

TEMPORARY ABOLITION OF PHOTOTROPISM IN LIMAX AFTER FEEDING.

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I.

The chance observation was made several years ago that the slug *Limax maximus* becomes temporarily non-reactive to light after feeding upon boiled potato. Raw potato did not have this effect. At the time, it was a matter of practical importance merely to avoid complications of this kind while seeking to measure the circus movements of *Limax* as a function of light intensity (Crozier and Cole, 1923). The result of feeding upon boiled potato has been verified upon a number of occasions. We have made a preliminary study of the matter with the idea that it should assist toward an understanding of temporary phases of non-reactiveness to light such as occasionally appear in each slug repeatedly tested. The problem of reversal of phototropism likewise enters, for Frandsen (1901) states that *Limax maximus* is normally photopositive toward light of very low intensities; and we have occasionally found instances of apparent positive phototropism, although we are not quite certain that this is their correct interpretation.

The general idea involved is, simply, that internal variations of the composition of body juices, for example, connected with feeding and nutrition, may determine the exhibition and the direction of phototropic orientation. This notion is of course familiar. Loeb (1889) long ago described the practical loss of heliotropism in the larvæ of *Porthesia* after their first meal. Other definite changes in behavior after feeding may be mentioned, as in connection with the geotropism of *Planaria* (Olmsted, 1917) and in relation to the homing activities of

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Onchidium (Arey and Crozier, 1921). The phototropism of *Limulus* seems also to supply a case in point. Cole (1922-23) found these animals positively phototropic when freshly collected, and (1923-24) that during the first 48 hours of laboratory confinement a great increase occurs in the percentage of photopositive responses; at the end of a week, about 50 per cent of the individuals are indifferent to light. This may be related to the fact that in *Limulus* and other forms, according to Morgulis (1922, 1923), brief laboratory confinement suffices to produce notable diminution in the proportion of sugar and of non-protein nitrogen in the blood. In a general way the interpretation of such facts is probably similar to that of the induction of phototropic behavior by the addition of various agents (CO₂, esters, alkaloids) to the environment of photically indifferent aquatic animals (Loeb, 1906; Moore, 1912). With *Limax* it has been shown (Crozier and Federighi, 1924-25) that strychnine may be used to abolish phototropism for a time. But for the understanding of a clear-cut instance of physiological state brought about by feeding, it has seemed desirable to analyze the consequences of *Limax* eating boiled potato, and to identify as far as possible the particular substance responsible for the effect.

II.

To obtain a rough measure of photic reactivity the animal was allowed to creep upon a moistened sheet of glass under which was a system of circular and radial coordinates on white paper. The slug was induced to creep in a line perpendicular to the path of a beam of light; after it had crept for about 15 cm., thus approaching the center of the observation stage, the light was admitted and the subsequent path of the animal was charted upon small scale record sheets. A number of the animals had one eye-tentacle removed a week or more before the experiments began; with these the light was admitted upon the eye-bearing side. The observations were made in a dark room, in which the slugs were kept in individual glass jars with pieces of moist rotting wood, which contributes especially fungi to the slug's diet.

When illuminated in the way described, *Limax* usually turns sharply at an angle of about 90° away from the light and then travels in the path of the beam. Rarely, an individual fails to respond; such

a slug if again tested after an interval usually reacts diagrammatically. The light intensity used in these tests was approximately 200 m.c. Sometimes a higher intensity is required to call forth the sharpest orientation. These are but aspects of a fluctuating state of phototropic responsiveness such as any animal exhibits. The feeding experiments with *Limax* suggest a means of their interpretation.

