THE EFFECT OF LUMINOUS INTENSITY ON THE RELATION BETWEEN STIMULATING EFFICIENCY AND FLASH-FREQUENCY OF INTERMITTENT LIGHT IN THE DRONE FLY, ERISTALIS TENAX.

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It has been demonstrated in observations on the butterfly, Vanessa antiopa, and the tachina fly, Archytas aterrima, that the stimulating efficiency of intermittent light depends upon the flash-frequency and that it may be greater than, less than, or equal to that of continuous light (1), (2).

Mast (3) maintains that the fact that intermittent light has at certain flash-frequencies a higher stimulating efficiency than continuous light indicates that the processes involved in stimulation are not continuous, that there are in the nervous system alternate sensitive and refractory periods, stimulation occurring during the former and restitution during the latter. He holds, moreover, that a given quantity of energy must be received by the receptors during each of the sensitive periods and that the length of these periods consequently depends upon the luminous intensity,—the higher the intensity the shorter the period. If all this be true, then it is evident that the flash-frequency for maximum stimulation ought to be higher in strong light than in weak light. The experiments described in the following pages deal primarily with this problem.

Eristalis tenax was selected for the work because it can readily be procured and kept in excellent condition, and because it responds promptly and definitely and orients very precisely.

METHODS. At Woods Hole Eristalis was found in abundance on various flowers during the summer months. Here it was caught by net and taken to the laboratory where after clipping the wings it was kept in darkness to avoid excessive activity. A little dry granulated sugar occasionally was thrown into the finger bowls containing the flies. This was eaten freely. No water was added, but this would probably be required in drier regions. The flies remained in very good condition for a number of days so that the same individuals could be used day after day in extended series of observations.

The observations were all made on a table in a dark room in a field of light composed of two horizontal beams produced by two 100, 400 or 1000 watt stereopticon lamps so situated that the beams crossed at right angles. One of the lamps was mounted on a track in a long light-tight box so that the illumination could be easily varied by moving it back and forth. The other lamp was mounted in a light-tight cubical box which was placed on a small table. The boxes were painted dead black inside so as to reduce reflection, and each contained an opening which was screened in such a way as to produce a well-defined beam of light. Other screens were set up at various intervals in the two beams of light so as to make the field of light where they crossed 14 cm. square. The scattering of light by reflection was everywhere reduced as much as possible by means of dead black paper and velvet curtains. A rotating sectored disk was interposed in each beam. One of these was run at high speed (approximately 125 revolutions per second) by a motor connected directly with the lighting system. The other was run by a motor connected with an Edison storage battery with an adjustable rheostat in the circuit so that the rate of rotation could readily be varied and accurately controlled (fig. 1). The two disks were precisely the same, one-fourth being removed in both. The dark periods were consequently in all cases three times as long as the light periods. At the intersection of the two beams there was thus produced a field of light consisting of intermittent rays entering at right angles, the flash-frequency of those from one direction being constant and very high, and that of those from the other direction varying as desired.

It is known that if the light in the two beams in such a field is constant and equal, Eristalis will go toward a point half-way between them, and that if it is unequal it will go toward a point nearer the more intense beam. It may consequently be concluded that whenever the flies go toward a point half-way between two horizontal beams of light crossing at right angles the stimulating effect of the light in these beams is equal, regardless of the relation in quality or quantity. On the basis of this conclusion it was definitely proved in a preliminary set of tests that, with the illuminations used in the following experiments, the stimulating efficiency of intermittent light with a flash-frequency of 125 or over per second is practically equal to that of continuous light. Consequently, since the flash-frequency of the light in one of the beams in the field was always higher than this, it is evident that the effect of the light in this beam was the same as it would have been if it had been continuous and in the following experiment we shall, for the sake of simplicity, refer to it as continuous.

Intermittent light of high flash-frequency was used in place of continuous light in this beam because this made it possible to have the two lamps at the same distance from the field of observation resulting in images in the two eyes of the same size; and it also greatly simplified measurements and adjustments necessary to insure equal illumination from them. To obtain this it was only necessary to ascertain the candle power of the two lamps, adjust them so that the luminous intensity produced by them at the center of the field was equal and insert the rotating sectors. Under these conditions the amount of light received from the two beams per unit of time remained equal regardless of the relation in flash-frequency in them. Consequently, to ascertain the effect of flash-frequency on stimulating efficiency it was merely necessary to change the rate of rotation of one of the sectored disks; and to ascertain the effect of intensity it was only necessary to change the distance of the two lamps from the field and to note the direction of movement of the flies in the field. For, as previously stated, if their path bisects the angle between the beams the stimulating effect of the light in them is equal and if it does not it is unequal.

