Thus far, in speaking of variation of performance, we have discussed chiefly the relative variability of $\theta$, on the ground that for these cases the precision of the mean of the observations should be limited in the same way as the mean angle $\theta$ itself, which analysis permits us to regard as the measure of excitation (Crozier and Pincus, 1929-30, b). The direct control of excitation, however, should be proportional to $\sin \alpha$ (careful test shows no effect of weight of individual, or sex, other things equal, so far as $\theta$ is concerned). We therefore look for the slope $\Delta \sigma_\theta/\Delta \sin \alpha$ to be constant in each series of measurements. Clearly, a variation index (of slightly different meaning from the one hitherto used) should be computable on this basis also. The plots in Fig. 13, 14, 15 demonstrate that this expectation is satisfactorily met by all the available measurements, including those previously published. For subsequent reference, we may include here results with line $K$ as well.

When dealing with the reaction-time or latent period for geotropic response (in snails) it is found that $\sigma_t$ is directly proportional to the latent period, both being influenced in the same manner by $\sin \alpha$ (Hoagland and Crozier, 1930–31); the case is similar with $\theta$ and $\sigma_\theta$ in the gravitational orientation of $Uca$ (Kropp and Crozier, 1928–29) and of ants (Barnes, 1929), where $-\Delta \sigma_\theta/\Delta \sin \alpha$ is constant. The extension of this method of analysis to other types of occurrences (Crozier, 1929; Crozier, Stier, and Pincus, 1929; Pincus, 1930–31) is important, because it is obvious that no predisposition of the ob-
server could achieve by conspiracy or accident a state of affairs in which the scatter of the observations is such that the standard deviations of their means shall obey rational rules (in the present case, 3 distinct and specific rules), in some instances not looked for until long after the data were recorded! It has been emphasized (Crozier, 1929) that where tests of this character can be applied it is no longer per-

2 Or rather, of two observers; we have made a practice of dividing the labor of recording, so far as possible. The variability number is independent of the observer when series by each are compared.
It is notable that, when several series of observations are available, as with line A and in other material at our disposal but not here considered, in which the effect of casual variations of mean θ's is reduced by having n sufficiently large, the dispersion of the mean θ's tends conspicuously to be confined, in the plot against log sin α, to a band with definite marginal delimitations. The "width" of such a band is very nearly constant, if not indeed absolutely so, in the direction parallel to the log sin α axis; the indication is that with plotted points of equivalent weight the "width" would be quite constant. This must be a reflection of the "unmodifiable" fraction of the total variation of performance (i.e., independent of log sin α). It signifies that...
to produce an unequivocal increase of mean $\theta$, the inclination of
surface ($\alpha$) must be increased by an amount which in terms of $\sin \alpha$ is a
definite fraction of the lowest $\sin \alpha$ which unequivocally invokes the
lower $\theta$. Lest it be mistakenly assumed that this is the Weber-Fechner
Rule in some sort of disguise, we hasten to point out that a definite
fractional increase of $\sin \alpha$ thus leads to a statistically significant step
in $\theta$, but that the magnitude of the resulting $\Delta \theta$ is manifestly a func-
tion of the magnitude of $\sin \alpha$. Another way of describing this state
of affairs is, that the latitude of variation in $\sin \alpha$ over which a statisti-
cally constant $\theta$ may be expected in a uniform population is a con-
stant fraction of the mean $\sin \alpha$ associated with this orientation-angle.
For line $A$ this latitude is ca. 10 per cent of $\sin \alpha$, for mean $\theta$'s of the
given weights, and in line $B$ also. This type of dispersion imposes
definite conditions upon the methods permissible in fitting curves to
the observations.

