempt to deal with these points in greater detail is of course hindered by the experimental difficulty of locating threshold slopes precisely, and of attempting the reconstruction of the missing portion of Curve 1; but even in comparing the results with lines $A$ and $B$ it can be predicted, on the basis of the forms of Curve 1 in the two cases, that if (as found with $A$ and $K$) the respective group 1's are inherited alternatively in crosses involving $A$ and $B$, that the rats possessing a "$B$" group 1 will also orient at $\alpha = 15^\circ$, those with "$A$" group 1 not until about $\alpha = 20^\circ$ is reached.

The question of the nature of the indices of variation of $\theta$ can be approached in a similar way. The areas under the differential curves (Fig. 7) indicate the numbers of effective receptor units above the threshold for response, in terms of the analysis we have employed. A given departure from mean $\theta$ is less likely to occur if the functional receptor units are more numerous. Consequently $\Delta \frac{P.E.\theta}{\Delta \sin \alpha}$
(cf. Figs. 2, 3) should be greater with larger total area under the differential curve, since the bringing in of relatively more receptor units by a given increase of \( \sin \alpha \) should cause \( P.E.0 \) to decrease more rapidly. For \( A, B, P, \Delta P.E.0/\Delta \sin \alpha \) is respectively (weighted means) 0.93, 1.11, 0.89 (calculated with \( \Delta \sin \alpha = 0.4 \)); for \( K \), with the area in same units = 17.4, \( \Delta P.E.0/\Delta \sin \alpha = 1.6 \pm \) or a little larger. The correlation demanded is thus met about as precisely as could be expected. The correspondence is perhaps the more convincing since the actual orientation-angles are so much higher in \( B \) than \( A \) or \( P \), while the differential curves are so nearly alike in \( B \) and \( P \). In a similar way we might expect the proportionate relative variation to be greater in \( K \) than for \( B \) or \( P \), which is clearly the fact; whereas with \( A \) the higher threshold \( \alpha \) prevents direct comparison. The mean total relative variations with \( K, B, \) and \( P \) (corrected for \( N \) and \( n \)) are respectively 2.8, 1.5, and 1.9 units; that for \( A \) falls into place in the series if its orientation-threshold is extrapolated to \( \alpha = 15^\circ \). The net result is to indicate that "geotropic sensitivity" is about equal in lines \( A \) and \( P \), higher in \( B \), still higher in \( K \). It is to be noticed that this order is in no simple way correlated with the threshold slope \( (\alpha) \) for response, nor is it reflected in the magnitude of the response at threshold—criteria often employed in the comparative evaluation of reactivities. It is obviously related, however, to the maximal response obtainable under comparable conditions \( (i.e., \) without added loads). All of the relations indicated are rationally accounted for in terms of the frequency distributions of thresholds for activation of receptor units, and the indices of variation as dependent upon the total number of these units. The examination of this matter will be considered in a later paper.

**SUMMARY**

The geotropic orientation of young rats of a closely inbred line \( P \), separated 6 years ago from a stock which gave rise also to the closely inbred lines \( A \) and \( B \) previously studied, has been measured. The curve connecting orientation-angle with inclination of substratum is in a general way similar to those for \( A, B \), and with them differs markedly from that for race \( K \) of totally different ancestry. The variability of the response exhibits similar affinities. Although the
orientation-angles are rather close to those obtained with $A$, the threshold slope for $P$ is that for $B$; analysis of the curve discloses how this fact is related to the character of the presumptive distributions of thresholds for the respective arrays of tension-receptor units. It is pointed out that these considerations prevent loose comparisons of "geotropic sensitivity" in different lines of rats, but make it plain why comparisons in terms of thresholds for response or of magnitude of response at the same threshold are ineffective. The estimated "number of excitation units," however, is found to correspond to the variability of orientation, and to the manner and extent whereby the dispersions of the measured orientation-angles are governed by the magnitude of the gravitational vector.

CITATIONS

Crozier, W. J., 1929, in Foundations of experimental psychology, Worcester, Clark University Press, ch. II.