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No. 321.

THE RELATION OF PHOTOTROPISM TO SWARMING IN
THE HONEY-BEE, APIS MELLIFERA L.

BY DWIGHT E. MINNICH.

FROM THE JOURNAL OF PSYCHOLOGY, VOL. II, No. 2.

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THE RELATION OF PHOTOTROPISM TO SWARMING IN THE HONEY BEE, *APIS MELLIFERA* L.¹

DWIGHT E. MINNICH

The honey bee is remarkable for the extent to which many of its activities are controlled by light. Observations and experiments demonstrating the strong photopositive responses of this animal have been detailed by Lubbock ('82, p. 278, 279, 284), Graber ('84) and Hess ('13a, '13b, '17). And indeed this feature of behavior must have been patent to many of the earlier workers, so strikingly and constantly is it exhibited.

While conducting some experiments on the photic behavior of bees several years ago, I was greatly impressed by the strong, positive reaction to light which normal individuals almost invariably displayed. Bees in an active state of locomotion, or easily excited to such, exhibited an orientation which, for its rapidity of accomplishment and its accuracy of maintenance, was most spectacular. I say bees exhibiting vigorous locomotion, for, obviously, bees which are torpid and do not move freely—a condition frequently encountered during cool, damp weather—cannot show phototropism. Even the moribund condition seemed often to intensify rather than to weaken photic behavior, and bees scarcely able to creep were observed making a final struggle toward the light.

My experiments were carried on well into the autumn, when it became more and more difficult to obtain bees in the field as the flowers became less abundant. I, therefore, installed a single comb of worker bees without queen, in a glass observation hive. The hive was kept darkened by means of small wooden covers fitted to the glass sides, and the exit was covered with a bit of screen wire to prevent the escape of the bees. Animals

¹ Contributions from the Zoölogical Laboratory of the Museum of Comparative Zoölogy at Harvard College. No. 321.

could be kept in this way in reasonably good condition for a month to six weeks, food being provided in case there was not sufficient in the comb. It was on these bees that I made the observations to be detailed in the present note, which I believe afford some evidence on the question of swarming and its relation to light.

The strong positive phototropism of individual bees is also characteristic of certain activities of the hive as a whole. Kellogg ('03) was the first to call attention to the fact that swarming bees are strongly positive to light. He says (p. 694), "That the issuance from the hive at swarming time depends upon a sudden extra development of positive heliotropism seems obvious. The ecstasy comes and the bees crowd for the one spot of light in the normal hive, namely, the entrance opening. But when the covering jacket² is lifted and the light comes strongly in from above—my hive was under a skylight—they rush toward the top, that is toward the light. Jacket on and light shut off from above, down they rush; jacket off and light stronger from above than below and they respond like iron filings in front of an electro-magnet which has its current suddenly turned on." These observations leave no doubt as to the strong positive phototropism of swarming bees. The statement, however, that the issuance of the swarm is dependent upon a "*sudden extra development*" of positive phototropism has met with some difference of opinion.

Thus von Buttler-Reepen has objected to this interpretation on the ground of a particular swarm instinct. He says ('15, p. 168)" . . . so ist in diesen Momenten [the emergence from the hive at swarming] nicht ein besonders starker Heliotropismus die Ursache, sondern die Schwärminstinkte drängen die Bienen in das Freie." Another objection, and I believe a much more important one, is suggested by a statement of Hess ('13a, p. 663). "Meine Versuche zeigen, dass die Neigung der Bienen, zum Hellen zu gehen, nicht auf die Zeit des Hochzeitsfluges beschränkt ist." This contention of Hess—that the

² Kellogg had a glass observation hive covered with a black cloth jacket.

manifestation of photopositiveness is not confined to any given period, such as the nuptial flight, has been amply confirmed in my observations. I have already called attention to the fact that among individual bees an active animal exhibits, almost without exception, strong positive phototropism. Large aggregates of bees also show marked positive light reactions quite aside from swarm activities, as the following observations clearly show.