VII

In races $K$, $A$, and in $R. rattus$ (Crozier and Pincus, 1926–27) $\Delta$
$\cos \theta/\Delta \sin \alpha$ was sensibly constant. Crosses between $K$ and $A$
showed that this need not be true in all cases (Crozier and Pincus,
1929–30, b). We were inclined to disregard certain indications in the
data for line $B$ (1929–30, b), because we then had at our disposal only
one series of measurements. The present material on line $B$, and data
on other lines which we shall discuss in later papers, force the recogni-
tion in $B$ of a state of affairs like that experimentally produced in our crosses
$K \times A$ and in back crosses with these. This has been referred to in
the first section of the present paper. We now record the condition
in these lines for convenience of reference in our subsequent account
of the results of crossing lines $A$ and $B$ (cf. Fig. 16). The $B$ line defi-
nitely shows a lesser slope ($\Delta \cos \theta/\Delta \sin \alpha$) at the high-$\alpha$ end than at
lower $\alpha$'s. The reason for this becomes apparent in the subsequent
discussion. The straightness of the graph up to $\alpha = 48^\circ$ is less clear
when the data from several tests is plotted together, since there are slight
tendencies for one set to show higher $\theta$'s than another; this cannot be
properly taken care of by averaging $\cos \theta$'s. The slope of the line
drawn averages the slopes for the individual sets. It should be noted
that although a rough derivation of the relation between $\theta$ and $\alpha$ has
been suggested in outline, from the standpoint of the theory of the
geotrophic orientation (Crozier and Pincus, 1926–27), and can be given
in more rigorous form, it has not been used save as a method of repre-
sentation which is for certain purposes convenient (Crozier and Pincus,
1929–30, a, b); its more exact use requires recognition of the three
regions of action of discrete groups of excitation-units. It happens

![Graph](https://via.placeholder.com/150)

**Fig. 16.** Cos $\theta$ vs. $\sin \alpha$, line B. See text. (Approximate rectilinearity is observed empirically up to an inclination $\alpha = \text{about } 48^\circ$. The plot really indicates, however, three distinct straight portions, the two below $\alpha = 48^\circ$ being for B rats, as for K, A, etc., practically confluent.)

that for A and K rats the three regions of the graph have about the
same slope. For B this is almost true for Groups 1 and 2, but not for
Groups 2 and 3.

**VIII**

The argument leading to the analysis of the curves $\theta \cdot \log \sin \alpha$ need
not be reproduced (cf. Crozier and Pincus, 1929–30, b); reason has been
FIG. 17. \((\Delta \theta)/(\Delta \log \sin \alpha)\) as function of \(\sin \alpha\), for line \(A\). See text. The graph is resolved into three constituent areas, labelled 1, 2, 3. In terms of the analysis given, these areas represent frequency distributions of thresholds for excitation-units.

FIG. 18. \((\Delta \theta)/(\Delta \log \sin \alpha)\) vs. \(\sin \alpha\), for line \(B\).
given for considering the plotting of $\Delta \theta / \Delta \log \sin \alpha$ against $\sin \alpha$ as providing a picture of the population of receptors concerned in the response in terms of their thresholds for excitation. The limitations of the assumptions employed have been considered (1929–30, b). The most searching test of the adequacy of this interpretation has been given by breeding tests, and is amply consistent with it. The differential curves for lines A and B can now be given more precisely than was possible previously (Figs. 17, 18). These curves do not differ in any material way from those previously published, however. They show that A and B rats are in a general way similar as regards the forms of the three sub-curves ("groups of receptors") into which the differential curves may be resolved, but that Groups 2 and 3 are definitely smaller in B than in A, "3" being about one-half the corresponding area in A; Group 1, however, is definitely larger in B, even when allowance is made for the lower threshold inclination which obtains with B. The maxima for the corresponding sub-curves for the two races turn out to fall at almost identical values of $\sin \alpha$. The areas under the 3 sub-curves are, in arbitrary planimeter units on an identical scale:

<table>
<thead>
<tr>
<th>Race</th>
<th>Areas of &quot;Groups of receptors&quot;</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>1</td>
<td>2</td>
</tr>
<tr>
<td>A</td>
<td>3.10</td>
<td>6.18</td>
</tr>
<tr>
<td>B</td>
<td>4.46</td>
<td>4.10</td>
</tr>
</tbody>
</table>

