PHOTOKINESIS AND TONIC EFFECT OF LIGHT IN UNIONICOLA

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Orientation responses of plants and animals to light are often related in a simple direct manner to the light intensity or to the logarithm of the light intensity. If the reaction is directly proportional to the light intensity and to time the reaction is often said to obey the Bunsen-Roscoe law; if proportional to the logarithm of the light intensity the response has usually been considered to agree with the so called Weber-Fechner law. In the case of free-moving organisms, responsive to light, it has been debated whether light had any appreciable effect other than on primary orientation. Certain investigators, notably Patten (1917), Moore and Cole (1921), and Cole (1922), found a kinetic effect of light, while Dolley (1917) and Mast and Gover (1922) failed to find an effect of light intensity on rate of progression and denied the probability that there was such an effect.

It has been demonstrated in the case of larvae of the mussel-crab *Pinnotheres maculatus* (Welsh, 1932) that light has a decided effect on rate of locomotion, and that over a certain range of intensities the velocity of progression increases as a definite function of the light intensity. The relationship, however, is not simple and obeys neither the Bunsen-Roscoe law nor the so called Weber-Fechner law.

Speed of progression in a free-moving organism is due to a combined effect of amplitude and frequency of movement of locomotor appendages, or of muscles concerned in locomotion. One or both of these factors might change with changing intensity of illumination, and the relation of either one to intensity might perhaps be simpler than that between velocity of progression and intensity. A change in amplitude of leg movement dependent upon light intensity would be due to a change in muscle tonus, thus lending support to the theory upheld by Loeb (1918), Garrey (1918–19), Crozier and Cole (1923), Crozier and Federighi (1924–25, *a* and *b*), to cite only a few of the instances where differential muscle tonus, due to light, has been proposed or definitely shown to account for posture and orientation. The question of frequency and extent of muscular contraction, and of posture, as related to the external stimulus, is important for the understanding of tropistic behavior and it was considered desirable to study further the photokinetic effect of light.

The swimming appendages of *Pinnotheres* larvae are too small to be easily seen and another more suitable form was selected. The water mite, *Unionicola ypsilophorus* var. *haldemani* Piers, found living as a parasite on the gills of *Anodonta cataracta* Say is, when free from host material, distinctly positive to light (Welsh, 1930). It progresses by using only the middle two of four pairs of legs; the first pair is extended forward, the fourth pair drags behind as balancers. When these animals travel in water, on a suitable surface such as ground glass, their rate of locomotion is very constant in light of a constant intensity, and they proceed in a straight line toward a source of light. It is possible to obtain uniform data on velocity of progression as a function of light intensity and at the same time to determine the frequency and extent of leg movements.

The experiments were carried on under essentially the same conditions as in the work on the larvae of *Pinnotheres*. The mites were placed individually in a glass trough 30 × 4 × 4 cm., having a ground glass bottom and polished sides. The bottom was divided into 5 cm. lengths. The trough was partially submerged in a water bath kept at 18.7°C. ± 0.2° to eliminate temperature changes. The light sources were 6 volt, ribbon filament lamps, one at either end of the tank, arranged to yield parallel beams of light of the dimensions of the inside of the trough. The illumination toward which the animals were attracted and adapted before each trial was 21.7 foot candles at the center of the trough. The variable light source, without filters, gave an illumination of 255 foot candles at the middle of the trough, and by means of Wratten neutral tint filters this could be reduced to 68.0, 10.6, 1.95, or 0.185 foot candles.

In a test an animal was attracted toward the adapting light and after 2 to 3 minutes the light beams were reversed, the animal allowed to travel 10 cm., and then timed for the next 10 cm. With this procedure, time consumed in primary orientation did not enter, and a uniform rate of movement had been acquired before measurement was begun. Leg movements could be counted easily at the four higher intensities, but below 1.95 foot candles, while it was possible to see the animals clearly, it was not possible to count the leg movements.

Table I gives velocities, expressed as the reciprocal of the time to travel 1.0 cm., for three individuals. These have been selected as representative of several series which it was found inadvisable to average. Each velocity is the average of five determinations at a

TABLE I

Velocities of progression (centimeters per second) for three individuals at five different intensities of light. Temperature 18.7° ± 0.2°.

