

THE RELATIVE STIMULATING EFFICIENCY OF CONTINUOUS AND INTERMITTENT LIGHT IN VANESSA ANTIOPA

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I. INTRODUCTION

Many investigators have studied the effect of intermittent light on the human eye, while but few have investigated its effect upon other eyes. In the work on the human eye the following four questions have been prominent:

1. Does intermittent light of high flash-frequency have the same stimulating efficiency as continuous light?
2. What is the flash-frequency at which the "flicker" of intermittent light becomes imperceptible?
3. What is the shortest perceptible time interval between two flashes of light?
4. What is the comparative apparent brightness of a given light acting for various lengths of time?

The first of these questions concerns Talbot's law. This law has been stated by Helmholtz (1896, p. 483) as follows:

If any part of the retina is excited with intermittent light recurring periodically and regularly in the same way, and if the period is suffi-

ciently short, a continuous impression will result, which is the same as that which would result if the total light received in each period were uniformly distributed throughout the whole period.

Nearly all of those who have tested this law have concluded that it holds for the effect of intermittent light of high flash-frequency.

Plateau (1835, p. 457), Helmholtz (1896), Kleiner (1878, p. 542), Wiedemann and Messerschmitt (1888, p. 465), and Lummer and Brodhun (1896, p. 299-307) verified the law to within the range of their experimental error.

Fick (1863, p. 739) concluded that with intense illumination the action of intermittent light is stronger than it should be according to Talbot's law and that with very weak illumination the reverse is probably true.

Aubert (1864), however, maintains that the deviation from Talbot's law which Fick found is of the same order of magnitude as his experimental error and that therefore his results verify the law to within the limit of accuracy of his experiments.

Ferry (1893, p. 338) verified the law for white light but found quite large errors when the light transmitted through the rotating sector disk was of a bluer quality than that incident on the other side of the photometer screen.

Hyde (1906, pp. 1-32), however, as the result of an extremely thorough piece of work, came to the conclusion that Talbot's law, in its application to a rotating sector disk, holds for white light for all total angular openings between 288 and 10 degrees to within a possible error of 0.3 per cent, which he states probably expresses the limit of accuracy of his experiments. He also concluded that Talbot's law is verified for red, green, and blue light though not to such a high accuracy as for white light.

Parker and Patten (1912, pp. 22-29) on the contrary concluded that intermittent light is measureably less efficient as a stimulus for the eye than continuous light. Pfund, however, points out that Parker and Patten's methods were at fault and says (1914, p. 117): "It is therefore established by methods that are entirely free from objections that Talbot's law holds to a high degree of accuracy for the human eye."

Most of the investigators mentioned above used a fairly high flash-frequency. Lummer and Brodhun used a frequency of interruption of from 27 to 200 per second. Parker and Patten tested the effects of flash-frequencies of from 36 to 196 per second but in most of their tests used a flash-frequency of over 116 per second. Hyde states that in his work no attention was paid to the number of flashes per second except to prevent all possibility of a flicker. The flash-frequencies used by the other workers are not available.

The flash-frequency at which the "flicker" of intermittent light becomes imperceptible, the "Verschmelzungsfrequenz" of von Kries, depends upon the illumination. Baader (1891) states that at a flash-frequency of 18.96 per second the flicker of intermittent light of an illumination designated as "1" cannot be perceived and that the fusion-frequency rises gradually with increasing illumination until at an illumination of "1800" the frequency of interruption must be 50.24 per second before the flicker disappears. According to Helmholtz the fusion-frequency in strong lamp light is 24 per second, while that in full moon light is only 10 per second. Kleiner (1874) also concluded that the frequency at which the flashes of light fuse into a continuous impression varies with the illumination.

The fusion-frequency has also been shown to depend on the condition of adaptation of the eye. Schaternikoff (1902) and Charpentier (1887) state that with increasing dark adaptation the fusion-frequency rises from about 10 to about 17 per second if weak lights are used. The reverse is true if strong lights are used, according to von Kries and Schaternikoff. In this connection it is interesting to note that the fusion-frequency for totally color-blind individuals does not rise higher than 20 per second (von Kries, 1905, p. 255).

The fusion-frequency depends also upon the relative duration of the periods of light and darkness in intermittent light according to Dunlap, who maintains (1915, p. 230) that for the dark adapted eye the fusion-frequency rises from 28.17 to about 50 flashes per second, as the ratio between the duration of the flashes and of the interval between the flashes changes from 35/1 to

1/1, and decreases from about 50 to 34.04 flashes per second, as the ratio between the duration of the flashes and of the interval changes from 1/1 to 1/35. Schenck (1897, p. 54) states that if in intermittent light a grey period is interposed between the periods of darkness and of light the fusion-frequency increases, while Helmholtz (1896, p. 489) and Plateau maintain that the fusion-frequency is not affected by changes in the relative duration of the light and dark periods of intermittent light.

According to von Kries the results of Baader and Schenck show that in intermittent light consisting of alternate strong and weak flashes the fusion-frequency depends on the relative brightness of the flashes. As the relative brightness decreases the fusion-frequency decreases no matter whether the average illumination is unchanged or increases.

The first to investigate the shortest perceptible time-interval between two flashes of light was Exner who, working with electric sparks, found visual time-thresholds at 44/1000 seconds at 280 mm. distance and 21/1000 seconds at 640 mm. Weyer (1899), who also used electric sparks, states that the visual time-threshold is only 12/1000 seconds. If a series of stimulations is used, he holds that according to adaptation and other conditions, the flicker-threshold varies from 25/1000 to 87/1000 seconds and the threshold for separation of a series varies from 42/1000 to 105/1000 seconds.

Basler (1911), using a rotating black disk on which were painted white sectors states that the time-threshold is about 40/1000 seconds with two visual stimulations and for a series of stimulations it is about one-third as much. Dunlap, whose careful investigations have shown the difficulties of this problem, states that with two stimulations the time threshold decreases with increase in the length of the flashes and that this decrease seems to be altogether a function of the duration of the first flash. He also comes to the following conclusions as to the visual time-threshold (1915, pp. 247-248):

1. The effects of brightness of the light are variable, depending on the other factors in such a way that no conclusion can be drawn as yet concerning their effects.

2. The threshold is lower for the light-adapted eye than for the dark-adapted eye. This holds, at least, for certain light-adaptations.

3. The threshold is lower for an interval marked by flashes added to a continuous stimulation, than flashes in a dark field. This holds for a wide range of constant illumination, the threshold varying usually with the brightness of the constant illumination up to the point where the additions lose in distinctness.

The fourth question mentioned above, as to the relative apparent brightness of light acting for various lengths of time, has been answered differently by different investigators, who have also revealed several other interesting phenomena. The chief attempts in this direction have centered around the "action-time" of light, i.e., the time during which light must act in order to produce its maximum effect in point of apparent intensity. Exner (1868, p. 601), Martius (1902), and McDougall (1904, pp. 151-189) maintain that the action-time of light varies inversely with the illumination, while Swan maintains that it does not. According to McDougall the action-time of light is 0.2 seconds when the stimulus is so weak as to be barely perceptible, and decreases to 0.03 seconds when the intensity of the stimulus is sufficiently increased. He also states that the action-times of red, green, and blue lights of the same intensity differ but little or not at all. Kunkle (1874, p. 197) however holds that the action-time of red, green, and blue light differs.

The effect of light acting for longer than its action-time has been investigated by McDougall (1904), who concludes that when light of a certain illumination acts upon the human retina for longer than its action time the apparent brightness of the light remains equal to, and then becomes less than that of the same light acting for only its action-time. McDougall also states that when two lights of the same illumination act for different periods both however for longer than the action-time, the one of the shorter duration seems to the human eye to be the brighter.

The effect of light acting for less than its action-time seems to vary directly with the duration of the action of the light. This contention is supported by the work of McDougall, Swan (1849), Bloch (1885), and Charpentier (1887), McDougall says (1904, p. 177):

I am strongly disposed to believe that the law that the intensity of the sensation varies directly with the duration of the action of the light of given intensity holds good for all durations less than the action-time of the light.

In this connection and in view of the facts described in this paper it is also of especial interest to note the following results. Flickering lights of certain flash-frequencies seem to have a greater stimulating efficiency for the human eye than have the lights of the same illumination but of different flash-frequencies. von Kries says (1905, p. 232):

Hat man auf einer rotierenden Scheibe Ringe mit verschiedenen Zahlen schwarzer und weisser Sektoren, so bemerkt man bei passenden Rotationsgeschwindigkeiten, dass ein stark flimmernder Ring im ganzen beträchtlich heller erscheint als ein vollkommen stetig gesehener. Brücke gab an, dass bei einer Frequenz der Reizanstösse von etwa 17,5 in der Sekunde die Helligkeit am grössten erscheine.

Hyde and Cady (1906, pp. 415-437) confirm these results, for in an investigation of the mean horizontal intensity of incandescent lamps by the rotating lamp method they found that when certain types of incandescent lamps were rotated at three revolutions per second a flickering light was produced, which to some observers appeared of an intensity 4 per cent too high and to others 3 per cent too low. Ferry also confirms these results for he says (1894, p. 344): "But it was noticed that if the (rotating sectored) disc did not revolve rapidly enough to produce a perfectly steady illumination of the photometer screen, *more* light appeared to go through the sectored disc than theoretically should." Thus, apparently to the human eye intermittent light in which the flashes of a certain duration are perceptible seems stronger than it really is.