The experiments were carried out as follows: The two lamps and the rheostat were adjusted so as to produce the intensity and the flash-frequency desired. A sheet of jet black paper (25×25 cm.) was placed at the intersection of the two beams on a horizontal platform slightly lower than the lower edge of the luminous filaments in the lamps; after which the field of light, where the beams crossed, was outlined with a pencil indicating the direction of the rays in each, and a line drawn bisecting the angle between these beams. A fly which oriented accurately in a single beam of light was now selected and placed facing the light in one of the beams near the inner edge and about 5 cm. from the corner of the field farthest from the sources of light (fig. 1 x). Its path was recorded by following it with a black pencil which was long enough to make it possible to keep the hand above the beams so as not to affect the direction of movement by reflected light. After it had crossed the field it was allowed to walk on a small piece of black cardboard with which it was transferred to the other beam and another path made and recorded as before. Thus the specimen selected was allowed to make 4 paths, beginning each one in the same relative place alternately in the two beams so as to neutralize the effect of entering the field from one side. Upon the completion of these 4 trials the fly was placed in darkness, the black sheet replaced by another, the flash-frequency changed to 200 per second and then, after the specimen had been in darkness 10 minutes, 4 more trials were given as before to serve as a control. This was repeated until series of paths were obtained for flash-frequencies of 66, 50, 40, 33, 25, 20, 14, 10, 5 and 2 per second with a series of control paths for each. The whole process was repeated with this specimen in other intensities and with other specimens in various intensities as indicated in tables 1 and 2.

Results and conclusions. The results obtained are presented in tables 1 and 2 and in figure 2. In tabulating these results the angle of deflection from the line bisecting the angle between the beams was ascertained for each path. All those in which the deflection was toward the continuous light were labeled *c* and all those in which it was toward the intermittent light, *i*. Consequently in all paths with angles of deflection labeled *c* the stimulating effect of the continuous was greater than that of the intermittent light, and in all labeled *i* it was less.

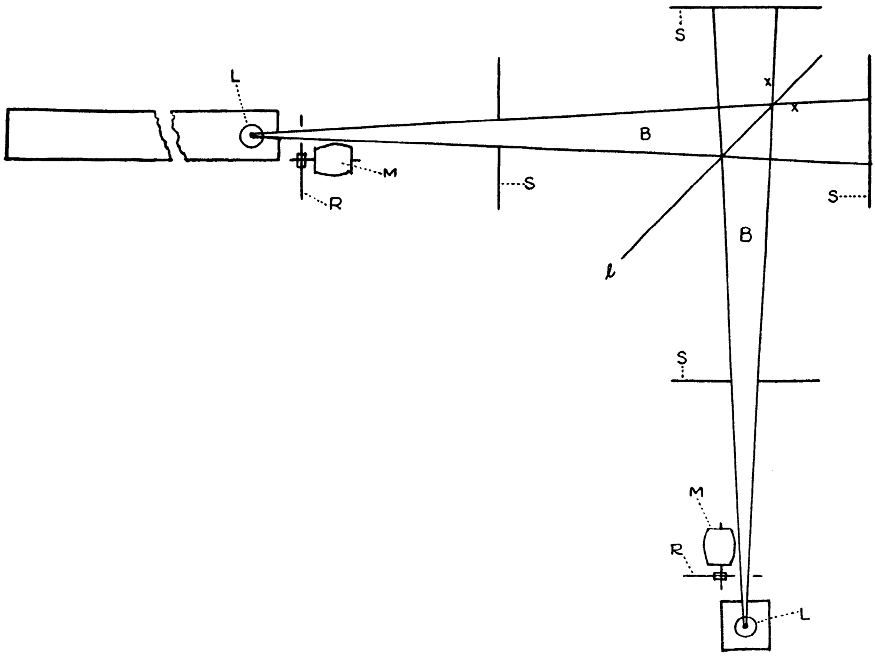

Fig. 1. Arrangement of apparatus used in ascertaining the effect of luminous intensity on flash-frequency for maximum stimulating efficiency. *L*, lamps in light-tight boxes; *R*, rotating sectors; *M*, motors; *S*, screens; *B*, beams of light; *l*, line bisecting angle between beams of light; *x*, *x'*, starting points in all trials.