It is instructive to compare these areas with the relative variations of response. Including corresponding indices for the K line, from data previously published, we have:

<table>
<thead>
<tr>
<th>Line</th>
<th>Area $\theta / (\log \sin \alpha)$</th>
<th>Total variation (mean)</th>
<th>Proportion of variation modifiable (mean)</th>
<th>Variability number (mean)</th>
</tr>
</thead>
<tbody>
<tr>
<td>K</td>
<td>17.3</td>
<td>2.8</td>
<td>85</td>
<td>5.85</td>
</tr>
<tr>
<td>A</td>
<td>10.4</td>
<td>1.3</td>
<td>56</td>
<td>2.82</td>
</tr>
<tr>
<td>B</td>
<td>9.20</td>
<td>1.5</td>
<td>72</td>
<td>3.32</td>
</tr>
</tbody>
</table>
Since a larger range of observed θ’s, and of usable sin α’s, tends automatically to increase all these quantities save the variability number, it might be suspected that “number of receptor units,” total variation of response, and proportion modifiable according to excitation, should be parallel. This notion would be supported by noting that in F₁ hybrids of K × A (Crozier and Pincus, 1929–30, a), where θ-area is intermediate between those for the parental stocks, total variation and percentage controllable (α 15° to 70°) are also intermediate, but the variability number is below that for A. Other data on different lines, however, seriously disturb these apparent correlations. There is no necessary correspondence among the indices of variation and the “number of receptor units” when different lines are compared, although when dealing with individuals of a given stock such parallelism may well be expected. Since the method of estimating the “number of receptors” implicitly defines the number in terms of functional units, this situation is entirely reasonable. The parallelism of proportionate relative variation to areal measure of quantity of excitation units is closer if one ventures to extrapolate to the “ideal” threshold for excitation of the receptors of Group 1 which may be supposed to undergo excitation at threshold slope. This question is better examined with other lines of rats; it is closely connected with the relation of threshold sin α to θ at the threshold.

The remaining point to be examined is the possibility of homologous modification of the specific curves for different homozygous lines under similar experimental change of the conditions determining θ as a function of α. This should supply a test of the kind of analysis accorded the two curves. We have shown (1929-30, b) that when a mass of about 2 gm. is attached at the saddle of young rats of line K the curve connecting θ with log sin α is distorted in a way which can be understood if a good number of receptors of Group 2 are brought into action, owing to the presence of the attached mass, at a much lower inclination of substratum than otherwise suffices to do so. The question then is, concretely: Will the curve for A exhibit a similar distortion when rats of this line similarly carry an added load of about 2 gm.? The test of this point also supplies certain criteria for the variability
number and associated indices. It should be obvious that modification of this sort, if resulting in an entirely comparable disturbance of the analytical structure of the $\theta$-curve, would add considerably to the force of the assumption that the structure is competent. A corollary which likewise must be examined is, that a similar mass carried in a different position on the body must distort the usual $\theta$-$\alpha$ curve in a different way. Experiments with rats of line $A$ give results which show that by these tests the differential arrays of "receptor groups" (Figs. 19, 22) afford a rational picture of the situation as regards geo-

TABLE VI

Data from tests for extent of upward orientation, with a mass of 2.12 gm. attached at saddle position ("posterior weight"); young rats of line $A$, 13 days after birth; $\theta = 21.3^\circ \pm 0.6^\circ$. For litter $A_{19}$, $N = 4$ (2 $\sigma$, 2 $\varphi$), weighing 16.0 to 18.5 gm., for $A_{19a}$, $N = 2$ (1 $\sigma$, 1 $\varphi$), for $A_{19b}$, $N = 3$ (all $\varphi$), weights 17.0 to 18.0 gm.; $n = 20$ throughout. See text.