The effect of intermittent light upon organisms other than man has been studied but little and most of the investigators have been interested in the first of the problems mentioned above, i.e., the applicability of Talbot's law. Loeb, Ewald (1914), and Wastenays (1917) state that this law holds for *Eudendrium*; Ewald (1914) maintains that it holds for *Daphnia*; Loeb and

Northrup (1917) that it holds for *Balanus* larvae; Patten (1915) that it holds for blow-fly larvae and Clark (1913), Blaauw (1909), Fröschel (1910), and Fitting (1905) that it holds for certain plants.

In these tests, as in those previously mentioned, the flash-frequency was usually high. For example, in the work of Loeb and Northrup the intermittent light was of a flash-frequency of from 50 to over 83 per second, while Patten used a frequency of interruption of 115 per second.

Apparently Ewald alone has investigated the effect upon an animal other than man of intermittent light of low flash-frequency. He states (1914) that *Daphnia* orients in intermittent light as it does in continuous light independently of whether the frequency of interruption is 1 or 30 per second, but that, in reference to the orientation of the eye of *Daphnia*, intermittent light of lower frequencies of interruption has a weaker effect than continuous light. He says (1913, p. 237):

In some cases I got a marked reaction of the eye on change from constant to intermittent light of equal energy when the speed of the sector-wheel was about one-tenth of a second per revolution. The deviation becomes more marked the slower the speed.

In harmony with the results described above are those obtained in certain investigations on the effect of light upon photographic plates. Abney, Kron, Helmic, and Newcomer state that the blackening of photographic plates by light does not depend solely upon the total energy received. Helmic (1918, p. 374) maintains that it "is dependent upon the rate of flow of energy, with total energy constant; and that for each brand of plate and quantity of total energy there is a maximum blackening given by a certain rate of flow of energy." According to Helmic, Abney (1901, p. 395) and Kron (1913, p. 755) reached the same conclusions. Moreover, Newcomer (1919, p. 243) asserts that intermittent light produced by a rotating sector disk with a 72 degree aperture produces less blackening of a photographic plate than continuous light of equal total energy. He does not state the flash-frequency used but it was presumably low.

In view of the slight information available as to the effect of intermittent light upon organisms other than man it seemed desirable to make a thorough study of this question in some of the lower forms. The mourning cloak butterfly, *Vanessa antiopa*, was chosen because its reactions to light are fairly well known and because it lives well in captivity and is not difficult to obtain in large quantities.

Before entering upon a discussion of these experiments I wish to express my very sincere appreciation of the kindness of Professor S. O. Mast whose many suggestions and unselfish aid have made this work possible. It is a pleasure also to acknowledge my indebtedness to Dr. H. E. Howe for the loan of apparatus and for other kindnesses and to Mrs. O. F. Hiser, who supplied me with the larvae from which the butterflies were reared.

II. METHODS

The butterflies used were all reared in the laboratory from larvae secured from both the June and August broods in Iowa. They were kept in a large wire cage, which was protected to some extent by a tree which partially shaded it. They were fed upon decaying fruit and a weak solution of maple syrup in water. The wings of those butterflies used in the tests were clipped to prevent their escape. This was not injurious, for animals with clipped wings live and thrive as well as normal specimens, and they behaved in the same manner.

Two slightly differing methods were used. Those used in all of the experiments, except those described in section V of this paper, were as follows. The observations were all made on a table in a dark room in a field of light composed of two small horizontal beams, produced by two 100 Watt Edison gas filled lamps, so situated that the beams crossed at right angles. The lamps were mounted in front of a small opening in a light proof box that was painted dead black inside. By means of screens the light from these lamps was so cut down as to produce sharply defined beams of the size desired. These beams were the only light in the room, and this was in large part absorbed

by means of black cloth which covered the walls of the room. There was consequently very little light in the room aside from that in the beams. One of the lamps was in an adjoining room, and the beam from it passed through an aperture in the intervening wall. The other lamp was placed upon a support so that its position could be easily changed. In some of the experiments the light in one of the beams was intermittent. The intermittent light was produced by means of a rotating sector disk connected with a small motor which was run on Edison storage batteries. The motor and sector disk as well as the lamp were all placed in an adjoining room, separated by a 30 cm. thick brick wall from the room in which the experiments were performed, so as to reduce vibration as much as possible. The flash-frequency and the duration of the flashes and of the dark periods between the flashes of the intermittent light was controlled by using different disks with apertures of various sizes and by varying the number of revolutions per second.

Not only was the behavior of the animals observed closely by the investigator but the butterflies themselves were forced to make permanent records of their own behavior. This was done by allowing them to walk on sheets of paper (15 by 21 cm.) which had been covered with soot from an oil lamp. The tracings made by the insects were made permanent by means of a coat of shellac. Tests showed that the behavior was not affected by the soot. Upon the sheets bearing the tracings of the insects were also marked the limits and direction of the beams of light. Individuals were given a varying number of trials under the same conditions. Sometimes 5 were given and at other times more. An insect was never allowed to make more than 10 tracings on one sheet. Where more trials were given other sheets were used. Usually an animal was given 5 consecutive trials from a point facing one source of light. It was then given 5 trials from a point facing the other source. In analyzing the tracings made a line was drawn bisecting the angle made by the rays of light in the center of each beam. The angle that each tracing made with this line was then measured. If, for example, the tracing was at an angle of 10 degrees with the line bisecting the angle

between the beams, it was marked "plus" or "minus" 10 degrees, depending upon whether the butterfly deflected toward the right or the left. The intermittent light was always to the right. Deflection toward it was consequently always "plus" (see figure 1).

The methods used in the experiments described in section V of this paper were similar to those described above except that the light conditions were slightly different and other means of recording the movements of the animals were used. As light sources two small 36 candle power automobile lamps run on storage batteries were used. The motor, sector disk, and lamps were all in the same room as that in which the experiments

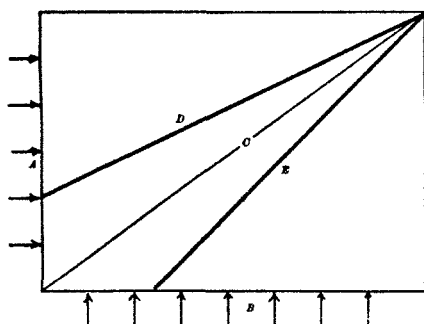


FIG. 1. Diagram to show methods used in recording the reactions of *Vanessa* in a field of light composed of two horizontal beams crossing at right angles (Reduced by three-fourths). Arrows, direction of rays of light; A, intermittent light; B, continuous light; C, line bisecting the angle made by the two beams; D, path of butterfly making an angle of +10 degrees; E, path of butterfly making an angle of -10 degrees.

were performed. The vibration caused by the motor was very slight and did not affect the results, as was shown by tests. Instead of using sheets of paper covered with soot to record the movements of the animals, very fine charcoal dust was sprinkled on the sheets mentioned above with a pepper shaker. After an insect had moved across a sheet so prepared a pencil was drawn along the trail left by the organism. After removal of the charcoal the sheet with no further treatment bore a permanent record of the reactions of the animal.

The candle power of the lamps used in the experiments was measured by means of a Sharp-Millar photometer by Prof. H. E. Howe of the Physics department of Cornell University, who also approved the arrangement of the experiments. The candle power of the lamps used in the experiments described in sections II, IV, VI, and VII was not measured until about a year after the experiments were performed. During the interim they were not used however and the depreciation due to age was probably slight.

III. ORIENTATION IN CONTINUOUS LIGHT FROM TWO SOURCES

Since the object of the experiments described in this paper was to ascertain the effect of intermittent light on orientation in *Vanessa* it was first necessary to know the effect of continuous light on orientation. This was ascertained in the following manner. Two horizontal beams of light were arranged, as described previously, so that they crossed at right angles. A sheet of paper covered with soot from an oil lamp was placed in the field of light common to the two beams, so that it was illuminated by an equal amount of light energy from each of the sources. A butterfly with clipped wings was picked up in the fingers and gently placed so that it faced a point about halfway between the two sources, care being taken to avoid excessive stimulation by handling. The insect moved across the sheet of paper leaving a trail in the soot. When it had completed this trial it was immediately picked up, placed again at about the same starting point, and allowed to complete another trial. In the same way 20 consecutive trials were given under these conditions. The direction of the rays of light was then marked on the sheet, and it was removed to be later coated with shellac, as described above. Similarly the same individual was given 20 consecutive trials with the relative illumination of the two beams of light in the following ratios respectively, 3 to 4, 2 to 1, and 1 to 4. An interval of at least thirty minutes separated each of the series of tests under the above four different light conditions. Thirteen butterflies were used, most of them being given all of the tests described above. The results obtained are given in table 1.

