

## ON THE GEOTROPIC ORIENTATION OF YOUNG MAMMALS.

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(Accepted for publication, April 5, 1928.)

### I.

An account of geotropic orientation in young rats and mice has been given in several preceding papers.<sup>1</sup> The points made were essentially these: upon a plane inclined at angle  $\alpha$  with the horizontal the path of steady progression is at a mean angle  $\theta$  to the intersection of the plane with the horizontal; the magnitude of  $\theta$  is roughly proportional to  $\log \sin \alpha$ ; more precisely,  $\cos \theta$  is a linear function of  $\sin \alpha$ ; the speed of progression obeys similar rules. These relationships were tested by a large number of observations, and specifically by the composition of fields in which the geotropic excitation was exactly counter-balanced by phototropic stimulation,<sup>2</sup> and by means of the effect of masses attached to the base of the tail. The precision with which such data may be obtained, under good conditions of temperature, age of animals, absence of photic stimulation, and selection of vigorous litters from among genetically uniform families, encouraged the attempt to investigate by their aid the possible relations in heredity of quantitative aspects of conduct. It was found that representatives of inbred lines belonging to different species of rats gave results agreeing with the equations already stated, but with various values of the respective constants.

In the papers previously published<sup>1</sup> we have relied upon measurements made with homogeneous groups of small numbers of individuals, although stating that these were given as illustrative. For the proposed investigation, however, it was first necessary to discover if with animals of a given strain, initially well inbred, the same values

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<sup>1</sup> Crozier and Pincus (1926; 1926-27, *a, b, c*); Pincus (1926-27); Crozier and Oxnard (1927-28); Keeler (1927-28); Crozier (1928).

<sup>2</sup> Crozier and Pincus (1926-27, *c*).

of the descriptive constants could be recovered with successive generations. We then sought other strains in which either the slope of the relation between  $\theta$  and  $\alpha$  might be different, or the magnitudes of the intercepts on the axes of the  $\cos \theta$  vs.  $\sin \alpha$  plot, or both. It was found that the values of the constants in the strain initially used are indeed recoverable at intervals over 15 months; and that strains differing in the desired ways are in fact procurable.

## II.

The families of *R. norvegicus* first used<sup>1</sup> were of a backcross stock between King inbred albinos and a dark-eyed (hooded) stock, labelled line *K*. This line was continued, and in two groups of experiments series of tests were again made, at different periods and with slight differences of technic, to determine the relation of the amount of orientation to the inclination of the creeping surface. The first extensive repetition of the original tests was made by a method slightly different from the one previously followed. At the beginning of each run a rat, 13 days after birth and with eyelids still unopened, was placed in a dark room at 19°–21°C. upon a large horizontal plane covered with tightly stretched wire screen of small mesh. The plane was hinged at one margin to a rigid support. When the effect of handling had more or less worn off, and the animal had begun to creep, the plane was slowly brought to a predetermined inclination to the horizontal. At the desired angle the lateral margin of the plane was held by a notched tongue of wood. In slipping into a notch a slight jarring of the plane was unavoidable, and the creeping of the rats seemed in consequence unusually variable, by comparison with series employing the older technic. The average values of  $\theta$  agreed quite well with those earlier obtained, though the variability was somewhat greater, proportionately; the slope of the best line connecting  $\theta$  and  $\log \sin \alpha$  was practically identical with that in previous tests, but the values of  $\theta$  were consistently a little lower. This was probably due in part to the lower temperature ( $20^\circ \pm 1.0$ ) prevailing in the later tests (*cf.* 23°–25° in Series I, III, etc.).

The newer technic was improved by eliminating the "catch" mechanism and substituting for it a stout cord working over a smooth pulley. The cord could be held fast at definite points corresponding to known elevations of the plane.

A series of tests with one litter of four individuals is summarized in Table I. The averages are here based upon 40 records of orientation at each value of  $\alpha$ , as in the earlier published series of measurements with 2 individuals. These conditions were chosen for the sake of a test shortly to be applied to the measurements of variability of  $\theta$ .

The manner in which the averages in Table I agree with the results of typical earlier tests is evident in Fig. 1. Here the series with line *K* already published (Crozier and Pincus, 1926-27, *a*; a confirmatory series is given in Pincus, 1926-27) is labelled "Series I," the present test (Table I) is "Series III." (Series II, previously referred to,

TABLE I.

