ON THE PLACE OF PHOTIC ADAPTATION.

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I.

As a method for the investigation of photic adaptation in a phototropic organism we have employed the measurement of phototropic divergence from the vertical path of geotropic creeping of the slugs *Agriolimax campestris* upon a perpendicular plate, the source of light being at one side (Wolf and Crozier, 1927-28). This divergence decreases with time, and in a manner easily accounted for by the simplest assumptions. The point we now discuss concerns the assumption that the decreasing effectiveness of light in driving the animal away from its course in darkness is due to photic adaptation of the eye. Clearly, there are at least two general possibilities in such a case. Either the continuous interplay of the inner (central) mechanisms respectively concerned with the geotropic and with the phototropic orientations results in the gradual establishment of a condition which internally "blocks" impulses arising in the eye; or else the photic irritability of the eye declines with continued exposure to light. The manner in which the behavior simulates "learning" is worthy of note.

It is important to obtain some means of deciding between the two alternatives, on the one hand of a (presumptively central nervous) adjustment resulting from competitive excitations, on the other a purely peripheral sensory adaptation.

The test relied upon to further a decision is of a very elementary kind. It consists in comparing the forced angular divergences from vertical creeping in the case of (1) slugs exposed to light while on a vertical surface, as in the experiments previously discussed, and (2) exposed to light of the same intensity while on a horizontal surface,

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until the moment of testing. While it might be thought necessary to study also the rôle of adaptation or exhaustion with respect to continuing geotropic excitation, we find it not imperative to do so,—because continued successive tests of geotropic orientation yield, within the limits required, no evidence of geotropic fatigue; and especially because the waning influence of light, with continuous exposure, leads to greater and greater amplitude of the geotropic response. The required evidence, therefore, must show whether the extent or the apparent rate of photic adaptation is due in any way to the concurrent geotropic excitation. When under the conditions of these tests the slugs creep vertically, with no detectable influence of the lateral light, they still (for a time) orient when illuminated upon a horizontal plane (as when the creeping plate is lowered). This signifies, as we have already intimated (Wolf and Crozier, 1927-28), that a sort of threshold must be recognized for the balancing of the phototropic effect by a geotropic one; its nature can be investigated by means of observations at different inclinations of the plane of creeping, but it in no way interferes with the proposed test.

The experiments were made by placing slugs, dark-adapted over night or longer, upon a moistened plate of ground glass. The plate was horizontal, light falling upon one side of the animal. By gentle rotation of the plate, keeping pace with the negatively phototropic orientation, light was maintained upon that side for a known time (estimated by a stop-watch). The plate was then tilted so as to be vertical, and the angle of orientation during creeping is charted exactly during the next 0.5 minute. As in previous experiments (Wolf and Crozier, 1927–28), the angle of deviation from vertical, measured to 0.5°, is then considered to be that appropriate to the mid-time of execution of the trail. By suitable spacing of the intervals of exposure, data are obtained in successive trials with each of a number of individuals. Occasionally it is necessary to start the animal creeping by stroking it with a moist camel's hair brush. Such manipulation does not affect the amount of orientation. The temperature of the dark room was 20–21°.

II.

After a variety of preliminary trials, which gave results in no way inconsistent with those here recorded in detail, a final experiment was made with 81 individuals. The intensity of the testing light was constantly 29.4 f.c. Table I contains the mean angles of orientation (β) away from the vertical, with their probable errors, after different intervals of exposure to light upon a horizontal surface. During the time elapsing up to the moment of testing, therefore, there can be no question of adjustment as between geotropic and phototropic impulses. It was previously shown that for photic orientation during light adaptation, in which the phototropic vector decreases in magnitude, the angle β should be expected to vary in such a way that the logarithm of its tangent decreases linearly with time (Wolf and Crozier, 1927–28).

TABLE I.

The angle of departure of *Agriolimax* from straight upward creeping upon a vertical plate illuminated from one side decreases with exposure time. Data from experiments with 81 individuals, the creeping plane being horizontal except during execution of the trails from which β is measured. Orienting light = 29.4 f.c. The calculated values are obtained from the curve fitting earlier data secured under continuous geotropic excitation.