The glass observation hive with its single comb of bees was situated at a south window where it was exposed to the sun during the morning hours. With the oncoming of the cool days of late October and early November, the bees became much less active. On bright days, however, the exposure to the warmth of the sun, and the corresponding rise of temperature within the hive, served to activate the colony until most of the bees were moving about the walls of the hive in a rapid uneasy manner. If at such a time the cover was removed from the end nearer the window, thus admitting the light, there was with the first penetrating rays, a sudden increase of the hum within. Thereupon ensued a scene no less spectacular than that described by Kellogg ('03, p. 693). His words picture it exactly, ". . . . the whole community of excited bees flowed—that is the word for it, so perfectly aligned and so evenly moving were all the individuals of the bee current—," toward the illuminated side. A few hours later, however, when the sun had passed from the hive and the temperature had fallen, particularly on the cooler days, the uncovering of one end of the hive elicited no such response. With perhaps the exception of a very few individuals, the bees remained quietly in the swarm cluster. Nor was this failure to obtain a response a result of the lowered intensity of light, for the active worker bee responds to a fairly low intensity. It must, therefore, have been due to the difference in temperature.

These facts, together with those previously stated, demonstrate conclusively that the pronounced phototropism, so conspicuous in swarming bees, is not confined to the period of swarming. This condition of photosensitivity appears to remain fairly constant at all times in the animal, although active locomo-

tion and the absence of other strong, distracting stimuli are necessary to its demonstration. The situation here differs from that described by Loeb ('90) for winged male and female ants, in which positive phototropism is confined exclusively to the period of the nuptial flight.

We may agree with Kellogg, therefore, that the issuance of bees from the hive at swarming may be a simple exhibition of positive phototropism, but it is not the result of a sudden increase in phototropism. The sudden increase is in the activity of the animals. Consequently, the fundamental factors in swarm behavior are those which effect a condition of heightened activity, a condition in which locomotion is generally controlled by light. In my own observations the state of heightened activity doubtless arose from the conditions of temperature and the prevention of the bees from making their accustomed flights for defecation, etc. The factors which activate the swarm are not known. They may consist of particular swarm instincts, as von Buttel-Reepen ('15) has suggested, or they may even be more simple reflexes of as yet unknown nature. In any case, the evidence seems clear that, although phototropism may be an important feature of swarm behavior, it is neither peculiar to this activity nor the primary causal agent of it.

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BY DWIGHT E. MINNICH.

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THE PHOTIC REACTIONS OF THE HONEY-BEE, APIS MELLIFERA L.¹

DWIGHT E. MINNICH

SEVENTEEN FIGURES

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I. INTRODUCTION

The circus movements produced by blackening one eye in certain arthropods have long been familiar to zoölogists. It was not, however, until the advent of more recent interpretations of behavior, that they received any considerable attention. Then for the first, the significance of their relationship to normal orientation was recognized. It became apparent that the nature of the stimulus involved in the two cases was the same. Obviously, therefore, the application of any general theory of photic orientation to those forms in which circus movements occurred depended upon its ability to explain this phenomenon satisfactorily. This consideration has led, within the last few years, to a number of more or less extensive investigations of these reactions.

When the present researches were begun there had been no attempt to study circus movements quantitatively. During the

¹ Contributions from the Zoölogical Laboratory of the Museum of Comparative Zoölogy at Harvard College, no. 320.

progress of the experiments, however, Dolley ('16) has published a contribution to this phase of the subject. His methods as well as his results, on *Vanessa*, differ widely from those to be described for the honey-bee. Although in his experiments, as in mine, the illumination employed is defined as non-directive, it was very unlike in the two instances. The results obtained by Dolley are described in terms of circus movements of greater or lesser 'angles of curvature;' those obtained by the writer, in terms of degrees turned per centimeter. The conclusions drawn in the two papers are also widely divergent.