<table>
<thead>
<tr>
<th>Litter</th>
<th>$\alpha$, degrees</th>
<th>$\theta$, degrees</th>
</tr>
</thead>
<tbody>
<tr>
<td>$A_{19}$</td>
<td>20</td>
<td>64.14 $\pm$ 1.10</td>
</tr>
<tr>
<td></td>
<td>30</td>
<td>69.94 $\pm$ 0.986</td>
</tr>
<tr>
<td></td>
<td>35</td>
<td>69.13 $\pm$ 0.936</td>
</tr>
<tr>
<td></td>
<td>45</td>
<td>73.46 $\pm$ 0.830</td>
</tr>
<tr>
<td></td>
<td>55</td>
<td>78.44 $\pm$ 0.616</td>
</tr>
<tr>
<td></td>
<td>70</td>
<td>73.08 $\pm$ 0.580</td>
</tr>
<tr>
<td>$A_{19a}$</td>
<td>25</td>
<td>66.37 $\pm$ 1.16</td>
</tr>
<tr>
<td>$A_{19b}$</td>
<td>25</td>
<td>65.32 $\pm$ 0.976</td>
</tr>
</tbody>
</table>

tropic excitation and orientation in both line $K$ and $A$. The further extension of these analytical experiments with added loads will be considered at some length later on.

Tests were made with $A$ litters, each rat carrying a brass weight attached with chicle on the back at the saddle position; the total mass added was 2.12 to 2.13 gm. (cf. Crozier and Pincus, 1929-30, b, Fig. 21). It is to be noted that the looseness of the skin makes it impossible, even with flat weights of sheet brass, to be sure of constancy in the mode of pull exerted by the added load. Even with this handicap, however, the results are unequivocal (Table VI; Fig. 19). The manner
Fig. 19. Orientation-angle $\theta$ as function of slope of substratum, when a mass of 2.12 gm. is attached at saddle position of rats of line A. The curve for unloaded rats is transferred from Fig. 4.

Fig. 20. Variability of orientation-angle in A rats with posterior load ($A_{19}$ solid circles); V.N.$\theta$ = 3.06. For $A_{16}$, without load (open circles), V.N.$\theta$ = 2.29; and for $A_{16}$, without load, 2.58.
in which the $\theta$-log $\sin \alpha$ curve is distorted by the additional mass carried is precisely that exhibited by the $K$ curve with the same added mass carried in the same position. A low-$\theta$ segment is lifted, made a little less steep; a flat portion is apparent in the mid-region; the high-$\theta$ end of the curve cuts below that for orientation without the weight.

As with $K$, at given $\alpha$ the variation of $\theta$ ($n$ and $N$ equivalent) is less with load than in its absence. At equal $\theta$'s the variation is about the

\[ \frac{\Delta \phi}{\Delta (\log \sin \alpha)} \]

**Fig. 21.** $(\Delta \phi)/(\Delta \log \sin \alpha)$ vs. $\sin \alpha$ for $A$ rats with posterior load. The corresponding graph for the unloaded rats is transferred from Fig. 17.

The differential curve, Fig. 21, is of the type found for $K$ individuals
with the load similarly placed. The effect of the posterior weight is exerted through action upon each of the three groups of receptors, but particularly upon I and 2; the dissection of Group 2 from Group I is in this way made clear.

The area under the differential curve is 7.12 units, as compared with 10.3 units in the absence of load. The ratio $10.3/7.12 = 1.45$ cor-

**TABLE VII**

Two series of tests, rats of line A, 13 days after birth, 2.12 gm. on back at shoulder level ("anterior position"); A$_{18}$ ($n = 20, N = 3$), A$_{19}$ ($n = 20, N = 2$); temperature $20.5^\circ \pm 1.0^\circ$. (These individuals also tested for orientation with posterior weight, and for orientation without added load.) Inclination of surface = $\alpha$, mean orientation angle = $\theta$. See Fig. 22.