By referring to these tables and the figure it will be seen at once that in any given illumination the angle of deflection depends upon the flash-frequency. Take, for example, specimen I in 227 m.c. Here we find that as the flash-frequency decreased from 66 to 2 per second the angle of deflection increased from 4.87° toward the intermittent light at flash-frequency of 66 to 17.62° at *25* and then decreased to 7.5° at *10*, after which it increased to 18° toward the continuous light at *2*. At a flash-frequency of 200 per second the angle remained nearly zero throughout the whole series of tests, the average for the different sets of tests at this flash-frequency, beginning above, being 2.12° *i*, 8.75° *i*, 3.37° *c*, 4.12° *c*, 7.62° *c*, 3.75° *c*, 6.50° *c*, 1.20° *c*, 0°, 4.87° *c*; total average, 2.05° *c*.

A further study of the tables shows that the results obtained in all of the tests are in harmony with this. These results support the conclusion reached by Dolley (1), (2) in experiments on Vanessa and Archytas, namely: that the stimulating effect of a given amount of intermittent light is at certain flash-frequencies greater than that of the same amount of continuous light.

TABLES 1 AND 2

Relation between flash-frequency, stimulating efficiency and luminous intensity. The numbers indicate the degree of deflection from the line bisecting the angle between two beams, one of continuous and the other of intermittent light. *i*, deflection toward the source of intermittent light; *c*, deflection toward the source of continuous light. The numbers under "average angle of deflection" are averages of 4 trials in all cases except those following flash-frequency 200 which are averages of 32 or more trials. Illumination in the two beams equal in all tests.

Compare the total average angles of deflection in the different intensities and note that the stimulating efficiency of intermittent light depends upon the flash-frequency and upon the intensity.

TABLE 1

FLASH FREQUENCY PER SECOND	AVERAGE ANGLE OF DEFLECTION DESIGNATION OF FLIES					TOTAL AVERAGE ANGLES
	D	E	A	C	B	
Illumination 550 m.c.						
66	2.00 c	6.37 c	5.25 c	12.12 c	1.62 i	4.82 c
50	13.62 i	5.12 c	6.25 i	9.75 c	4.50 c	0.10 i
40	5.00 i	11.12 c	10.75 i	21.62 i	2.12 c	4.82 i
33	11.50 i	9.37 i	21.62 i	29.00 i	12.00 i	**16.69 i**
25	1.87 i	1.50 i	25.62 i	33.00 i	4.50 i	**13.29 i**
20	2.87 i	0.75 i	13.12 i	3.00 c	15.62 i	5.87 i
14	5.50 c	6.50 c	22.75 i	0.87 i	6.87 i	3.69 i
10	22.75 c	24.50 c	11.25 c	21.87 c	0.12 c	16.09 c
200	9.78 c	11.32 c	1.51 c	0.96 c	2.84 i	4.14 c
Illumination 9.46 m.c.						
66	5.37 c	5.37 c	1.00 c	2.12 c	5.25 i	1.72 c
50	0.87 i	15.87 c	19.87 i	3.62 c	7.12 i	1.67 i
40	3.25 c	8.25 c	2.50 c	7.12 c	7.62 c	5.74 c
33	10.62 c	18.37 c	8.75 i	5.00 c	6.37 i	3.77 c
25	8.50 c	8.25 c	1.62 c	0.62 c	9.12 i	1.97 c
20	2.00 i	2.62 c	4.50 i	2.00 i	15.25 i	4.22 i
14	20.87 i	9.37 c	5.00 i	20.75 i	3.50 i	**8.15 i**
10	3.62 i	9.87 c	9.00 c	17.37 i	14.50 i	3.32 i
200	7.65 c	13.57 c	3.09 i	6.20 c	0.39 i	4.78 c