Mean angles  $\theta$  of paths of negatively geotropic orientation of 4 individuals (litter mates) of *Rattus norvegicus*, line *K*. The inclinations of the creeping stage are given in the first column.

$\alpha$	$\theta$
20°	43.70° ± 2.05
25°	53.73° ± 2.24
30°	55.98° ± 1.72
35°	62.50° ± 1.21
45°	69.89° ± 1.18
55°	81.80° ± 0.81
70°	86.76° ± 0.43

agrees well with these but the p.e. are too large, owing to the low temperature and to the mechanical disturbances there connected with elevating one edge of the creeping platform.) In Fig. 1 it is apparent that to a reasonable approximation  $\Delta \theta / \Delta \log \sin \alpha$  is constant over the whole working range. But it is equally clear that, with these coordinates, the curve is in reality a long-drawn *S*. Every series of tests has shown this to be true. The meaning of this relationship will be discussed in a different connection.

As demonstrated previously,<sup>1</sup> the function involving  $\theta$  and  $\alpha$  which gives a rectilinear plot is  $\Delta \cos \theta / \Delta \sin \alpha = \text{constant}$ . Measurements of Series I and III are given in this form in Fig. 2.

## III.

It has been objected (Hunter, 1927) that successive readings of  $\theta$  in such experiments may give bimodal frequency distributions, or

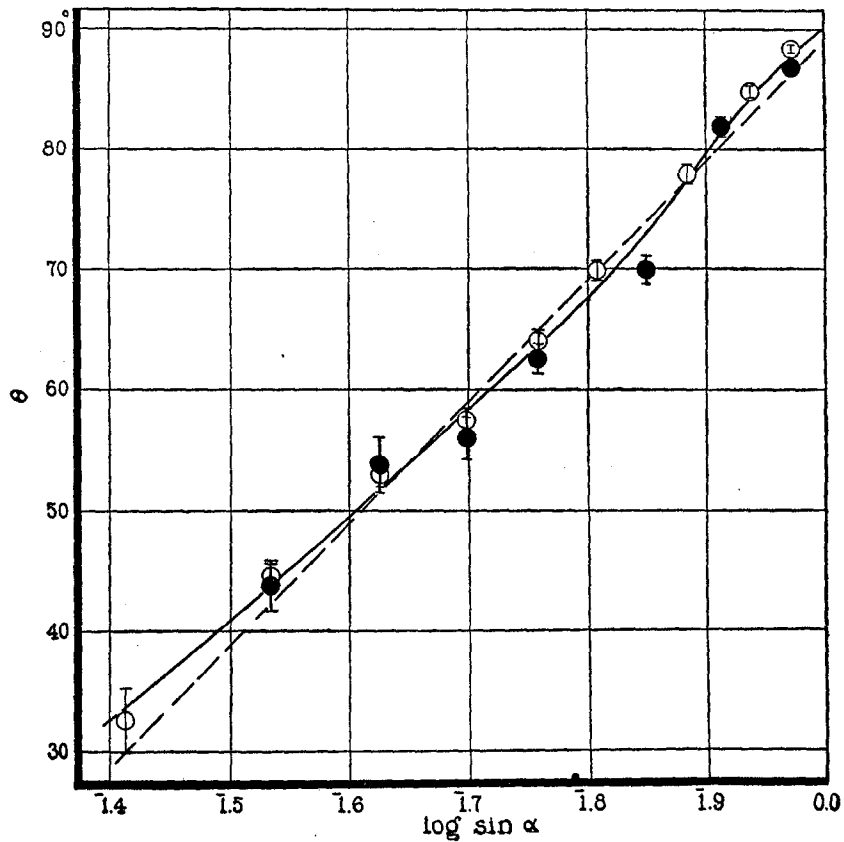


FIG. 1. Showing the agreement in the relation between amplitude of negatively geotropic orientation  $\theta$  and  $\log \sin \alpha$ , where  $\alpha$  is the angle between plane of creeping and the horizontal, in two series of tests with young rats (*R. norvegicus*, line K; see text) made 15 months apart. The height of the vertical bars = 2 P.E. For certain purposes the relation may be regarded as effectively rectilinear, though in reality sigmoid.

distributions quite asymmetrical. If proper and reasonable precautions are taken, and attention paid to the geometry of + and -  $\theta$ ,

we have found this not to be true. Certain effects which may produce such results have already been commented upon (Crozier, 1928; Crozier and Stier, 1927-28). For the present data, Series I and III, we may as a direct test consider certain properties of the measured