<table>
<thead>
<tr>
<th>$\alpha$, degrees</th>
<th>$\theta$, degrees</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>A$_{18}$ degrees</td>
</tr>
<tr>
<td>20</td>
<td>51.25 ± 1.18</td>
</tr>
<tr>
<td>25</td>
<td>55.22 ± 1.24</td>
</tr>
<tr>
<td>30</td>
<td>61.13 ± 1.07</td>
</tr>
<tr>
<td>35</td>
<td></td>
</tr>
<tr>
<td>40</td>
<td></td>
</tr>
<tr>
<td>45</td>
<td>78.21 ± 0.758</td>
</tr>
<tr>
<td>50</td>
<td>81.16 ± 0.602</td>
</tr>
<tr>
<td>55</td>
<td></td>
</tr>
<tr>
<td>60</td>
<td></td>
</tr>
<tr>
<td>70</td>
<td></td>
</tr>
</tbody>
</table>

responds closely to the ratio of the total proportionate variations in the two cases: $56/39.5 = 1.42$.

The same additional weight differently disposed could not produce the same effect upon the $\theta$-curve, if our understanding of the case is adequate thus far. Tests were made with the same mass (2.13 gm.)
attached on the back at shoulder level. The data are given in Table VII, plotted in Fig. 22. In this figure the central lines for $\theta$ without added weights, and for $\theta$ with the weight posteriorly located, have been included. The differences are obvious.

When the added mass is carried anteriorly the conditions are mechanically altered in two respects: an added load is moved, and the center of gravity is shifted toward the head and upward. The latter change tends to endanger stability; regardless of the total mass moved, the rat must then turn to a higher $\theta$, at given (high) $\alpha$, to achieve sensory equivalence of tension excitation on the two sides of the body. This effect must be combined with the influence of a differently excited
array of receptor units. The situation is to this extent not unlike that in *Uca* (Kropp and Crozier, 1928–29). The net result of both effects is to produce a much more rapid general increase of $\theta$ with increasing $\alpha$ than in the absence of the anterior load. Since the posteriorly located weight moves the centroid caudally, it should not affect mechanical stability during progression to anything like the same extent. We need not expect, then, that the curves with posterior and with anterior weights will be in all respects comparable, since additional new types of tensions may be brought into play by the weight anteriorly placed. The unravelling of these effects requires, for one thing, experiments in which a mass of 1 gm. is carried at the saddle, and 1 gm. at shoulder level; but these need not concern us at the moment, since all we look for now is indication that diversely located weights act diversely upon our array of receptors, and par-

![Graph](image-url)

**Fig. 23.** $(\Delta \theta) / (\Delta \log \sin \alpha)$ vs. $\sin \alpha$, for $A$ rats with added load at shoulder level. The curve is resolved into the three typical sub-areas, shifted from their positions in the absence of anterior load, plus area $2a$; see text.
particularly upon the three large groups distinguished in the antecedent analysis. Fig. 23 shows that the search is not unrewarded.

With the mass carried anteriorly, the variation of $\theta$ is not materially affected; the variability number, figured as $\Delta \frac{P.E.}{\theta}/\Delta \theta$, and corrected as before for $n$ and $N$, is (Fig. 24) 2.36 to 2.84; this cannot be held really divergent from the corresponding index in the absence of loads, or even when the load is in the posterior position (vide supra). It is to be remarked that the way in which the variation of performance keeps parallel in its behavior to $\theta$ is entirely consistent with the idea that $\theta$ is a measure of the excitation at orientation.