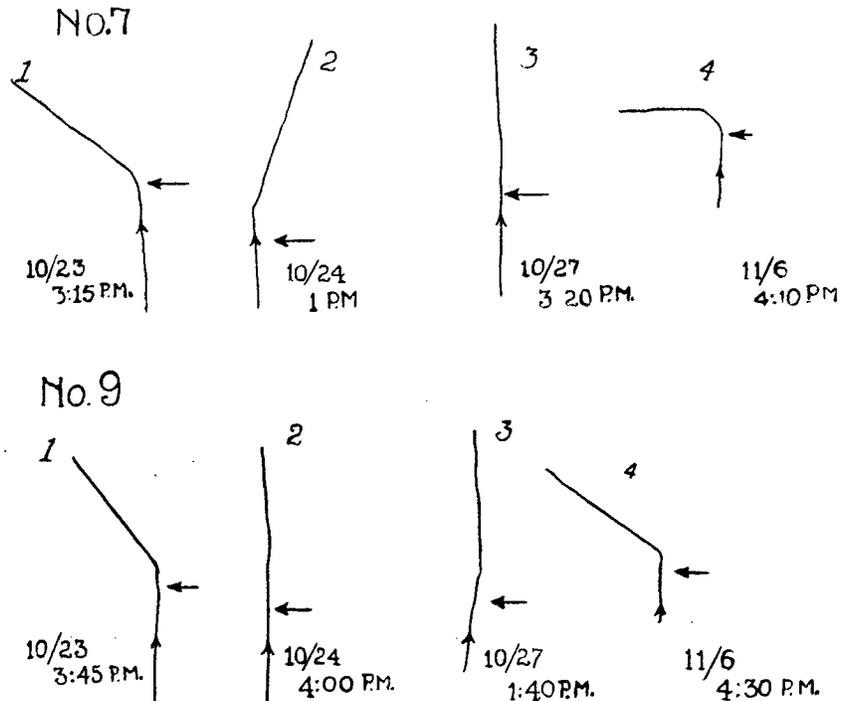


FIG. 1. Tracings of records obtained with two slugs (Nos. 7 and 9) before (1) during (2, 3) and after recovery from (4) a diet of cooked potato. The potatoes were boiled for 15 minutes. The arrows indicate the direction of illumination and the point on the path at which light was admitted. Scale 1:10.

Typically illustrative experiments serve to indicate the nature of the results. Fig. 1 contains graphic records of the behavior of individuals No. 7 and No. 9. On October 23rd their phototropism was tested, and found decided and negative. When tested in this way, with horizontal light, slugs with but one eye-tentacle may not react with such diagrammatic completeness (*i.e.* 90° turn) as do normal

ones. They were then put in jars each with a boiled potato, of which they ate considerable quantities. On the next afternoon these slugs were indifferent to light, or even in some trials (of which one is given) slightly photopositive. They were left with the potatoes, and ate further; next day the tests were repeated, with the same result. They were then removed to jars provided with bits of rotting wood, and in several days were found again normally photonegative in behavior. The average deflection of slugs repeatedly tested on the day of a boiled

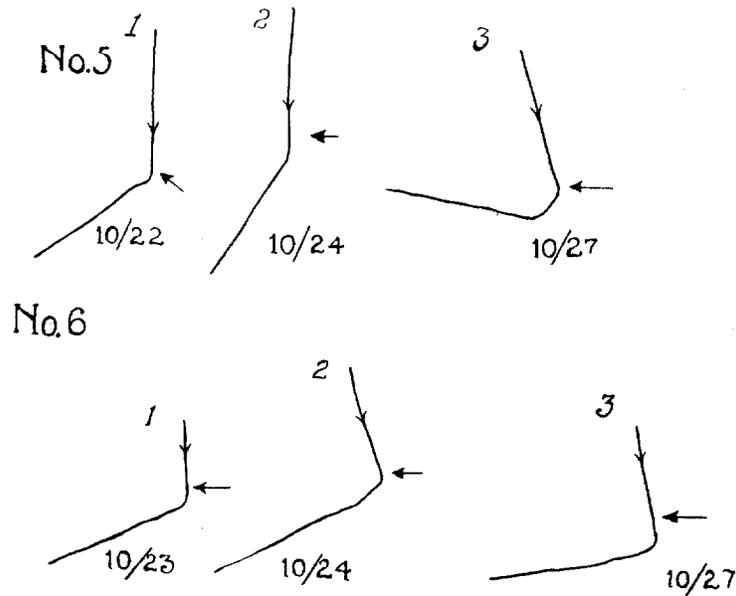


FIG. 2. Showing that a diet of raw potato, even continued for 5 days, does not suppress phototropism.

Individuals 7, 9, 5, and 6, had one eye-tentacle removed. Scale 1:10.

potato meal was 3.7° away from the light. The tests were all made at the same time of day. Raw potato is eaten just as readily as cooked, but does not result in the disappearance of phototropism. Typical results are shown in Fig. 2. The mean photonegative deflection of slugs fed on rotting wood was 54° , of those fed on raw potato 50° .

Suitable control tests showed that the skin of the potato was not concerned with these effects; that other (raw) foods, such as cabbage or apple, did not interfere with phototropism; and that starvation (for as much as 3 weeks) does not materially influence phototropism.

III.