Table 1 shows that when the illumination in the two beams was equal the average angle made by 11 butterflies was $+0.78$ degrees, indicating that the butterflies tended to move in general toward a point halfway between the two sources of light; and that when the illumination in one beam was greater than that in

TABLE 1

Orientation in continuous light from two sources. The numbers indicate the degree of deflection from a line bisecting the 90 degree angle between the two beams. "Plus," deflection toward right beam. If beams are of unequal illumination the stronger one is to the right of the insect. "Minus," deflection toward other beam

DESIGNATION OF BUTTERFLIES	AVERAGE ANGLE OF DEFLECTION (20 TRIALS FOR EACH AVERAGE), IN FOLLOWING ILLUMINATION							
	Right beam	Left beam	Right beam	Left beam	Right beam	Left beam	Right beam	Left beam
	14 m. c.	3 5 m. c.	14 m. c.	7 m. c.	14 m. c.	10 5 m. c.	14 m. c.	14 m. c.
13	-10.7		+12.6		-13.0		-13.7	
6	+18.55		+8.25					
8					-10.8		-9.0	
25	+13.10		+9.3		+9.9		+8.3	
23	+16.2		+17.9		+8.65		+7.5	
21	-7.8		-2.7		+1.55		+2.2	
16	+9.45		+14.1		-5.6		+4.57	
15	+4.05		+0.6		-6.4		-4.1	
14	+14.4		+12.45		+6.0		+5.35	
12	+17.35		+6.02		+17.8		+16.3	
11			-4.5		-14.25			
9	-5.1		+5.35		-10.05		-13.85	
7	+10.45		+4.95		+12.8		+5.1	
Total average angles.....	+7.27		+7.03		-0.28		+0.78	

the other they moved toward a point nearer the source of stronger light. This conclusion is evident from a comparison of the total average angles made in beams differing in relative illumination. The only apparent exception is the average angle made in two beams one of which was three-fourths as strong as the other. Although the total average angle made by all of the butterflies in this test was only -0.28 degrees, 63.6 per cent or 7 out of the 11 animals tested under the two conditions, first, in two beams of equal illumination and second, in two beams, one three-fourths

as strong as the other, deflected more toward the stronger beam in the latter test than they deflected toward either beam in the former test. An examination of table 1 shows also that the butterflies exhibited great variation in their reactions. For example, the average angles made by the different insects in two beams of equal illumination varied from -13.85 to $+16.3$ degrees. The causes of this variation are discussed later. It is clear however that in spite of great variation Vanessa when exposed to two beams of continuous light which cross at right angles tends in general to move toward a point between the sources, the location of which depends upon the relative illumination in the beams. This seems to indicate that the effect of light on orientation varies with the illumination.

This conclusion is supported by the results obtained with many other organisms by Mast (1907 and 1911), Ewald (1913), Patten (1914), and Loeb and Northrup (1917).

IV. VARIATION IN REACTIONS TO LIGHT

As stated above, Vanessa shows great variation in its reactions to light. This is evident both in its reactions in continuous and in intermittent light. Different individuals react differently, as is shown by an examination of tables 1, 3, and 5. A given insect also at times may show great variation in successive trials under the same conditions. This is well illustrated in table 2.

Table 2 shows that with the light from the two sources equal the angles made in the individual trails varied from -14 to $+21$ degrees; that with the illumination in one beam three-fourths that in the other the angles of the individual trails varied from -21 to $+30$ degrees; that with the illumination in one beam twice that in the other the angles of the individual trails varied from 0 to $+37$ degrees; and that with the illumination in one beam four times that in the other the angles made in the individual trails varied from 0 to $+32$ degrees. It is consequently evident that Vanessa may show great variation under the same conditions when reacting to two sources of continuous light. In spite of this variation the average angle made increased, in gen-

eral, as the difference between the illumination of the two beams increased, for, as the last line in table 2 shows, the average angle made in 20 trials when the light from the two sources was equal

TABLE 2

Showing the variation exhibited by a specimen of Vanessa (butterfly 14) in successive trials under the same conditions. The numbers indicate the degree of deflection from a line bisecting the 90 degree angle between two beams of continuous light. "Plus," deflection toward right beam. If beams are of unequal illumination the stronger one is to right of the insect. "Minus," deflection toward other beam

SERIAL ORDER OF TRIALS	ANGLES IN DEGREES OF EACH OF THE 20 TRIALS							
	Illumination in meter-candles							
	Right beam	Left beam	Right beam	Left beam	Right beam	Left beam	Right beam	Left beam
	14	14	14	10.5	14	7	14	3.5
1	+19		+12		+10		+18	
2	+19		+9		+6		+18	
3	+19		+8		+8		+32	
4	+11		+8		+8		+21	
5	+11		0		+7		+26	
6	0		0		0		+22	
7	0		0		+8		+13	
8	0		-11		+7		+32	
9	0		-21		0		+28	
10	0		+0.5		0		+22	
11	+13		+10		+16		0	
12	+21		+15		+37		0	
13	+7		+30		+36		+9	
14	+8		+22		+12		+9	
15	0		+20		0		+10	
16	0		0		+36		+10	
17	0		0		+22		0	
18	0		+6		+22		+4	
19	-14		+6		+7		+7	
20	-7		+6		+7		+7	
Average angle made in 20 trials.....	+5.35		+6.02		+12.45		+14.4	

was +5.35 degrees; when the illumination in one beam was three-fourths that in the other the average angle of 20 trials was +6.02 degrees; when the illumination in one beam was twice that in the other the average angle was +12.45 degrees; and when

the illumination in one beam was three times that in the other the average angle was $+14.4$ degrees. This conclusion is supported by the data presented in table 1, as is shown in the preceding section. This seems to show that, in spite of the enormous variation described, conclusions based upon averages of numerous tests are trustworthy. We have consequently in the work described in the following pages continuously dealt with such averages.

The cause of the variations mentioned is in itself an exceedingly interesting problem. Why, for example, does a butterfly under given conditions deflect zero degrees in one test and $+36$ degrees in the following test? We assume that this change is due to internal changes of some sort or other. What these changes are is not known, but we shall demonstrate later that they are at times, at least, associated with the past experiences of the individuals involved.

V. RELATIVE STIMULATING EFFICIENCY OF INTERMITTENT AND CONTINUOUS LIGHT

In the following experiments it was found that at certain flash-frequencies the stimulating effect of intermittent light is greater than that of continuous light of equal illumination; at other flash-frequencies it is less than that of continuous light; and at still others it is equal to that of continuous light.

In these experiments the butterflies were exposed at the intersection of two horizontal beams of light which crossed at right angles, as in the preceding experiments. The paths of the insects were recorded by allowing them to walk over sheets of paper covered with charcoal dust, as described previously. Each one of 10 animals was given the following tests. An individual was first given 5 trials in two beams of continuous light of equal illumination. Before each trial the insect was placed so that it faced a point about halfway between the two sources. As soon as it had walked across the field of light it was gently picked up in the fingers and placed again at the starting point preparatory for another trial. Care was taken not to pinch the animal or to

stimulate it by handling. When the five trials were completed a water glass was inverted over the insect to prevent its escape. A pencil was then drawn along the trails made on the record sheet: the direction of the rays of light was marked on it: and it was replaced by a fresh sheet. A sector disk with one-fourth removed, rotating at the rate of 100 revolutions per second, was next interposed in one of the beams, and the illumination in the other beam was decreased by changing the position of its source until the amount of light received from the two sources was equal, as in the preceding tests, that from one, however, being intermittent and that from the other continuous. The butterfly was then given 5 consecutive trials just as in the preceding test. After an interval of about five minutes, 5 more consecutive trials were given with the flash-frequency of the intermittent light 60 per second. Similarly, tests were made with the flash-frequency of the intermittent light 50, 40, 30, 20, 10, 5, and 2 per second respectively. The results obtained may be illustrated by a detailed description of a typical experiment.

In this experiment the butterfly was first given 5 trials in two beams of continuous light of equal illumination. It deflected somewhat toward the source to its right, making an average angle of $+12.3$ degrees with the line bisecting the angle made by the two beams of light. It was then exposed to two beams of equal illumination, one of them being of continuous and the other of intermittent light. The flash-frequency of the intermittent light was 100 per second. The organism made the same average angle that it had made in two beams of continuous light of equal illumination, $+12.3$ degrees. The insect was next given tests in intermittent light of flash-frequencies of 60, 50, 40, and 30 per second. It made the following average angles respectively: $+4.4$, $+6$, $+19.8$, and $+15.6$ degrees, thus reacting to intermittent light of high flash-frequency in general as it did to continuous light. A test in intermittent light of a flash-frequency of 20 per second followed. The butterfly made a much larger average angle, $+29.7$ degrees, indicating that the stimulating efficiency of intermittent light of this flash-frequency was greater than that of continuous light. The effect of intermittent light of

a frequency of interruption of 10 per second was next tested and was found to be about equal to that of continuous light, for the average angle made was $+12.8$ degrees, about the same as that made in two beams of continuous light of equal illumination. Tests in light of flash-frequencies of 5 and 2 per second were next given. The angles of deflection made were -1.4 and -23.4 degrees, respectively, showing that the stimulating efficiency of intermittent light of these flash-frequencies was less than that of continuous light.

Consequently, the reactions of this individual indicate: (1) that intermittent light of a flash-frequency of 20 per second has a higher stimulating efficiency in Vanessa than continuous light, i.e., a given amount of intermittent light has a greater stimulating effect than the same amount of continuous light, (2) that intermittent light of flash-frequencies of 5 and 2 per second has a lower stimulating efficiency than continuous light, and (3) that the stimulating efficiency of intermittent light of flash-frequencies of 100, 60, 50, 40, 30, and 10 per second is approximately equal to that of continuous light. These conclusions are in general strongly supported by the results of all of the tests made which are presented in tables 3 and 4.