TABLE 2

FLASH FREQUENCY PER SECOND	AVERAGE ANGLE OF DEFLECTION DESIGNATION OF FLIES					TOTAL AVERAGE ANGLES
	E	K	L	I	M	
Illumination 227 m.c.						
66	6.12 c			4.87 i	4.37 i	1.04 i
50	19.85 c	3.50 i	5.62 c	5.12 i	31.12 i	2.85 i
40	16.12 c	0.87 i	0.62 i	11.62 i	21.12 i	3.62 i
33	8.62 c	6.75 i	12.37 i	14.75 i	13.00 i	7.65 i
25	0.75 i	17.75 i	13.12 i	17.62 i	27.37 i	**15.32 i**
20	5.62 i	18.87 i	7.00 i	11.75 i	18.50 i	**12.34 i**
14	14.62 i	4.62 i	0.50 c	13.12 i	14.25 i	9.22 i
10	8.50 c	9.12 c	6.62 c	7.50 i	10.00 i	1.34 c
5	1.50 c	7.12 c	21.62 c	9.12 c	25.87 c	13.04 c
2	8.87 c	22.00 c	26.00 c	18.00 c	16.00 c	18.17 c
200	1.98 c	1.19 c	4.19 c	2.05 c	3.13 c	2.50 c
Illumination 92.19 m.c.						
50	0.37 i	0.75 i	3.37 i	5.37 i	4.12 i	2.79 i
40	2.12 i	4.12 c	16.00 c	16.62 i	5.75 i	0.87 i
33	5.62 i	7.75 i	2.00 i	14.37 i	9.00 i	7.74 i
25	6.37 i	5.75 i	3.87 c	12.62 i	19.00 i	7.97 i
20	7.25 i	16.37 i	5.37 i	20.37 i	7.75 i	**11.42 i**
14	5.12 i	10.12 i	6.75 i	23.00 i	8.00 i	**10.59 i**
10	6.50 c	6.50 i	11.62 c	2.37 i	8.62 i	0.12 c
5	11.25 c	26.37 c	29.87 c	12.12 c	23.12 c	20.54 c
2	16.75 c	29.37 c	24.16 c	1.12 i	18.87 c	17.60 c
200	1.26 i	5.52 c	5.97 c	1.40 i	7.90 c	3.34 c

If the averages for the angle of deflection in different luminous intensities are compared it will be seen that the flash-frequency for maximum deflection toward the intermittent light differs greatly, it being approximately 30° in 550 m.c., 23° in 227 m.c., 18° in 92.19 m.c. and 14° in 9.46 m.c. (fig. 2). This indicates that the higher the intensity is the higher the flash-frequency for maximum stimulating efficiency will be.

These results are in complete harmony with the hypothesis previously presented, that there are in the receptors or the nervous system of insects alternate sensitive and refractory periods, and that in continuous illumination light does not act continuously but only during the sensitive periods, restitution occurring during the refractory periods. In accord with this hypothesis the illumination of a photo-receptor results in certain changes, probably photochemical in nature; these proceed in a certain direction and continue until a quantitatively definite amount of change has occurred; then a reverse change sets in (restitution) regardless as to whether illumination continues or not. In continuous illumination the light which is received during the refractory period is consequently neutral in its effect. Intermittent light of such a nature that the dark periods