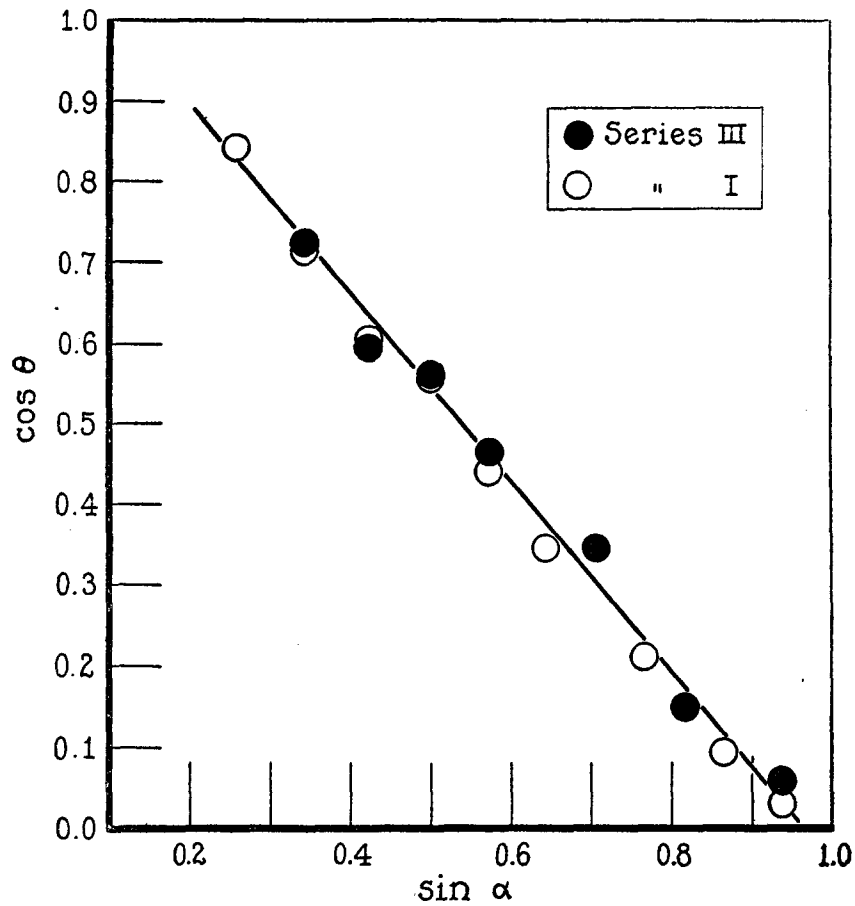


FIG. 2. The agreement of two independent series, I and III, in terms of a linear connection between  $\cos \theta$  and  $\sin \alpha$ . See text.

variability of  $\theta$  in the two series, and also the relation between *median* magnitudes of  $\theta$  from combined frequency distributions of Series I and III. Figs 3 and 4 show that the median values of  $\theta$  are related to

$\log \sin \alpha$ , and of  $\cos \theta$  med. to  $\sin \alpha$ , exactly as are the means (Figs. 1 and 2). The evidence from the P.E. of  $\theta$  is perhaps not so obvious, but is even more powerful. We already know that  $C.V. \theta$  (or,  $n$  being constant, P.E.  $\times 100$ ) decreases rectilinearly with  $\log \sin \alpha$ .