By referring to table 3 it will be seen at once that the results presented in the last two columns show that the efficiency of intermittent light of low flash-frequency (5 and 2 per second) is clearly lower than that of continuous illumination. Only in two individuals was there any indication of an exception to this; "H" and "C" both deflected less toward intermittent light of 5 flashes per second than they did toward continuous light of the same illumination. In all of the other flash-frequencies the variation in deflection in different individuals is so great that the meaning of the results is not immediately evident. For example, in specimen F the greatest stimulating efficiency appears to have been at 100 flashes per second; in B at 50; in L at 40; in J at 10; in C and in E at 30; and in N, I, G, and H at 20. A thorough analysis of these results shows however that in spite of this variation the results are quite clear. Such an analysis is presented in the last line in table 3 and in table 4.

Examination of these shows that the stimulating efficiency of intermittent light of a flash-frequency of 20 per second is higher than that of continuous light. This statement is based on two facts: first, the average angle of deflection of all 10 insects in intermittent light of 20 flashes per second (+7.83 degrees) was greater than that made in continuous light; and second, 80 per

TABLE 3

Comparative stimulating efficiency of continuous and intermittent light. The numbers indicate the degree of deflection from the line bisecting the angle between two beams crossing at right angles. "Plus," deflection toward the source of intermittent light, or toward the right if both beams are continuous. "Minus," deflection toward the source of continuous light, or toward the left if both beams are continuous. Each figure given is the average angle of 5 trials

DESIGNATION OF BUTTERFLIES	LIGHT IN BOTH BEAMS CONTINUOUS: ILLUMINATION IN BOTH, EQUAL, 14 m. c.	ONE BEAM, CONTINUOUS; THE OTHER, INTERMITTENT: ILLUMINATION IN BOTH, EQUAL, 3.5 m. c.									
		Flash-frequency per second									
		100	60	50	40	30	20	10	5	2	
		Angles of deflection									
N	+12.3	+12.3	+4.4	+6.0	+19.8	+15.6	+29.7	+12.8	-1.4	-23.4	
L	+4.8	-2.2	+7.2	-9.6	+12.6	+5.2	+0.2	-13.8	-27.0	-48.6	
J	+5.2	+10.4	+20.4	+30.0	+8.4	+18.6	+16.3	+21.1	-36.0	-35.6	
I	+5.6	+12.8	+12.8	0	+3.4	+2.0	+14.0	-7.8	-10.2	-29.2	
H	-5.7	-1.0	+2.4	0	0	-3.6	+7.6	0	-1.6	-39.0	
G	-7.4	-11.6	-10.0	-12.0	-9.8	-12.2	-6.8	-27.6	-23.2	-32.6	
F	+4.4	+13.0	+9.6	+4.8	+1.6	+10.2	+8.7	-38.4	-25.4	-24.8	
E	+16.4	+15.4	+13.8	+13.8	+15.8	+24.8	+19.4	0	-12.4	-7.2	
C	+8.2	+18.4	+13.8	+20.4	+15.6	+32.0	+13.0	+39.8	+31.2	-7.6	
B	+14.6	-1.4	-2.6	+11.2	+8.0	-2.8	-23.8	-15.5	-16.0	-14.0	
Average		+5.84	+6.61	+7.18	+6.46	+7.54	+8.98	+7.83	-2.94	-12.2	-26.2

cent, or 8 out of the 10 insects tested, deflected more toward the source of intermittent light of this flash-frequency than they did toward either source when tested in two beams of continuous light of equal illumination.

Similarly, the stimulating efficiency of intermittent light of a flash-frequency of 30 per second seems to be greater than that of continuous light, for 70 per cent, or 7 out of the 10 insects tested

deflected more toward the source of intermittent light of this flash-frequency than they did toward either source when tested in two beams of continuous light of equal illumination. Moreover, the average angle of deflection of all 10 insects in light of 30 flashes per second (+8.98 degrees) was greater than that made in continuous light.

The efficiency of light of 100 flashes per second is apparently equal to that of continuous light for the average angle of deflec-

TABLE 4

Relative stimulating efficiency of intermittent light of various flash-frequencies and continuous light of equal illumination. This table is based upon the data given in table 3

FLASH-FREQUENCY OF INTERMITTENT LIGHT PER SECOND	PERCENTAGE OF BUTTERFLIES TESTED IN WHICH THE STIMULATING EFFICIENCY OF INTERMITTENT LIGHT WAS		
	Greater than that of continuous light	Less than that of con- tinuous light	Equal to that of con- tinuous light
100	50	40	10
60	60	40	0
50	40	60	0
40	50	50	0
30	70	30	0
20	80	20	0
10	40	60	0
5	20	80	0
2	0	100	0

tion of all 10 insects made in both sorts of light was approximately equal, being +6.61 degrees in the former and +5.84 degrees in the latter. This conclusion is supported by the fact that 50 per cent of the 10 animals deflected more toward the source of intermittent light than they deflected toward either source when tested in two beams of continuous light of equal illumination. Forty per cent deflected less, and 10 per cent deflected to an equal extent. It is therefore evident that for Vanessa the stimulating efficiency of intermittent light of a flash-frequency of 100 per second is approximately equal to that of continuous light.

A study of table 4 indicates that the same conclusion is to be drawn as to the stimulating efficiency of intermittent light of

flash-frequencies of 60, 50, 40, and 10 per second. However an examination of the averages presented in the last line in table 3 indicates that the stimulating efficiency of intermittent light begins to rise at a flash-frequency of about 60 per second, reaches a maximum at 30 per second, and then declines. According to these figures the efficiency of light of 10 per second is less than that of continuous light. If this is true the stimulating efficiency of intermittent light of a flash-frequency of somewhere between 10 and 20 per second is equal to that of continuous light. In the absence of more data it is probably wiser to assume that the conclusions drawn from table 4 are more nearly correct than those drawn from the last line in table 3.

The conclusion stated above that the stimulating efficiency of intermittent light varies with the flash-frequency is further supported by the results presented in table 5. This table shows that the total average angles of the butterflies tested in intermittent light produced by a sector disk with one-fourth removed and of the following flash-frequencies: 30, 20, 15, 10, 5, and 2 per second were respectively: +15.38, +7.67, -4.16, +0.84, -14.67, and -22.76 degrees. The angles of deflection of the butterflies tested in light produced by a disk with one-half removed and of the following flash-frequencies: 30, 20, 15, 10, 5, and 2 per second were respectively: +10.75, +6.73, -0.71, +0.92, -6.58, and -15.67 degrees. The angles of deflection of the butterflies tested in light produced by a disk with three-fourths removed were respectively +1.37, +0.11, +1.31, +0.07, -2.15, and -5.26 degrees. Thus, in all three sorts of light the angles of deflection decrease in general as the flash-frequency decreases from 30 to 2 per second. These angles are averaged from various numbers of insects but this fact does not invalidate the conclusions drawn from these average angles, for, while these insects showed great variation, an examination of the angles made by the different individuals leads to the same deduction. Moreover, the conclusions drawn thus far in this section are supported by numerous results presented in the following sections.

The statement that intermittent light of flash-frequencies of 20 and 30 per second has a higher stimulating efficiency in

TABLE 5

Relation between stimulating efficiency and flashes of low frequency. The numbers indicate the degree of deflection from the line bisecting the angle between two beams of equal illumination, crossing at right angles. One beam, continuous; the other, intermittent. "Plus," deflection toward source of intermittent light; "minus," deflection toward source of continuous light. This table is the summary of the results obtained in 3400 trials, each number given being the average angle made in 20 trials, except those for butterflies 13 and 8, which are the average of 10 trials

DESIGNATION OF BUTTER- FLIES	AVERAGE ILLUMINA- TION IN EACH BEAM IN METER- CANDLES	PORTION OF SEC- TORED DISK RE- MOVED	FLASH-FREQUENCY PER SECOND					
			30	20	15	10	5	2
			Angles of deflection					
13	3.5	$\frac{1}{4}$	+9.725	+9.725		-0.4	-25.3	-32.25
	7.0	$\frac{1}{2}$	+0.7	-4.5		-15.2	-16.2	-24.3
	10.5	$\frac{3}{4}$	-12.6	-13.45		-13.7	-17.3	-17.4
6	3.5	$\frac{1}{4}$	+27.65	+14.9		+4.2	-12.0	-29.5
	7.0	$\frac{1}{2}$	+14.85	+15.7		+18.15	-2.63	-39.8
	10.5	$\frac{3}{4}$						
8	10.5	$\frac{3}{4}$	-9.22	-9.5		-18.9	-23.8	-15.6
25	3.5	$\frac{1}{4}$	+11.6	+12.55		+2.45	-18.15	-22.3
	7.0	$\frac{1}{2}$	+11.65	+14.65		+1.9	-3.05	-13.15
	10.5	$\frac{3}{4}$	+4.95	+6.75		-1.4	+5.25	-6.95
23	3.5	$\frac{1}{4}$	+9.7	+5.2		-0.25	-17.1	-17.5
	7.0	$\frac{1}{2}$	+12.75	+13.85		+10.45	+3.95	+4.4
	10.5	$\frac{3}{4}$	+13.425	+4.6		+1.55	+6.0	+5.0
21	3.5	$\frac{1}{4}$	+29.5	+7.2		+1.75	-9.25	-23.95
	7.0	$\frac{1}{2}$	+12.25	+0.35		-6.75	-14.5	-28.35
	10.5	$\frac{3}{4}$	+4.05	+8.75		+8.4	-0.2	-6.25
20	3.5	$\frac{1}{4}$	+4.15	+11.8		-0.365	-22.3	-30.3
	7.0	$\frac{1}{2}$	+12.35	+11.35		+7.9	-5.55	-19.25
	10.5	$\frac{3}{4}$	+7.65	+3.75		+17.1	+5.6	+1.2
16	3.5	$\frac{1}{4}$		+8.9	-4.6	+8.95	-12.75	-21.4
	7.0	$\frac{1}{2}$		+8.9	+8.25	-2.15	-2.8	-6.2
	10.5	$\frac{3}{4}$		+5.9	-5.1	+0.7		-8.3
15	3.5	$\frac{1}{4}$		-7.1	-9.05	-0.3	-15.25	-18.2
	7.0	$\frac{1}{2}$		-1.2	+0.3	-6.1	-7.95	-15.05
	10.5	$\frac{3}{4}$		-3.45	-2.6	-4.65		-6.95