Illumination (foot candles)	Series 1	Series 2	Series 3
0.185	0.318	0.333	0.369
1.95	0.338	0.351	0.376
10.6	0.352	0.375	0.391
68.0	0.392	0.407	0.400
255.0	0.410	0.420	0.408

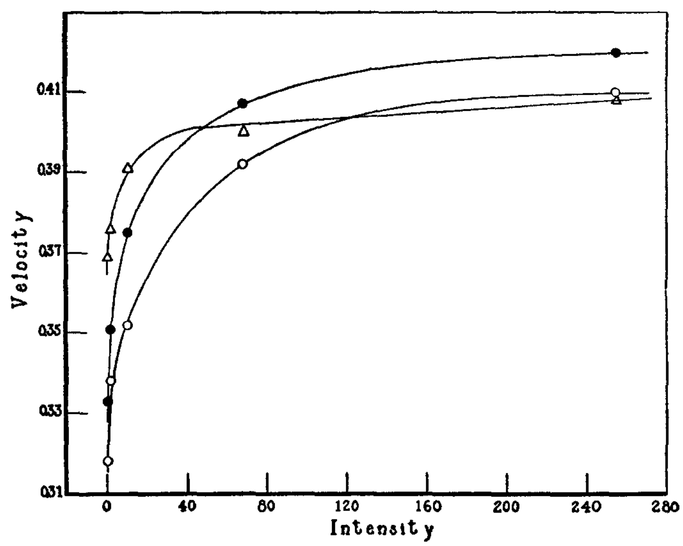

FIG. 1. Data of Table I plotted as velocity (cm. per second) against illumination (foot candles). Series 1, represented by open circles, and Series 2, represented by closed circles, were begun at the highest intensity. Series 3, represented by triangles, was begun at the lowest intensity.

given intensity. Series 1 and 2 were begun at the highest intensity and the illumination was diminished by successive steps; Series 3 was begun at the lowest intensity and the intensity was increased. As may be seen in Fig. 1, the results for the three mites are not identical, although in each case when velocity is plotted against intensity a smooth curve is obtained; the curves are essentially similar in shape but are far from straight lines. When the same data are plotted as velocity against the logarithm of the light intensity (Fig. 2) sigmoid curves are obtained, and it is more evident that there are minimum and maximum velocities below and above which changes in light intensity have no effect. It is quite possible that in instances where

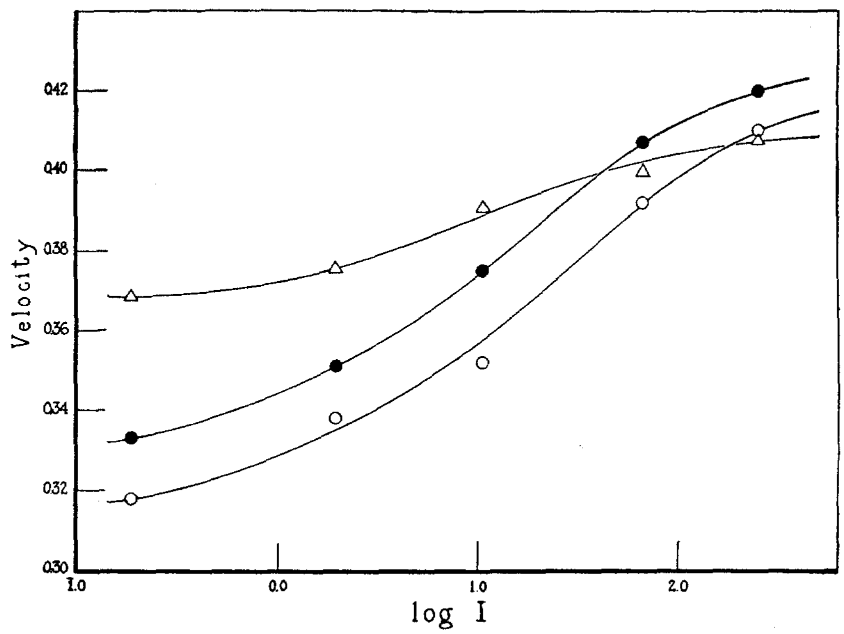

FIG. 2. Same data as in Fig. 1 plotted as velocity of movement against the logarithm of the light intensity.

such a relationship has been found to be rectilinear, and therefore considered to obey the Weber-Fechner law, that a middle range of intensities has been used which would yield essentially a straight line when rate of progression was plotted against the logarithm of light intensity. It is also possible that in cases where light has apparently had no effect on rate of progression a range of intensities above that necessary to elicit a maximum response has been used. It is evident that there is here no very simple relationship between speed of progression and light intensity; but as the "speed" is the result of a combined effect of light intensity; but as the "speed" is the result of a combined effect of amplitude of stride and frequency of stepping one would not necessarily expect a simple relation.