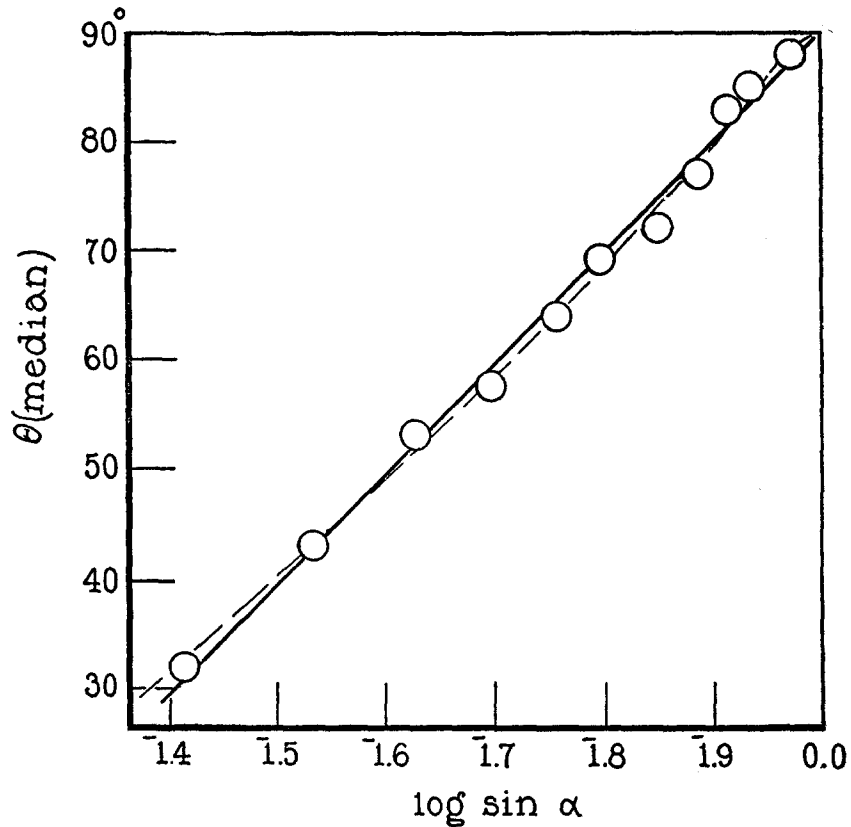


FIG. 3.  $\theta$  median from combined distributions of Series I and III bears the same relation to  $\log \sin \alpha$  as does mean  $\theta$ .

If in the course of the experiments two litters of like individuals are compared, the same number of observations ( $n$ ) being taken in each set at each value of  $\theta$ , but with more individuals in one set than in the other, then for the set with fewer individuals the relative variability should be found lower at a given value of  $\alpha$ , but should decrease less

rapidly as  $\alpha$  increases. The point is that if the experiments are properly conducted the method of averaging should eliminate all but "chance" values of  $\theta$  due to momentary individual causes; hence, since  $\Delta C.V./\Delta \log \sin \alpha$  is constant, and the gravitational vector must

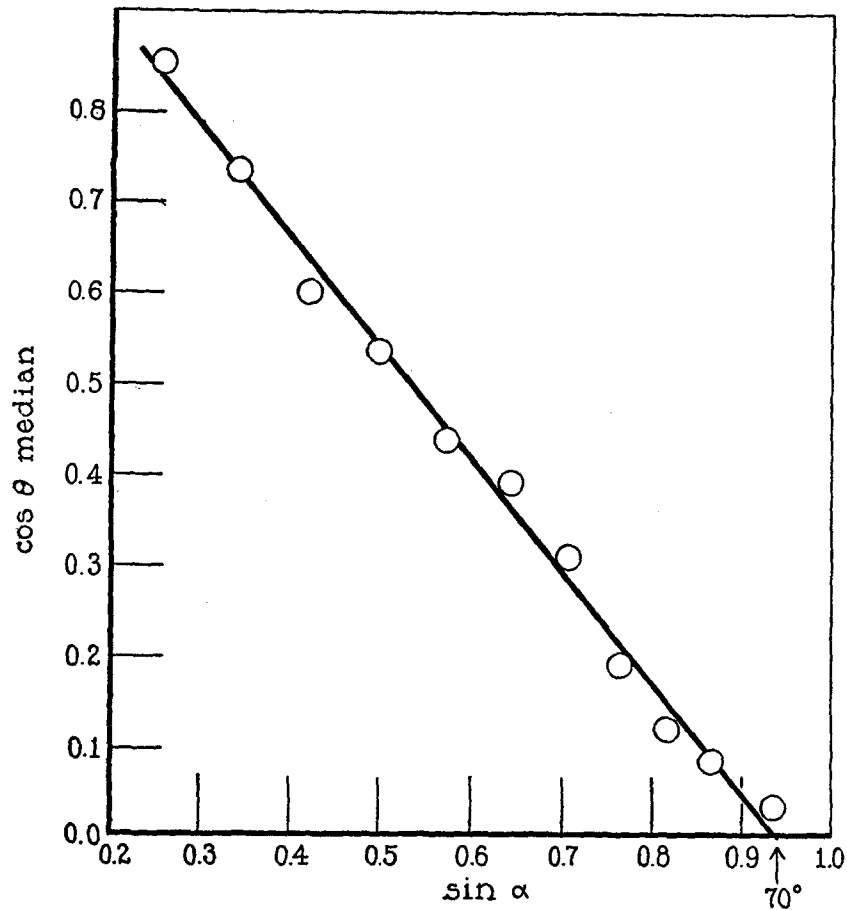


FIG. 4.  $\cos \theta$  median from combined measurements of Series I and III bears the same relation to  $\sin \alpha$  as does  $\cos \theta$  mean.