It is a pleasure here to acknowledge my deep indebtedness to Dr. G. H. Parker, at whose suggestion this research was undertaken and with whose helpful criticism it was carried on. I wish also to express my gratitude to Dr. E. L. Mark for the courtesies and privileges of the Zoölogical Laboratory.

II. LITERATURE

As early as 1796, Goeze² (p. 42) recorded the fact that a hornet in which one eye had been painted over with an opaque varnish always flew toward the uncovered eye. Some years later, Treviranus ('32, p. 194) described an experiment in which the lower half of the right cornea of a dragon-fly was carefully cut away from the optic nerve, with the result that the animal moved toward the left side.

Decidedly the most interesting of the earlier observations are those of Dubois ('86) on a phosphorescent elaterid beetle of the genus *Pyrophorus*. This insect responds positively to at least certain intensities of light, and according to Dubois (p. 209) it is most affected by the yellow-green rays, which also predominate in the spectrum of its own light. The photogenic organs are three in number, one occupying a median ventral position on the first abdominal segment, the other two being situated on opposite sides of the prothorax near its dorsolateral edges. Whenever the beetle begins to creep spontaneously in the dark, the prothoracic organs become luminous. During flight the abdominal organ does likewise.

² I have not had direct access to this work. The above reference is taken from a footnote in Treviranus ('32, p. 193).

Dubois (p. 208) found that upon completely obscuring the light from the prothoracic organ of one side of the body with a covering of black wax, the beetle no longer crept in a straight line. Smoked paper records, made in a dark room, showed that such individuals crept in circles toward the functional eye. A check experiment, moreover, showed that the results obtained were not due to the weight of the wax. If instead of eliminating one of the prothoracic organs, the cornea or the entire eye of one side was destroyed with a red-hot needle (p. 211), very similar results were obtained. When, however, both photogenic organs of the prothorax were obscured or both eyes were destroyed, the animal crept in a hesitant, irregular fashion, presently stopping altogether.

Dubois has interpreted these results from an anthropomorphic viewpoint, as evidenced by his original paper and by a more recent comment ('09). To the present writer, however, these responses of *Pyrophorus* afford not only a typical case of circus movements, but one of considerable theoretical importance as well. The tendency to circle attendant upon the suppression of one photogenic organ or the destruction of one eye may be attributed to the unequal stimulation on the two sides of the body. If this be correct, the case is indeed unique, for the beetle is oriented by its own luminosity. This, of course, in no wise affects behavior in the normal animal. With a photogenic organ on each side of the prothorax producing light of the same quality and intensity, it is always perfectly oriented with respect to its own light. But if the source of light or the photoreceptor of one side be eliminated, the beetle promptly orients toward the opposite side, the side which is receiving the greater stimulation.

In recent years, a steadily increasing number of arthropods have been shown to exhibit circus movements when one eye is blackened or destroyed. The researches of Bethe ('97 a), Axenfeld ('99), Holmes ('01, '05), Rádl ('01, '03), Parker ('03), Hadley ('08), Carpenter ('08), Brundin ('13), Holmes and McGraw ('13), Dolley ('16), and Garrey ('17), have demonstrated conclusively that among phototropic arthropods generally, unilateral photic stimulation results in a more or less asymmetric response.

These investigations have covered between fifty and sixty species, including the four chief classes of arthropods. Among the insects, where most of the work has been done, representatives of most of the larger orders have been experimented upon. These embrace Orthoptera, Blattoidea, Hymenoptera, Coleoptera, Odonata, Lepidoptera, Diptera, Homoptera, and Hemiptera. The phenomenon of circus movements—or perhaps better, asymmetrical response—must, therefore, be regarded as general rather than exceptional for the members of this phylum.

The form of response naturally varies with the peculiarities of locomotion in a given species. It is not the same for a sidewise moving crab, such as *Carcinus*, as it is for an insect which moves forward. With the usual type of forward locomotion, however, arthropods with one eye blackened generally circle toward the functional eye, if they are positively phototropic; toward the non-functional eye, if they are negatively phototropic.