If we examine the data on number of leg movements as a function of light intensity (Table II) it is interesting to note that as the intensity increases and the velocity likewise increases, the number of leg movements per 10 cm. path actually *decreases*. This indicates that the length of stride must increase with increasing intensity of illumination, while the frequency might or might not change. As may be seen in Table II, both amplitude of stride and frequency of leg movements increase as certain functions of light intensity. Fig. 3 shows plots of averages of both amplitude and frequency against the logarithm of the light intensity. Amplitude of stride is seen to be directly proportional

TABLE II

Numbers of leg movements in travelling 10 cm.; average length of stride; and frequency of leg movement, at four intensities of illumination.

Illumination (foot candles)	No. of leg movements per 10 cm. path				Length of stride	Frequency
	Series 1	Series 2	Series 3	Average		
					cm.	
1.95	60.1	60.2	59.6	59.96	0.167	2.125
10.6	58.4	59.2	57.2	58.26	0.172	2.162
68.0	56.2	57.4	56.0	56.53	0.177	2.260
255.0	55.2	56.0	54.5	55.23	0.181	2.281

to the logarithm of the light intensity, as the plot yields a straight line. Frequency of stepping, however, does not bear such a simple relation and yields a sigmoid curve. Combining the effects of two factors yields the velocity curves of Fig. 2, and accounts for the shape of the curves in Fig. 2.

A somewhat similar case was investigated by Crozier and Stier (1925–26). These authors found that the relation between temperature and speed of progression in *Malacosoma* larvae was not a simple one, but that when frequency and amplitude of movement of the anal prolegs were determined as functions of temperature the frequency was found to vary directly with the temperature while the amplitude of steps did not. It is possible that such a relation exists between leg movements and temperature in *Unionicola*.

The change in length of stride in *Unionicola* is due to tonus changes in the leg muscles; this is due to the tonic effect of light, and is directly proportional to the logarithm of the light intensity over the range employed. Such effects have been studied previously chiefly during orientation, or during the exhibition of circus movements resulting from blinding one eye. In any case, the muscle tonus theory upheld by Loeb and others seems the only explanation of the observed effects.

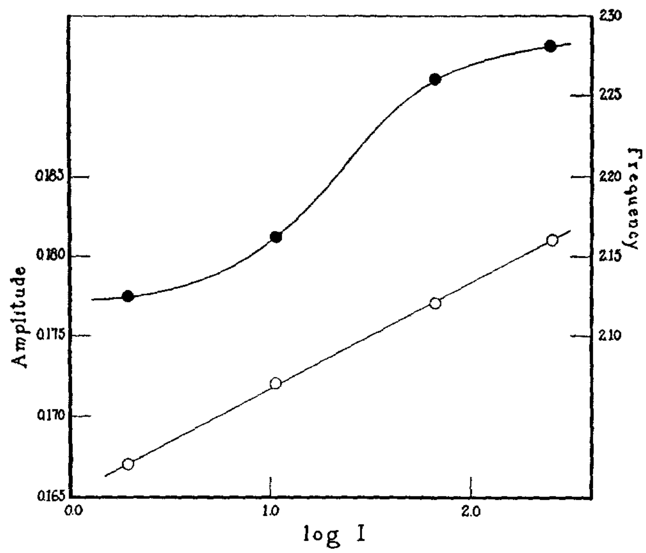

FIG. 3. Averages of amplitude of stride (open circles), and frequency of leg movement (closed circles), as function of the light intensity. Data from Table II. Combining these curves would produce a curve representing the average of those shown in Fig. 2.

SUMMARY

1. The speed of progression of *Unionicola*, a water mite, is influenced by light; and over a certain range increases as a function of the light intensity.

2. The relation between speed and light intensity is not a simple one, as the speed of progression is due to the combined effect of amplitude of steps and frequency of leg movement.

3. The amplitude of stride increases in direct proportion to the logarithm of the light intensity, while the frequency of stepping has no such simple relation to intensity.

4. The change in length of stride with changing light intensity indicates a tonic effect of light on the locomotor muscles. Such an effect has been observed previously in studies of orientation, due to unequal illumination, which produces changes in posture.

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