therefore be regarded as eliminating change influences of external forces capable of affecting the orientation, and according to exactly the same law as that by which  $\theta$  itself is controlled, the variability

of internal origin bulks relatively twice as large in a series with twice the number of individuals. Fig. 5 shows that in Series III, with 4 individuals, the decline of  $\frac{100 \times \text{P.E.}}{\theta}$  with increasing  $\log \sin \alpha$  is almost exactly twice as rapid as with Series I (2 individuals).

## IV.

Of great importance for the objective of these experiments is the finding of races of rats or mice in which the constants in the equations

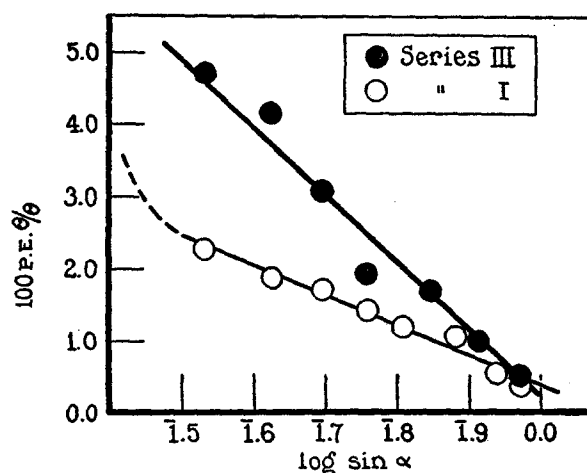


FIG. 5. The variability of  $\theta$ , expressed by P.E.  $\theta$  as a percentage of the mean (the number of variates being 40 in each case) declines directly as  $\log \sin \alpha$  increases. The rate of the decline is directly proportional to the number of individuals concerned: in Series I, 2 individuals, in Series III, 4, the slopes of the lines being in the ratio 1:2.1.

describing geotropic orientation are different from those found in the race thus far used. The genetic utilization of such differences, supposing them to be found, can provide upon the one hand a biological test of the reality of the behavior-constants, and upon the other a means for the consideration of certain concrete aspects of behavior in relation to inheritance. Two kinds of difference might be expected among races for which the general formulation already used is applicable. The slope of the rectilinear relationship between  $\cos \theta$  and  $\sin \alpha$



might be different; or, with equivalence of slope, the intercepts might not be the same. With *R. rattus* it was in fact found (Crozier and Pincus, 1927-28, *d*) that the constants in the equations differed from those gotten with *R. norvegicus*. Experiments with several strains