TABLE 5—*Concluded*

DESIGNATION OF BUTTER- FLIES	AVERAGE ILLUMINA- TION IN EACH BEAM IN METER- CANDLES	PORTION OF SEC- TORED DISK RE- MOVED	FLASH-FREQUENCY PER SECOND					
			30	20	15	10	5	2
			Angles of deflection					
14	3.5	$\frac{1}{4}$		+12.95	+9.9	-7.3	-5.3	-17.85
	7.0	$\frac{1}{2}$		+10.4	+6.75	+3.35	+7.13	-9.41
	10.5	$\frac{3}{4}$		+6.45	+5.55	+1.65	+1.25	+2.8
12	3.5	$\frac{1}{4}$				+5.05		-6.3
	7.0	$\frac{1}{2}$		+22.8		+9.3		+1.65
	10.5	$\frac{3}{4}$		+9.35	+20.25	+10.15	+6.85	+8.4
11	3.5	$\frac{1}{4}$						
	7.0	$\frac{1}{2}$		-9.6	-13.0	-5.15	-15.55	-18.9
	10.5	$\frac{3}{4}$		-9.7	-13.52			
9	3.5	$\frac{1}{4}$		+8.3	-13.8	-11.75	-9.45	-23.8
	7.0	$\frac{1}{2}$		-3.1	-11.05	-5.95	-16.6	-23.075
	10.5	$\frac{3}{4}$		-13.75	-4.15	-8.75	-7.85	-19.05
7	3.5	$\frac{1}{4}$		0.0	-3.25	-12.2	-14.6	-29.8
	7.0	$\frac{1}{2}$		+7.95	+4.45	+2.25	-5.3	-12.3
	10.5	$\frac{3}{4}$		+5.75	+8.8	+8.75	+2.65	-0.05
Total aver- age	3.5	$\frac{1}{4}$	+15.387	+7.67	-4.16	+0.84	-14.67	-22.76
	7.0	$\frac{1}{2}$	+10.75	+6.73	-0.71	+0.92	-6.58	-15.67
	10.5	$\frac{3}{4}$	+1.37	+0.11	+1.31	+0.075	-2.15	-5.26

Vanessa than continuous light is in harmony with the results obtained in experiments upon the human eye which have been described previously. If McDougall and others are correct in their contention that a given light acting for a given length of time upon the human retina appears brighter than the same light acting for a longer period, it is to be expected that intermittent light of a certain flash-frequency will have a greater stimulating efficiency upon the human eye than continuous light. This expectation is confirmed by the results of the investigations of von Kries and Brücke, who maintain that a disk upon which are painted black and white sectors when rotated at a certain rate appears brighter than when rotated at other more rapid rates. This is also confirmed by the results obtained by Hyde and

Cady. These investigators contend that the flickering light obtained by rotating certain types of incandescent lamps at a rate of 3 revolutions per second seems to some observers to be brighter than continuous light of the same illumination. Moreover, it is supported by the results obtained by Ferry on the human eye, which have been presented previously.

VI. THE RELATION BETWEEN STIMULATING EFFICIENCY AND THE
RATIO BETWEEN THE DURATION OF THE LIGHT AND DARK
PERIODS OF INTERMITTENT LIGHT

In the preceding section it was demonstrated that the stimulating efficiency of intermittent light varies with the flash-frequency. In this section it will be demonstrated that it also varies with the ratio between the duration of the flashes and the dark periods between the flashes.

In the experiments described below the butterflies were exposed at the intersection of two beams of light of equal illumination arranged as in the preceding experiments, the light in one beam being continuous and that in the other intermittent. They were given tests with the flash-frequency of the intermittent light 30, 20, 15, 10, 5 and 2 per second and with the ratio between the light and dark periods of the intermittent light $1/3$, $1/1$, and $3/1$. The intermittent light used was produced by means of three different rotating sectored disks, one in which one-fourth of the disk was removed, one in which one-half of the disk was removed, and one in which three-fourths of the disk was removed. In every test made the total illumination of the intermittent light was equal to that of the continuous light. In this way the stimulating efficiency was ascertained of light of various flash-frequencies in which the length of the light and dark periods were in the following ratios respectively, 1 to 3; 1 to 1; and 3 to 1. Fourteen butterflies were tested in all, some under nearly all of the above conditions and others under only a few of them. The results obtained varied considerably in different individuals. In some respects, however, there was but little variation.

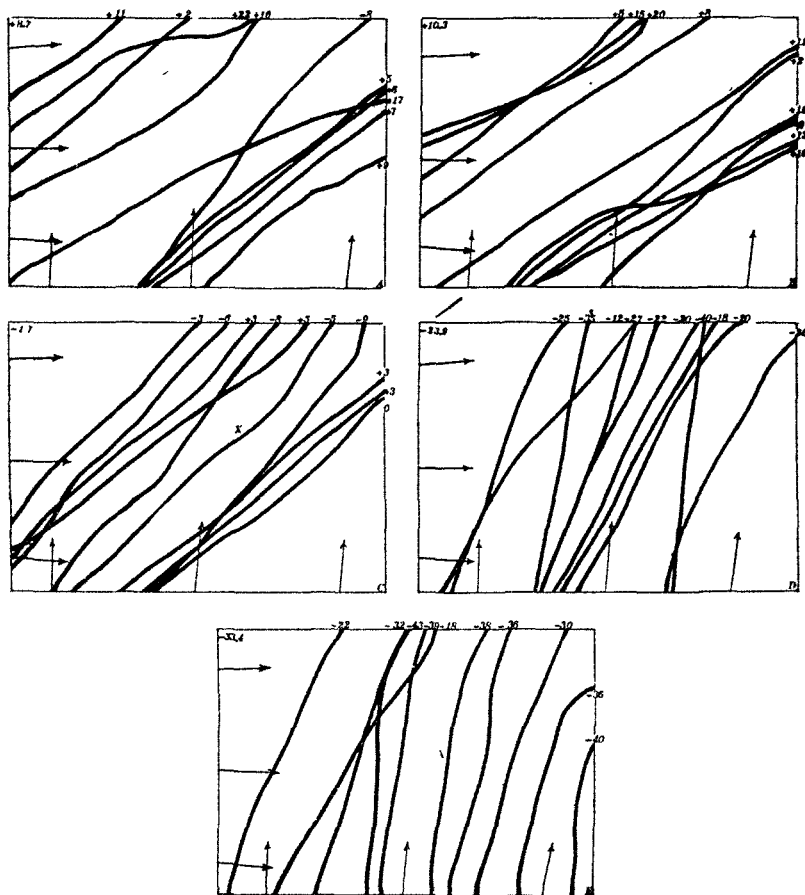


FIG. 2. Paths of a typical specimen of *Vanessa* in a field of light composed of two horizontal beams of equal illumination crossing at right angles, the light in one beam being continuous and that in the other intermittent. (Reduced by three-fourths). The intermittent light was produced by a rotating sector disk with one-fourth removed. Arrows to the left, direction of the rays of intermittent light; arrows below, direction of the rays of continuous light. Flash-frequency of intermittent light in A, 30; in B, 20; in C, 10; in D, 5; in E, 2 per second. Illumination in each beam, 3.5 m.c. Figures above and to right, degree of deflection in individual trials from line bisecting angle between the two beams. "Plus" indicates deflection toward source of intermittent light; "minus," toward source of continuous light. Figures in upper left hand corners indicate the average angle made in each group of 10 trials. The angles given in table 5 for this butterfly (25) are the average of 20 trials. In this figure only 10 of them under the different conditions are presented. Note that the degree of deflection varied with the flash-frequency. When the frequency of interruption was 2 per second the butterfly moved toward a point near the source of continuous light. When the frequency of interruption was 20 and 30 per second the organism moved toward a point some distance from the source of intermittent light. At intermediate flash-frequencies it moved toward points between the above.

The methods used and the results obtained may be elucidated by a detailed description of one of the numerous similar experiments performed. The animal used in this experiment was designated butterfly "25." This insect was first tested in the flash-frequencies mentioned above with the dark periods of the intermittent light three times as long as the light periods: after an interval of about 30 minutes it was tested with the dark periods of the intermittent light equal to the light periods: finally after another interval of about 30 minutes it was tested with the dark periods only one-third as long as the light periods.

With the ratio between the light and dark periods, $1/3$, and with a flash-frequency of 2 per second the average angle of deflection obtained for 20 trials was -23.3 degrees; with a flash-frequency of 5 per second the average angle of deflection was -18.15 degrees; with a flash-frequency of 10 per second the average angle of deflection was $+2.45$ degrees; with a flash-frequency of 20 per second the average angle of deflection was $+12.55$ degrees; and with a flash-frequency of 30 per second the average angle of deflection was $+11.6$ degrees (fig. 2).