Exposure time	β found	β calculated
min.		
0.5	63.0 ± 0.911°	65.2°
1.0	58.3 ± 1.19°	57.6°
2.0	42.6 ± 1.85°	41.0°
3.0	22.8 ± 1.06°	24.2°
4.0	14.1 ± 1.35°	13.7°

It is quite apparent that this relationship is accurately obeyed in the present case also, as shown by Fig. 1. The formula expressed by the graph in Fig. 1 results from the assumptions (1) that the geotropic effect is constant and (2) that the phototropic effect decreases exponentially with time. The nature of the present result indicates that the general character of the photic adaptation is independent of concurrent geotropic excitation.

The analysis can be carried further. It was shown that the *rate* of photic adaptation in these slugs is independent of season, and that data secured from separate lots of individuals under comparable conditions agree quantitatively (Wolf and Crozier, 1927–28). Such comparisons are facilitated in a practical way by the fact that the rate

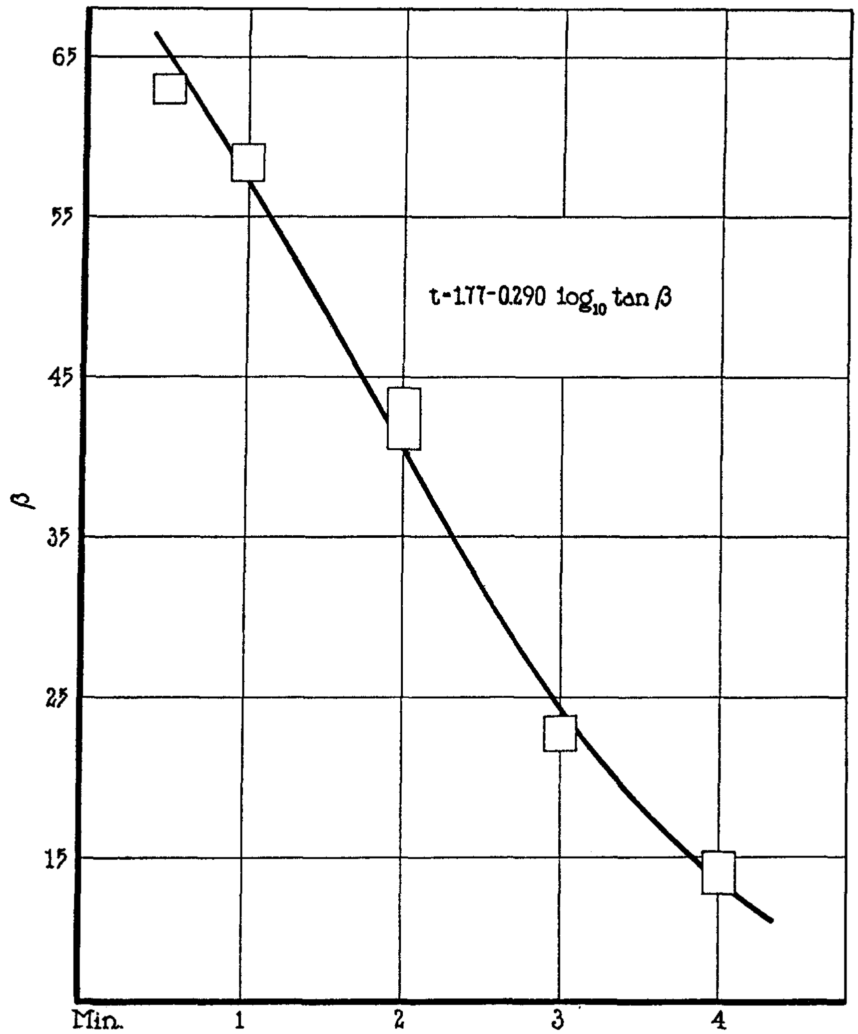

FIG. 1. The angle of orientation of *Agriolimax*, the departure (β) from a vertical path upon a vertical plane as forced by the phototropic effect of light from one side, after increasing periods of exposure to illumination of 29.4 f.c. The slugs were creeping upon a *horizontal* surface except during the half minute required to obtain the orientation trail. The observations are plotted as bars centered on the means, with height = 2 P.E. The curve is that of the equation

$$\text{time} = 1.77 - 0.290 \log_{10} \tan \beta,$$

and the agreement with the observations shows that, as found previously (Wolf and Crozier, 1927–28), log tan β decreases linearly with time.

of light adaptation is practically independent of temperature (within the range 15° to 22°). Legitimate comparison may therefore be made between the measurements of the present series and those already