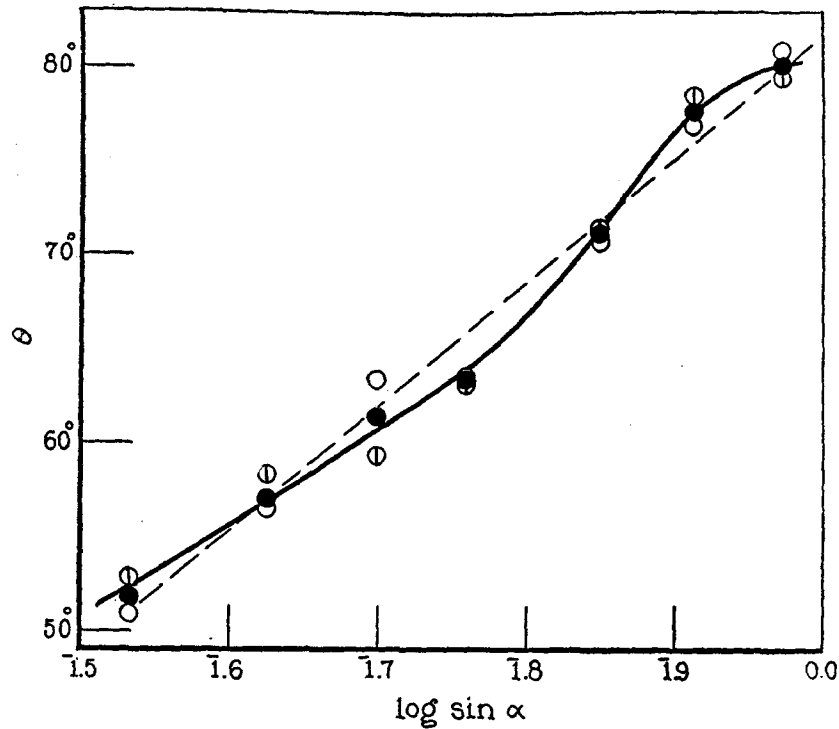


FIG. 6. Upward geotropic orientation of two series of rats of strain *A* (see text); Nos. 1-6, open circlets; Nos. 7-12, circlets with bar; means, 1-12, solid circlets. The ordinate scale is relatively larger than in Fig. 1, and the *S*-form of the relation between  $\theta$  and  $\log \sin \alpha$  is therefore more pronounced; the linear proportionality between  $\theta$  and  $\log \sin \alpha$  is still sufficiently close for some purposes.

have since shown that, independently of possible connections with body weight or slight differences of age, it is possible to obtain strains of rats and of mice in which both kinds of difference from *R. norvegicus*, strain *K* (Crozier and Pincus, 1926-27 *a*; and Pincus, 1926-27), are definite and specific. The strain most extensively used for compari-

son, labelled *A*, is characterized here in illustration of this point. This particular strain has been used with strain *K* in genetic experiments of the sort earlier forecast (Crozier and Pincus, 1926-27, *d*); the results will be considered in a subsequent paper. Strain *A* is a red-eyed yellow hooded race which had been bred brother to sister for ten generations after previous loose inbreeding.

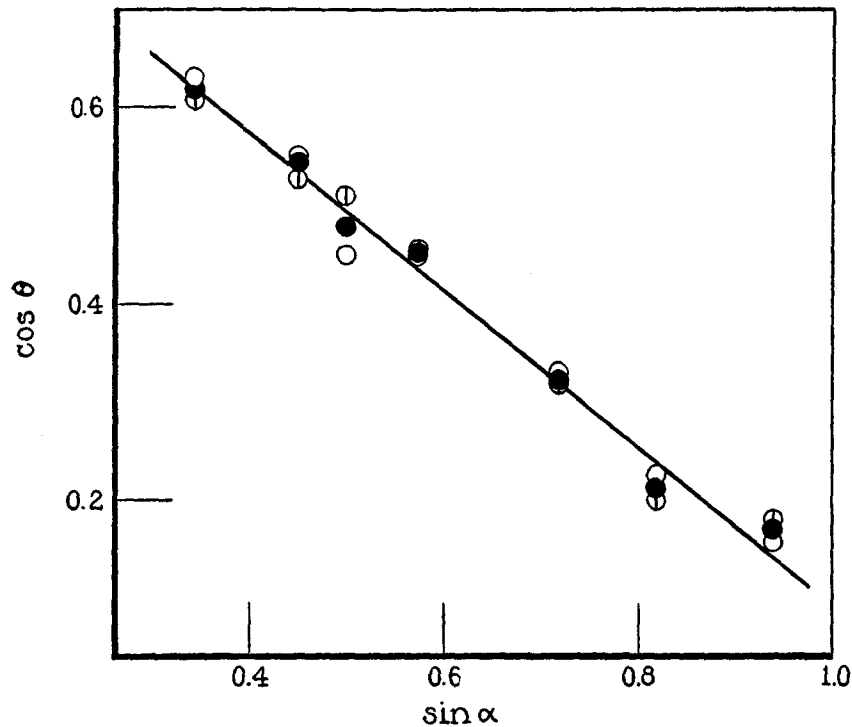


FIG. 7. The relationship between  $\cos \theta$  and  $\sin \alpha$  for strain *A*; individuals 1-6, open circlets; 7-12, circlets with bar; general means, solid circlets.