With the ratio between the light and dark periods, $1/1$, and with a flash-frequency of 2 per second the average angle of deflection obtained for 20 trials was -13.15 degrees; with a flash-frequency of 5 per second the average angle of deflection was -3.05 degrees; with a flash-frequency of 10 per second the average angle of deflection was $+1.9$ degrees; with a flash-frequency of 20 per second the average angle of deflection was $+14.65$ degrees; and with a flash-frequency of 30 per second the average angle of deflection was $+11.65$ degrees (fig. 3).

With the ratio between the light and dark periods, $3/1$ and with a flash-frequency of 2 per second the average angle of deflection obtained for 20 trials was -6.95 degrees; with a flash-frequency of 5 per second the average angle of deflection was $+5.25$ degrees; with a flash-frequency of 10 per second the average angle of deflection was -1.4 degrees; with a flash-frequency of 20 per second the average angle of deflection was $+6.75$ degrees; and with a flash-frequency of 30 per second the average angle of deflection was $+4.95$ degrees (fig. 4).

These results show that the stimulating efficiency of intermittent light depends not only on the flash-frequency but also on the ratio between the duration of the flashes and the intervals between the flashes. This conclusion is evident if the lights

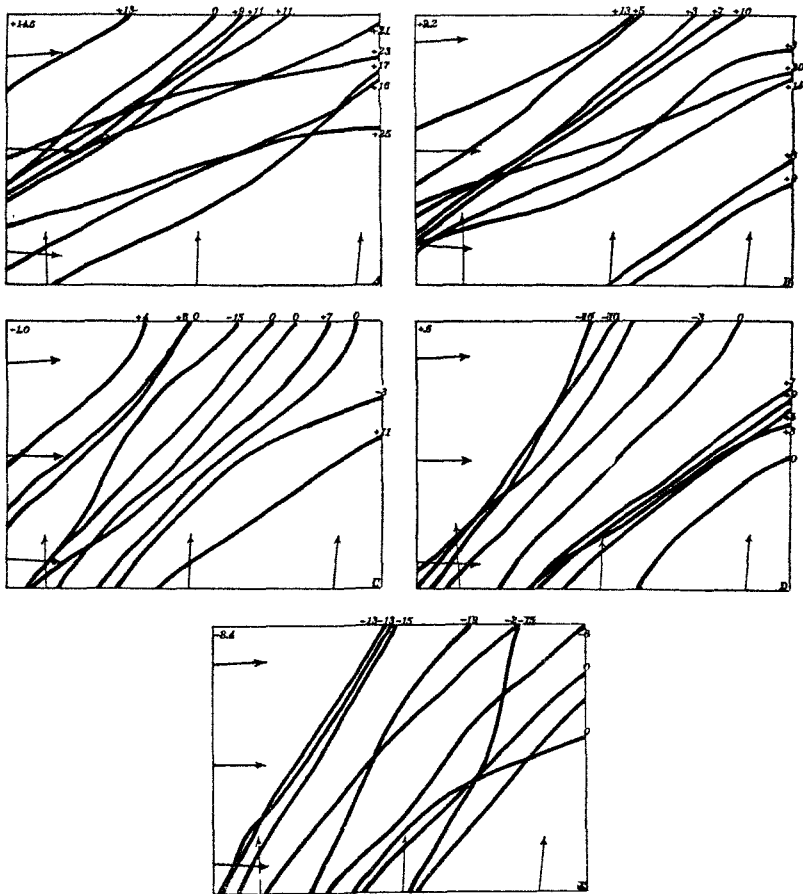


FIG. 3. Paths of a typical specimen of *Vanessa* in a field of light composed of two horizontal beams of equal illumination, 7 m.c. crossing at right angles, the light in one beam being continuous and that in the other intermittent. (Reduced by three-fourths). The intermittent light was produced by a disk with one-half removed. Other explanations of this figure are the same as those already given in the description of figure 2. Note here also that the degree of deflection varied with the flash-frequency.

of the same flash-frequency but of different ratios between the light and dark periods are arranged in order as to relative stimulating efficiency. When this is done it is apparent that those lights of flash-frequencies of 30, 20, and 10 per second in which

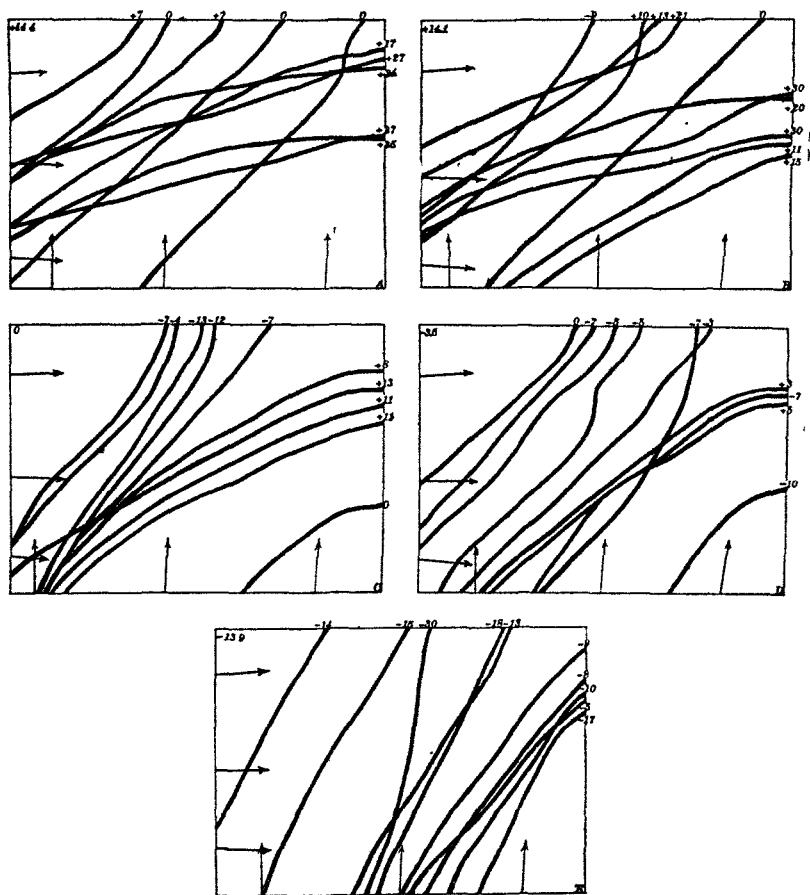


FIG. 4. Paths of a typical specimen of *Vanessa* in a field of light composed of two horizontal beams of equal illumination, 10.5 m.c., crossing at right angles, the light in one beam being continuous and that in the other intermittent. (Reduced by three-fourths). The intermittent light was produced by a disk with three-fourths removed. Other explanations of this figure are the same as those given in the description of figure 2. Note here also that the degree of deflection varied with the flash-frequency.

the ratio between the duration of the light and dark periods is $1/3$ are of higher stimulating efficiency than the lights of corresponding flash-frequency but in which the ratio between the light and dark periods is $1/1$ and $3/1$. Similarly, those lights of flash-frequencies of 5 and 2 per second in which the ratio between light and dark periods is $1/3$ are of lower stimulating efficiency than those lights of corresponding flash-frequency but in which the ratio between light and dark periods is $1/1$ and $3/1$. This indicates that the stimulating efficiency of intermittent light depends on the ratio between the duration of the light and dark periods and that the ratio at which it is most efficient at higher flash-frequencies is different from that at which it is most efficient at lower flash-frequencies. This conclusion is confirmed by the results obtained in all of the experiments made which are presented in tables 5 and 6. The significance of the results presented in table 5 is not evident, however, until the data are analyzed, as is done in table 6.

The data in table 6 may be made clearer by a brief explanation of those given for one of the lights, e.g., intermittent light of a flash-frequency of 15 per second produced by a disk with one-half removed. This is given the serial number "2" because 66.66 per cent, or 4 out of the 6 butterflies tested in this light and in the light of a flash-frequency of 15 per second produced by a disk with three-fourths removed deflected more toward the source of intermittent light in the former than in the latter. In the same way a greater proportion of butterflies deflected more in the same direction in the lights listed under serial order number "1" than in those under "2."

It is to be noted that the relative stimulating efficiency of many of the lights is determined by comparatively small percentages. For example, the light of a flash-frequency of 15 produced by a disk with one-fourth removed is assigned a higher stimulating efficiency than the light of a flash-frequency of 2 per second produced by a disk with three-fourths removed because only 60 per cent of the animals tested in both of these lights deflected more toward the source of intermittent light than toward the other source in the former than in the latter light.