The differentiation of the $\theta$-log $\sin \alpha$ curve for $A$ rats with anterior weight results in Fig. 23. The resolution of this graph can be made as indicated in the figure. The area of sub-curve 2, measured after the analysis, is 6.20 units, identical with the area (6.18) obtained for 2 in the absence of weight (Fig. 17). The form of 2 is very slightly
modified, however; the distribution is flattened a bit and as a whole moved to a slightly lower \( \sin \alpha \). The absence of group 3 from its usual position permits a test of the form of the curve for 2; it will be noticed that the right-hand margin of the symmetrical curve is simply the result of plotting \( \Delta \theta / \Delta \log \sin \alpha \) against \( \sin \alpha \); it is probably more than a coincidence that in spite of the chances of curve-fitting the areas of 2 should come out identical with the anterior weight and without. Group I area is again practically unchanged, its left-hand outline very slightly altered. Group 3 is brought into action at much lower slopes. The additional area 2a, 0.36 units, is required to complete the construction of the differential curve as found. Noticing that \( \theta_{\text{max}} \) (at \( \alpha = 70^\circ \)) is definitely greater with the anterior load, 83° as compared with 80° in the absence of load, it is natural to relate the increase to a greater number of receptor units involved. On this basis 83° - 80° = 3° = 0.36 excitation units, and 1° of orientation angle = 0.12 units of receptors. The total areas under the curves in Figs. 17 and 23 are respectively 10.3 and 11.0 units, almost exactly in proportion to the maximum \( \theta \)’s attained, whence 1°\( \theta \) = 0.13 units of area; sub-group 2a should thus correspond in area (0.36±) to about 3 orientation units brought into action above \( \alpha = 15^\circ \). In terms of the notion used for the curves with race K (Crozier and Pincus, 1929-30, b), the total areas under the differential curves (i.e., the numbers of excitation units), ought to be proportional to the differences between \( \theta_{\text{max}} \) and \( \theta \) at threshold slope; inaccurate location of lower thresholds for excitation, and disturbances due to shifts of centroid (particularly with weight in the anterior position) interfere with this estimation.

The nature to be ascribed to area 2a in Fig. 23 is of course obscure. It may perhaps correspond to the effect of the altered position of the center of gravity in bringing into play a “new” set of tension receptors; or it might represent a functional dissection of the asymmetry of our “Group 1” which is suggested at its left-hand side. In either case, if we subtract its area from the total, leaving 10.7– units, the ratio of increase of \( \theta \) above threshold response to area becomes 2.8, corresponding to 2.6 for the case without load, 2.25 with posterior load (assuming for the latter instance threshold \( \alpha = 20^\circ \), which is probably a little too high; if lower, the ratio would agree more nearly with the two others).
The effect of the anteriorly-located weight clearly suggests that sense-organ Group 3 is located in the anterior legs. The possibility of more detailed localizations is fairly obvious.

SUMMARY

Extension of analysis of the functional basis of geotropic excitation and response in young rats has made it desirable to obtain, for additional genetically stabilized lines, further tests of the quantitative reproducibility of orientation data as secured from successive generations in these lines over a period of several years; and of the measures of variation of performance as these are related to the exciting vector and to the extent of orientation. Procedures are illustrated whereby the significance of measurements can be checked automatically. It is shown that differences apparent in the geotropic behavior of three inbred lines of *R. norvegicus* are quantitatively recoverable over a period of nine generations. The constant, characteristic features for each inbred line concern: the extent of upward orientation, absolutely and as a function of the inclination of the substratum; the threshold slope for orientation; the dispersion of mean orientation-angles as governed by the slope of substratum; the dependence of the dispersion of the relative variation of observed orientation-angles upon the intensity of excitation; and the proportion of the total variation of response which is modifiable as a function of the slope of surface.

It is also shown that when for two lines of rats the curves connecting orientation-angle with inclination of substratum differ in position and in details of form, the curves none-the-less undergo distortions of homologous type when rats of these lines creep geotropically with the same additional load in the form of a mass attached at a corresponding position on the back; and that shifting this mass to another position induces a quite different modification of the curve.

These effects are discussed in terms of the view that orientation during geotropic creeping is controlled by the adjustment of sensorially equivalent tension-excitation in the legs of the two sides of the body, and that the frequency distributions of thresholds for excitation within the several groups of receptor units concerned differ quantitatively among the inbred stocks, but are statistically constant within each line.
CITATIONS

Barnes, T. C., 1929, *J. Gen. Psychol.*, 2, 517.