Occasional temporary geopositive orientation is observed in both the strains here considered. Such geopositive orientation is also amenable to quantitative treatment, but we do not attempt this at present. The initiation of a geopositive phase is marked by peculiar sidewise creeping during which the animal moves upward at a steadily decreasing angle, so that its path forms a curve. It may move hori-

zontally for a while, but, in any such case, it eventually turns downward and moves at an angle which is about equal to the angle ( $\theta$ ) of geonegative orientation characteristic of the angle of inclination employed. The change to a geopositive phase is almost always heralded by the peculiar sidewise movement described, during which the animal seems to be struggling between a tendency to move upward

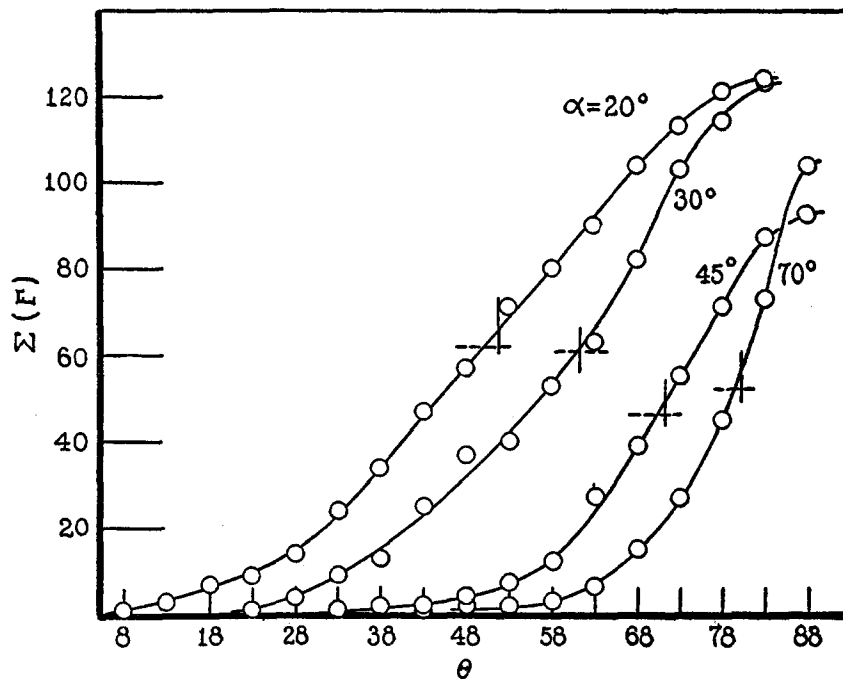


FIG. 8. Frequency distributions (line *A*, 12 individuals) of  $\theta$  at several values of  $\alpha$ . See text.

and an almost equal tendency to move downward. (Geopositive orientation seems to occur more frequently at lower angles of inclination.) Such orientation was found to occur much more frequently in line *A* than in line *K*. It is noteworthy in this connection that for line *K* measurements of  $\theta$  can be taken with some reliability at  $\alpha = 15^\circ$ , but that this is impossible with *A*. Thus there may be some connection between this greater sensitivity of line *K* to geotropic stimulation

(note also the steepness of the slope of the curve (Fig. 9)), and its infrequent geopositive orientation.

Two comparable litters of the tenth inbred generation of *A*, containing 6 individuals each, were tested independently. The weights, on the 12th day for Nos. 1-6, 13th day for Nos. 7-12, were respectively 13.0 to 15.5 gm. and 15.5 to 18.0 gm. As in earlier tests, there is no apparent correlation of geotropic performance with body weight. Differences of 2 days in age are likewise of no significance, as other experiments with individuals on successive days amply prove. Average

TABLE II.

Geotropic orientation of young rats of race *A*, 10th inbred generation (see text); 12 individuals, in 2 series of 6 each (the 2 series given separately in Fig. 6). The means from the single individuals being comparable, all are averaged together. The nature of the frequency distributions is indicated in Fig. 8.  $\alpha$  = inclination of the surface,  $\theta$  = angle of upward orientation,  $n$  = number of observations.