TABLE 6

Relation between stimulating efficiency and the ratio between the duration of the flashes and the dark periods between the flashes, as ascertained by an analysis of the data given in table 5. Lights of the same flash-frequency are arranged in groups. "y," arbitrary unit, amount of light energy emitted in a single flash of intermittent light of flash-frequency of 80 per second produced by rotating disk with one-fourth removed

GROUP	SERIAL ORDER OF STIMULATING EFFICIENCY	PORTION OF SECTORED DISK REMOVED	FLASH-FREQUENCY PER SECOND	RATIO BETWEEN THE DURATION OF THE FLASHES AND THE DARK PERIODS BETWEEN THE FLASHES	AMOUNT OF LIGHT ENERGY EMITTED IN ONE SECOND	PERCENTAGE OF BUTTERFLIES THAT DEFLECTED MORE TOWARD THE SOURCE OF INTERMITTENT LIGHT IN THE LIGHT OF THE PRECEDING THAN IN THAT OF THE SUCCEEDING SERIAL NUMBER
I	1	$\frac{1}{4}$	30	1/3	30 y	66 66
	1	$\frac{1}{2}$	30	1/1	120 y	
	4	$\frac{3}{4}$	30	3/1	270 y	
II	1	$\frac{1}{4}$	20	1/3	30 y	60.00
	1	$\frac{1}{2}$	20	1/1	120 y	83 33
	4	$\frac{3}{4}$	20	3/1	270 y	66 66
III	2	$\frac{1}{2}$	15	1/1	120 y	66.66
	3	$\frac{3}{4}$	15	3/1	270 y	60.00
	9	$\frac{1}{4}$	15	1/3	30 y	
IV	5	$\frac{3}{4}$	10	3/1	270 y	63.63
	6	$\frac{1}{2}$	10	1/1	120 y	66.66
	8	$\frac{1}{4}$	10	1/3	30 y	60.00
V	7	$\frac{3}{4}$	5	3/1	270 y	77.77
	10	$\frac{1}{2}$	5	1/1	120 y	91.66
	12	$\frac{1}{4}$	5	1/3	30 y	100 00
VI	10	$\frac{3}{4}$	2	3/1	270 y	90.90
	11	$\frac{1}{2}$	2	1/1	120 y	63.63
	13	$\frac{1}{4}$	2	1/3	30 y	

It is probable that tests of larger numbers of butterflies would change the relative stimulating efficiency assigned to several of the lights.

Table 6 shows that the differences in illumination of the various lights used does not cause the differences in stimulating efficiency of these lights, for lights differing greatly in the amount of light

energy emitted in a unit of time are of equal stimulating efficiency. For example, intermittent light of a flash-frequency of 20 per second produced by a disk with one-fourth removed and light of the same flash-frequency produced by a disk with one-half removed are of equal stimulating efficiency. Yet the latter of these two lights emits four times the amount of light energy in one second that the former does.

Table 6 also shows that the stimulating efficiency of the lights used depends on the ratio between the duration of the light and dark periods. This is evident when the members of each of the groups in this table are studied. For example, in group I are placed those lights of a flash-frequency of 30 per second and in group VI are placed those lights of a flash-frequency of 2 per second. Any difference in stimulating efficiency between the members of each group is therefore not due to differences in flash-frequency for this factor is the same in all. Hence differences in stimulating efficiency between the members of each group must be due to the ratio between the duration of the light and dark periods. In the first two groups the order of the stimulating efficiency of the lights of the three ratios is as follows: $1/3$, $1/1$, and $3/1$, i.e., in each of the first two groups the intermittent light in which the ratio of the duration of the light to the dark periods is $1/3$ is of the highest stimulating efficiency, and the intermittent light in which the ratio of the duration of the light to the dark periods is $3/1$ is of the lowest stimulating efficiency. Similarly, in the last three groups the order of the stimulating efficiency of the lights of the three ratios is as follows: $3/1$, $1/1$, and $1/3$. This shows that the stimulating efficiency of the intermittent light used in the experiments depends on the ratio between the duration of the light and dark periods and that the effect of the ratio is reversed at lower flash-frequencies.

VII. INFLUENCE OF MECHANICAL STIMULATION AND PREVIOUS EXPERIENCE ON THE REACTIONS OF VANESSA TO LIGHT

When two paths made under the same conditions differ in the angle made with the rays of light it indicates a change in the physiological state of the organism. Two factors were dis-

covered which may influence the physiological state of the organism and consequently the angle made in a field of light composed of two horizontal beams crossing at right angles. They are present stimulation and previous experience of the organism.

The effect of the first of these was demonstrated in the following manner. A butterfly designated "21" was given 10 trials in two beams of continuous light which crossed at right angles. The illumination in one beam was four times stronger than that in the other. The average angle made in these trials was -9.5 degrees (see fig. 5). After each trial the butterfly was allowed to walk onto a piece of cardboard by means of which it was

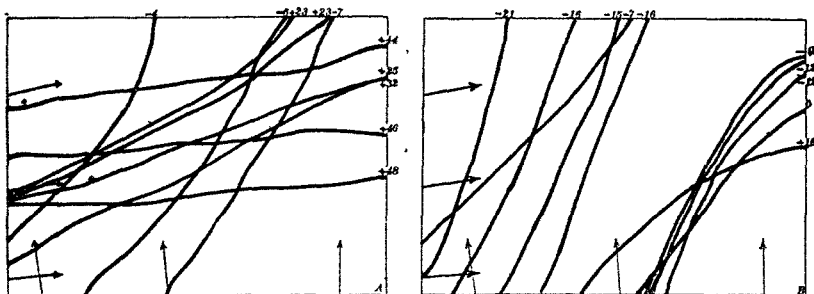


FIG. 5. Paths of a specimen of *Vanessa* (butterfly 21) showing effect of stimulation on orientation in a field of continuous light composed of two horizontal beams crossing at right angles. (Reduced by three-fourths). Illumination in beam to left, 3.5 m.c.; in beam below, 14 m.c. Figures above and to right, degree of deflection in individual trials from line bisecting angle between the two beams. "Plus" indicates deflection toward weaker light; "minus," toward stronger light. Conditions in A and in B were identical except that before each of the trials in B care was taken not to stimulate the insect, while before each of the trials in A the animal was stimulated by being shaken violently in the hollow of the hand. Note that stimulation caused the insect to react more strongly to the weak light and to react very slightly, if at all, to the strong light in 7 out of 10 trials.

carefully transferred to the starting point for a new trial so as to avoid stimulation as much as possible. After completion of these trials the organism was given 10 more trials under the same conditions, except that before each of these trials the insect was stimulated by being picked up in the fingers, placed in the hollow of the hand, and shaken violently. The average angle

made in these 10 trials was $+22.4$ degrees. This shows very clearly that mechanical stimulation may greatly affect the deflection in continuous light from two sources. Here "plus" indicates deflection toward weaker light and "minus" toward stronger light. Where used elsewhere in this paper "plus" indicates deflection toward stronger continuous light or toward intermittent light.

Stimulation also may affect the angle made in intermittent light. As is shown in figure 6, butterfly 21 was given 7 trials in intermittent light of a frequency of interruption of 5 per second by the method described previously. Care was taken, as in the tests in continuous light, not to stimulate the animal. The

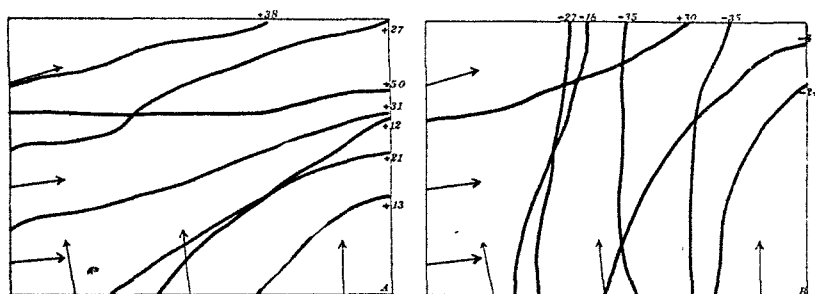


FIG. 6. Paths of a specimen of *Vanessa* (butterfly 21) showing effect of stimulation on orientation in intermittent light. The field of light is composed of two horizontal beams of equal illumination, 3.5 m.c., crossing at right angles, the light in one beam being continuous and that in the other intermittent. (Reduced by three-fourths). Intermittent light is of frequency of interruption of 5 per second produced by disk with one-fourth removed. Other explanations are the same as those given in the description of figure 2. Conditions in A and in B were identical except that before each of the trials in B care was taken not to stimulate the insect, while before each of the trials in A the animal was vigorously stimulated by handling. Note that stimulation caused the insect to react strongly to intermittent light and very slightly, if at all, to continuous light in 6 out of the 7 trials

average angle made in these trials was -16.4 degrees. Immediately afterwards the butterfly was given 7 trials under the same conditions, but before each of these the insect was stimulated by being shaken violently in the hand. The average angle made in these 7 trials was $+27.4$ degrees. This test shows clearly that stimulation may also greatly affect the angle made with the rays of light if the light in one of the beams is intermittent.

It is to be noted that in the tests in continuous light (fig. 5) stimulation of the butterfly had the effect of making the organism move almost directly toward the weaker source of light, although the illumination in the other beam was four times greater. Even when the animal began a trial facing the stronger source, it eventually turned toward the weaker source. This persistence in turning toward the same source may possibly be due to the fact that in the first five trials it faced the weaker source and in the succeeding trials, although started in each trial in the other direction, it turned in the same direction as that in which it had turned first. This is evident if previous experience may affect the reactions of this insect, as is shown below.

When the animal started toward the weaker source the nerve impulses aroused by light passed along certain nerves, and during this time the pathways were probably closed to other nerve impulses set up by the stronger light when the insect reached that point where it was exposed to the stronger illumination. If this is true, there is in this case a conflict between stimuli of the same nature, and while the butterfly is reacting to the first it does not react to the second, which may be stronger. This phenomenon is probably similar to that property of higher organisms generally known as "attention."