The fecal masses deposited by slugs which have eaten raw potato are whitish, firm, and bulky. They contain quantities of undigested starch grains. Fecal masses from *Limax* fed on boiled potato are much smaller, more slimy, and contain relatively few starch grains. (Data on the amolytic activity of the digestive secretions of pulmonates

No.14

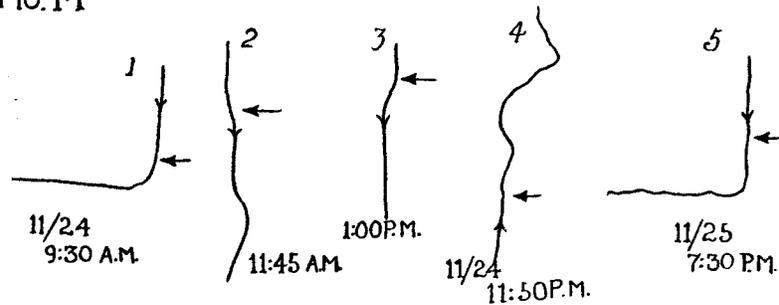


FIG. 3.

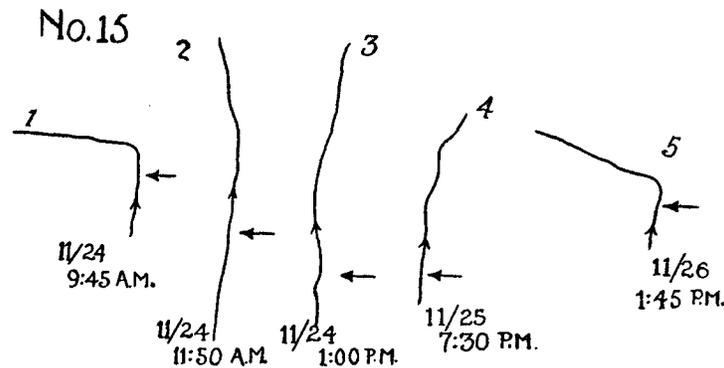


FIG. 4.

FIGS. 3 and 4. The effect of injecting 0.3 cc. of $m/4$ sucrose solution into the stomach of *Limax* No. 14. This animal had both optic tentacles intact. Trail 1, before injection; at 11:15 a.m. the sucrose solution was put down the esophagus, and 30 minutes later Trail 2 was obtained. Trails 3 and 4 show continuance of non-reactivity until 11:50 p.m. (tests were made at intervals of several hours); by 7:30 p.m. the next day negative phototropism was fully recovered.

A duplicate experiment, with Slug 15, is detailed in Fig. 4. The effect lasts about $1\frac{1}{2}$ days. Scale 1:10.

is reviewed by Jordan (1913).¹ It was assumed that the influence of cooked potato on phototropism might be due to an effect of carbohydrate metabolism. Cooked potato starch, and corn-starch, was fed to slugs previously starved for several days. At most $\frac{1}{4}$ teaspoonful was all that was eaten. No definite influence on phototropism was apparent, but this may be due to the fact that not much starch was ingested; moreover, tests were not made until 12 hours after feeding.

By moistening the oral field of a *Limax* with M/10 sugar solution the lips are caused to open widely and the mouth parts engage in feeding movements. A slender pipette can then be inserted into the stomach. In this way sugar solutions were injected. The history of two such experiments is given in Figs. 3 and 4. The results of other trials agreed perfectly with these. When tap water was injected no effect was detected.

It appears, then, that the ingestion of sucrose is followed by the definite suppression of phototropism, precisely as in the case of digestible starch in the cooked potato.

In order to complete the proof, sugar solutions were injected into the body cavity. The needle was inserted near the caudal keel, in order to avoid damage to the heart. Sucrose solution (0.5 cc. of M/10) had a relatively slight effect; several animals were made almost photically indifferent after about 2 hours, and remained so for 15 hours. A similar quantity of levulose solution, or of dextrose, led to complete photic indifference within 2 to 4 hours (during the 1st hour after injection much slime is secreted, and the animal does not creep well). A larger number of animals is required than is available at this season before the relative efficiencies of sucrose and of reducing sugars can be established, and to study the variations in blood sugar.

We are for the present unable to trace further the mechanism of the action of carbohydrate in suppressing phototropism. Two points we expect to study are (1) the possible decreased alkalinity of the body juices (or, locally, of nerve centers?) during sugar consumption; and (2) the possibility of reversing the effect.

¹ Jordan (1913), p. 298.

SUMMARY.

When fed upon *cooked* potato the slug *Limax maximus* becomes for a day or more indifferent to light—its natural negative phototropism is suppressed. This effect is not produced by raw potato or other diets; it can be duplicated by injection of sugar solutions into the stomach or into the body fluids, and seems to be due to sugar absorbed during the digestion of the cooked starch. The fact is of interest particularly for the suggestion which it affords as to the explanation of fluctuations in conduct.

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