$\alpha$	$n$	$\theta$
20°	125	51.88° ± 0.23
25°	118	56.97° ± 0.21
30°	123	61.39° ± 0.18
35°	112	63.19° ± 0.16
45°	92	71.24° ± 0.14
55°	113	77.69° ± 0.16
70°	109	80.17° ± 0.10

values of  $\theta$  derived from trials with rats one to six and seven to twelve are plotted in Figs. 6, 7. The two series again demonstrate the kind of concordance obtainable in these experiments. The average magnitudes of  $\theta$  from all observations are summarized in Table II. With so many individuals in one series, it is worth while to refer to the frequency distributions of  $\theta$  at constant values of  $\alpha$ . The distributions (as in Fig. 8) are slightly skewed, with a "tail" of low values of  $\theta$ . Modes and medians are close together. As with other series of measurements, we can expect that the observed frequencies of negative departures from the mode should decrease almost logarithmically with the extent of the departure. This should appear most clearly

at intermediate values of  $\alpha$ , since at low values of  $\alpha$  the "normal" spread of  $\theta$  is wide.<sup>3</sup>

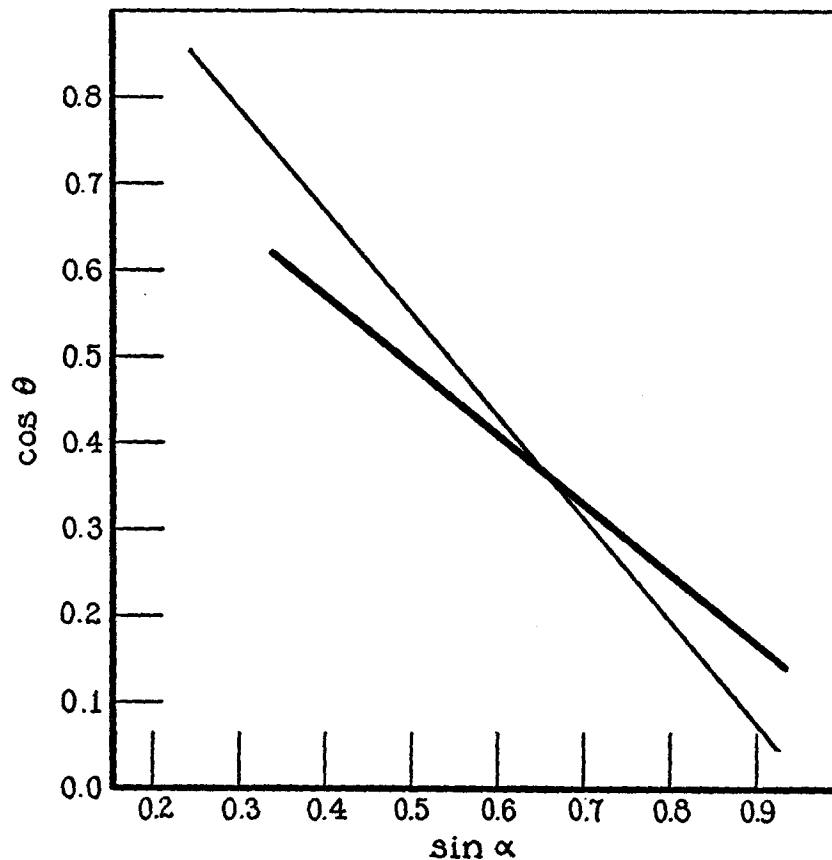


FIG. 9. Comparison of the lines connecting  $\cos \theta$  and  $\sin \alpha$ , for *R. norvegicus* line *K* and line *A*. Data from Figs. 2 and 7. See text.

Comparison of lines *K* and *A* is most easily made through Figs. 2 and 7. In Fig. 9 the lines fitting  $\cos \theta$  vs.  $\sin \alpha$  have been reproduced on one grid. The slopes are quite different, and the lines moreover

<sup>3</sup>On this basis it is possible to institute tests of series of such measurements, in a way which may be employed to discover the presence of extraneous (non-gravitational) excitation factors.

cross at  $\alpha = 35^\circ$ . This means that in comparing the geotropic reactivity of the two lines it is absolutely necessary to obtain data over the whole possible working range of  $\alpha$ . It is obvious that if the differences between lines *K* and *A* correspond to heritable differences, litters obtained by simple systems of crossing between *K* and *A* should be expected to exhibit considerable variability in the measurable relations of  $\theta$  to  $\alpha$ . On the other hand, these differences can be made the basis of a genetic analysis.

#### SUMMARY.

Constants in equations of curves describing the geotropic orientation of young rats are repeatedly obtainable from litters of successive generations of the same inbred strains. Different inbred strains have been obtained for which the respective constants are quite unlike.

Such findings show how necessary it is to employ biologically uniform material in experiments of this kind. And at the same time they are convenient as a starting point for genetic analysis.

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