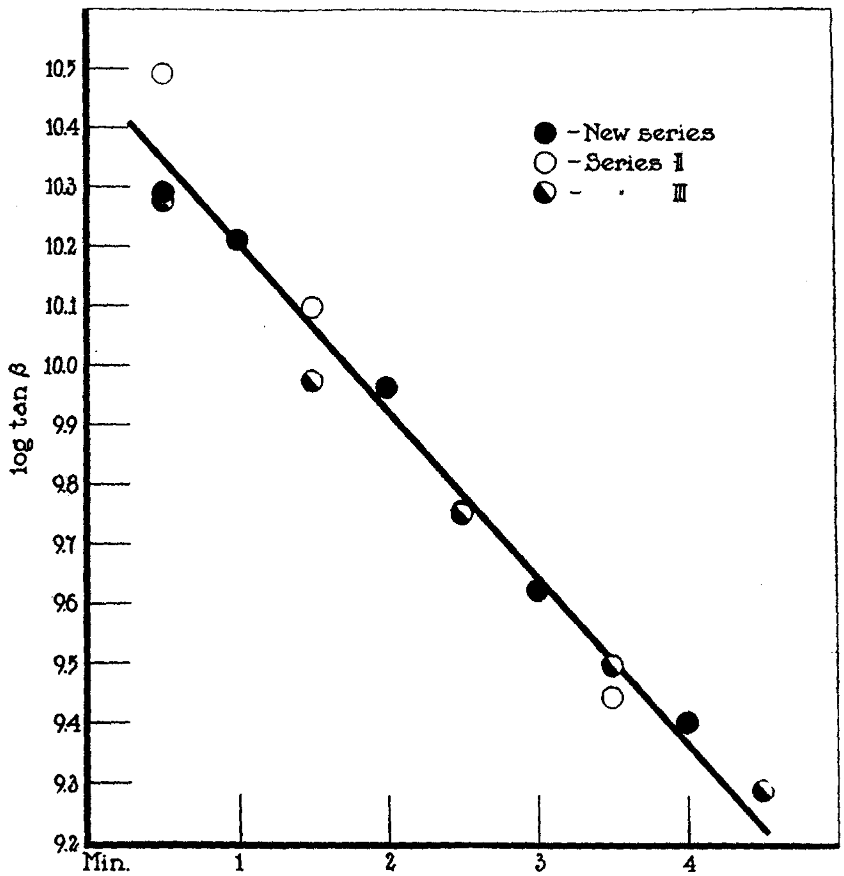

FIG. 2. Data from two earlier series (II, III) of experiments are plotted together with those of the present paper, to demonstrate the agreement in the extent and in the rate of photic adaptation, and thus their independence of continuous concurrent geotropic excitation, as practiced in Series II and III.

given in the previous paper for adaptation to light of the same intensity. It is evident from Fig. 2 that the two series are in excellent agreement, not only in their general course but also in every quantitative detail, including the important matter of the *rate* at which adaptation takes place. In fact, the curve in Fig. 1 is that obtained from the earlier observations.

III.

That adaptation to repeated or continued excitation is a matter of the sensory receptors concerned may seem to be so obvious as not to require proof. Yet a moment's consideration will show that in phenomena of phototropic excitation such as that we have considered, the conclusion is by no means self-evident. The manner in which, particularly in the presence of other modes of excitation, one form of response appears to gain ascendency over another clearly simulates the type of adjustment commonly evident in "learning." If it can be shown, as in the present instance, that the "adjustment" occurs in the absence of the competing stimulation, there is no recourse but to place the site of adjustment, not in the central nervous organ, but in the receptors. The case is thus somewhat different from that treated by Hecht (1918, 1918–19, 1922–23), in which it was shown that adapting changes in the responses of *Ciona* and *Mya* to repeated excitation by light are satisfactorily and quantitatively accounted for by the properties of a simple receptor mechanism, without appeal to "higher behavior." The difference lies in the fact that with *Agriolimax* there is involved the added complexity of another form of excitation, and the possibility of central nervous competition therefore given; from the nature of the phenomenon, moreover, it is possible to deal with the time factor in such conceivable competitions, which in certain earlier experiments (Crozier and Pincus, 1926–27) could not be managed.

SUMMARY.

The progress of photic adaptation of *Agriolimax*, when studied by the method of compounding phototropic and geotropic vectors, is shown to be uninfluenced by the concurrent gravitational excitation. Direct proof is thus obtained that the adaptation to light, manifest in its steadily decreasing effectiveness as a stimulus during the course of exposure, is not due to any central nervous adjustment simulating "learning," but is due to photochemical changes in the receptors.

CITATIONS.

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