A second factor which may influence the direction of the course taken in light from two sources is, as stated above, the previous experience of the butterfly. This is shown very beautifully in figure 7. Butterfly 25 was given, in the method described previously, 10 trials in two beams of continuous light, the illumination in one being 4 times that in the other. The average angle made was +9.6 degrees. Immediately after this the organism was given 10 trials in two beams of equal illumination, the light in one beam being continuous and that in the other intermittent of a flash-frequency of 30 per second produced by a disk with one-fourth removed. The average angle made in these trials was +16.7 degrees. Then the insect was given 10 more trials in continuous light under the same conditions as at first. The average angle made in these trials was +21.6 degrees. Why did the animal at one time make an

average angle of $+9.6$ degrees and then a little later under the same conditions make an average angle of $+21.6$ degrees? This difference is probably due to the fact that before the first test the organism had not been tested experimentally at all. Before the second series of trials it had just been tested in intermittent

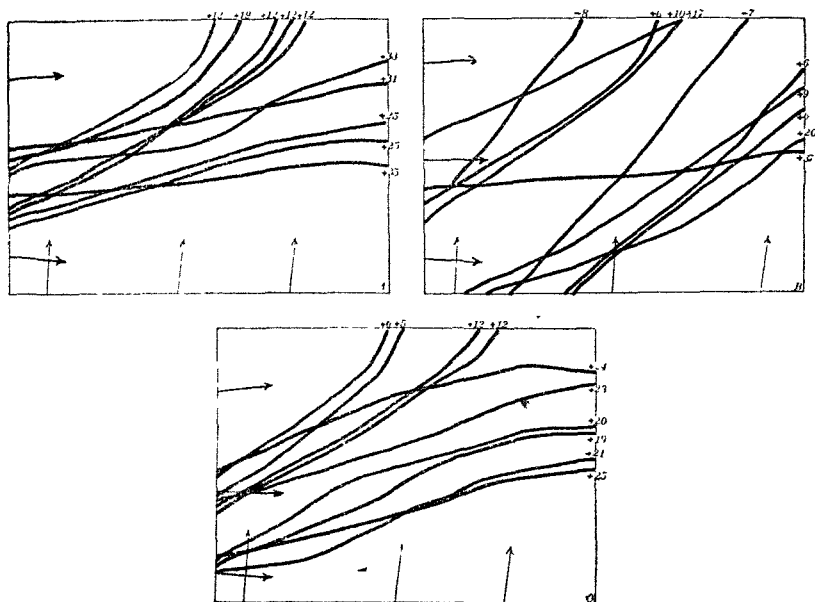


FIG. 7. Paths of a specimen of *Vanessa* (butterfly 25) showing the effect of previous experience on its reactions in a field of continuous light composed of two horizontal beams crossing at right angles. (Reduced by three-fourths.) Arrows to the left in A and in B, direction of rays of continuous light of illumination, 14 m.c.; arrows below in A and in B, direction of rays of continuous light of illumination, 3.5 m.c. Arrows to the left in C, direction of rays of intermittent light of flash-frequency of 30 per second produced by disk with one-fourth removed. Arrows below in C, direction of rays of continuous light. Illumination in each beam in C, 3.5 m.c. Figures have same significance as in preceding figures. In A and B "plus" indicates deflection toward stronger light; "minus," toward weaker light. In C, "plus" indicates deflection toward intermittent light; "minus," toward continuous light. Conditions in A and in B were exactly identical except that the butterfly had not been tested experimentally before the trials in B. It was however given the trials presented in C immediately before making the paths reproduced in A. Note the difference between the paths in A and in B. This difference is due to the fact that this organism in A was reacting, in part at least, to conditions which had ceased to exist, i.e., to the conditions to which it had just been reacting in C.

light of a flash-frequency of 30 per second, which has been shown to have a great stimulating effect upon this specimen of *Vanessa*, causing movement toward the source of intermittent light. The butterfly for 10 trials had reacted to this light from this direction, and then when the conditions were changed the

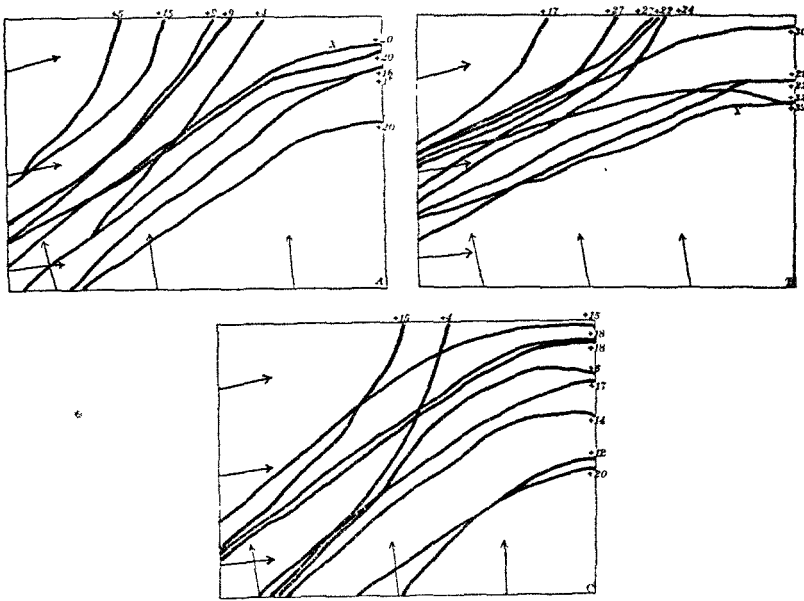


FIG. 8. Paths made by a specimen of *Vanessa* (butterfly 20) showing the effect of previous experience on its reactions in a field of light composed of two horizontal beams at right angles with each other. (Reduced by three fourths). Arrows to the left in A and in B, direction of rays of intermittent light. Arrows below in A and in B, direction of rays of continuous light. Illumination in each beam in A and B, 10.5 m.c. Arrows to left in C, direction of rays of continuous light, illumination, 14 m.c.; arrows below in C direction of rays of continuous light, illumination, 10.5 m.c. Intermittent light of flash-frequency of 2 and 10 per second in A and in B, respectively, produced by disk with three-fourths removed. Figures with prefixed signs have the same significance as in figure 7. While the animal was making trails marked X in A and in B the conditions were not the same as in the other trials in A and in B. During these two trials a beam of continuous light was substituted for the beam of intermittent light, thus changing the conditions to those which were present in C. Trails X were tenth in each series. Note that although the conditions were different, about the same angles were made in trails X as in the other trails in A and in B. Note also that in making trails X the insect was reacting in part to light conditions which had ceased to exist. In C are reproduced other trails made by this butterfly under exactly the same light conditions as those in which trails X were made.

insect continued to behave as it had just been doing. It deflected in the same direction. It was not reacting to the conditions which existed at that moment, but it was reacting to stimuli which had ceased to exist. This is probably an example of organic memory. This conclusion is confirmed by tests on another butterfly which are presented in figure 8.

This insect (fig. 8, C) was given 10 trials in two beams of continuous light, the illumination in one being 14 m.c. and that in the other 10.5 m.c. The angles made by the paths ranged from +4 to +20 degrees. It was then given 9 trials in two beams of equal illumination, 10.5 m.c., one of continuous and the other of intermittent light of a flash-frequency of 10 per second produced by a disk with three-fourths removed (fig. 8, B). The angles made by these paths ranged from +17 to +39 degrees. Suddenly the light conditions were changed so that they were the same as those in which the previous 10 trials had been made. The tenth trial was then given in these conditions (both beams of continuous light). The angle made was +32 degrees, an angle very nearly like those that had just been made under different light conditions and very unlike the angles that had previously been made under similar conditions. It is probable that in making this tenth trial the insect was reacting to light conditions that had ceased to exist. Its behavior was influenced still by its previous experience. If this is true it must be concluded that the orientation of *Vanessa* in light from two horizontal beams which cross at right angles depends upon its previous experience.

VIII. SUMMARY

1. When *Vanessa antiopa* is exposed to continuous light from two sources, the rays of which cross at right angles, it moves toward a point between the sources. The location of this point depends on the relation between the illumination received from the two sources.

2. The stimulating efficiency of intermittent light in the orientation of *Vanessa* varies with the flash-frequency. At flash-frequencies of 20 and 30 per second it is higher than that

of continuous light; at flash-frequencies of 5 and 2 per second it is lower than that of continuous light; and at flash-frequencies of 10, 100, 60, 50, and 40 per second it is approximately equal to that of continuous light.

3. The stimulating efficiency of intermittent light of relatively low flash-frequency depends on the ratio between the duration of the light periods and the dark periods. At flash-frequencies of 30 and 20 per second, intermittent light in which the ratio between the light and the dark periods is 3/1 is less efficient than light in which this ratio is 1/3 and 1/1. At these flash-frequencies the efficiency of the latter two sorts of light is apparently equal. At flash-frequencies of 10, 5, and 2 per second intermittent light in which the ratio between light and dark periods is 3/1 is more efficient than light in which this ratio is 1/1, and this light in turn is more efficient than light in which the ratio is 1/3.

4. Some specimens of *Vanessa* exhibit great variation in their reactions to light. This variation is shown to depend, in part at least, upon previous experience. Mechanical stimulation preceding exposure to light may cause butterflies to react more strongly to weak light than to strong light. It may also cause them to react more strongly to intermittent light of low flash-frequency than to continuous light of equal illumination. Moreover, butterflies after having reacted for some time to certain light conditions may continue to react in the same manner after the light conditions are suddenly changed.

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