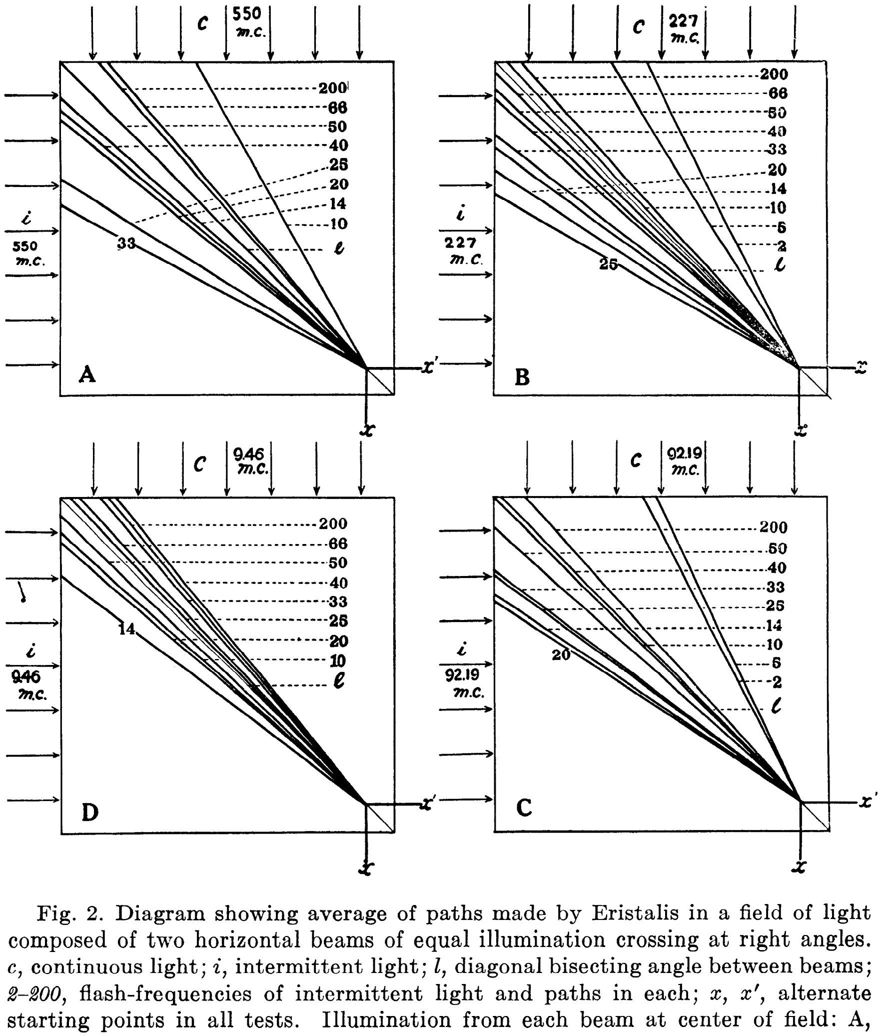

Fig. 2. Diagram showing average of paths made by Eristalis in a field of light composed of two horizontal beams of equal illumination crossing at right angles. *c*, continuous light; *i*, intermittent light; *l*, diagonal bisecting angle between beams; *2–200*, flash-frequencies of intermittent light and paths in each; *x*, *x'*, alternate starting points in all tests. Illumination from each beam at center of field: A, 550 m.c.; B, 227 m.c.; C, 92.19 m.c.; D, 9.46 m.c. Path 200 A, average of 160 trials; 200 B, 192; 200 C, 160; 200 D, 180; 66 B, 12; all others, 20.

Note that the deflection of the paths from the diagonal varies in each intensity with the flash-frequency of the intermittent light, and that for the same flash-frequency it varies with the intensity, the flash-frequency for greatest deflection toward the intermittent light, the optimum flash-frequency, being approximately 33 in 550 m.c.; 25 in 227 m.c.; 20 in 92.19 m.c. and 14 in 9.46 m.c.

coincide with the refractory periods therefore would be expected to have a higher stimulating efficiency than continuous light, i.e., the stimulating effect of a given amount of light received would be greater, and if the change induced by light during the sensitive period is specifically related to the amount of light received during this period it is evident that the more intense the light the shorter the sensitive period would be and consequently the higher the flash-frequency for maximum stimulating efficiency. This is precisely what was observed, as previously set forth.

A further comparison of the results presented in the tables shows also that the magnitude of the maximum deflection toward the intermittent light depends upon the intensity, it being approximately 16° in 550 m.c., 15° in 227 m.c., 11° in 92.19 m.c. and 8° in 9.46 m.c. That is, it is greatest in the highest intensity used.

If the length of the refractory period is independent of the luminous intensity, as would be expected, and the sensitive period increases as the intensity decreases it is evident that the difference between the stimulating efficiency of continuous and intermittent light would be less in low intensity than in high, provided there is a direct quantitative relation between the amount of light received during the sensitive period and the change induced by it, for the lower the intensity the shorter the dark period in relation to the light period; and the shorter the dark period in relation to the light period the smaller the relative amount of light received and wasted during the refractory period in continuous illumination. The fact then that the maximum stimulating efficiency of intermittent light in relation to that of continuous light decreases as the intensity decreases is in full accord with the hypothesis considered.

In further investigation now under way we shall deal quantitatively with the effect of luminous intensity on the relation between the length of the light and the dark periods in intermittent light of maximum stimulating efficiency and with the difference between the stimulating efficiency of continuous and intermittent light in different intensities. The results already at hand indicate that this investigation will further elucidate the processes involved in stimulation.

SUMMARY

1. The stimulating efficiency of intermittent light in the orientation of Eristalis varies with the flash-frequency, i.e., depending upon the flash-frequency the effect of intermittent light may be greater than, equal to, or less than that of continuous light of equal illumination.

2. In intermittent light the flash-frequency for maximum stimulating efficiency varies with the illumination. It is higher in strong light than in weak light. If this is true it follows that in insects exposed to continuous illumination, light does not act continuously.

3. The maximum stimulating efficiency of intermittent light in relation to that of continuous light decreases as the luminous intensity decreases.

4. These facts support the contention that there are in the photoreceptors or the nervous system of insects alternate sensitive and refractory periods and that continuous illumination does not act continuously in photic stimulation.

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