It is true there are cases which, on first examination, do not appear to conform to this generalization. Thus Holmes ('05, pp. 332–336) has demonstrated clearly that an animal with one eye blackened may at first perform circus movements in creeping toward a light, only to modify its behavior after a time and creep in a straight path. Such was true of both *Ranatra* and *Notonecta*. Axenfeld ('99, p. 375) had previously made similar observations, and more recently Brundin ('13, pp. 337, 346–348) and Dolley ('16, pp. 371–382) have demonstrated the same phenomenon in the species with which they worked.

There can be no doubt, therefore, that many arthropods with one eye blackened are able in time to modify their behavior to light. This, however, in no wise lessens the significance of the initial tendency of the animal to perform circus movements. In fact, this initial tendency is the all-important one as far as the question of orientation in the normal animal is concerned. I do not believe, therefore, that the presence of modifiability in an animal warrants considering its behavior as an exception to the general occurrence of circus movements.

A second difficulty in the way of any generalization concerning circus movements has been encountered in the behavior of cer-

tain flies. Thus Rádl ('03, p. 62) says, "Die Calliphora vomitoria bewegt sich fast ebenso gerade mit einem geschwärzten Auge, wie wenn sie aus beiden sieht, und es ist mir nicht leicht, diese Erscheinung zu erklären." Carpenter ('08, p. 486) states that *Drosophila* with one eye blackened "crept in a fairly direct path toward the light, although a tendency to deviate toward the side of the normal eye regularly occurred." It is possible, I believe, to interpret these cases as merely more extreme instances of modifiability, in which regulation occurs very rapidly instead of after a more or less prolonged experience.

That modifiability is operative, at least in the case of *Drosophila*, is evidenced by the following statement of Carpenter (p. 486). "The tendency to diverge from the direct path toward the side of the uncovered eye was overcome by a series of short, quick turns in the opposite direction, which kept them headed toward the light." Further evidence in the case is afforded by the behavior of one fly which, according to Carpenter, persisted in performing circus movements. This fly, however, (p. 486) "had long been active, and showed signs of fatigue." As will be shown later, very similar phenomena were observed in the honey-bee. In conditions, such as that of weakness, induced by long experiment, the bee frequently circled much more toward the functional eye than it had formerly done. It seems probable that in such states the animal approximates more nearly to a simple, reflex behavior. Factors effective in modifying behavior in the vigorous animal have ceased to be operative.

If these interpretations be correct, the conspicuous absence of circus movements in *Drosophila* is only an extreme case of modifiability, and offers no real objection to the general conclusion to be drawn from these reactions. However, further work is necessary upon both *Drosophila* and *Calliphora* before they may be disposed of with certainty.

Responses of still another kind have seemed perhaps the most formidable obstacle to any general conclusion as to the occurrence of circus movements. Thus Hadley ('08, p. 197) has shown that whereas the 'progressive orientation' of the lobster larva after the blinding of one eye is positive, the larva performs circus

movements or turns toward the injured side. Brundin ('13, p. 346) states that in positive specimens of *Orchestia traskiana*, circus movements will occur as often toward the blackened as toward the normal eye, while Holmes and McGraw ('13, p. 370) report the case of a positive skipper butterfly which almost invariably circled toward the blackened eye.

A very plausible explanation of these apparent anomalies, however, has been offered by Dolley ('16, pp. 394-399), who has shown that the contact stimulus afforded by the material covering the eye is sufficient to cause *Vanessa*, when in the dark, to turn continuously toward the covered eye. This tendency, moreover, exhibits little, if any, modification from day to day. The effect of such a contact stimulus is continuous. But in the presence of photic stimulation of moderate or high intensity, it is quite overwhelmed by the strong phototropism of the butterfly. In the case of animals of less certain phototropic index, this contact stimulus is, in all probability, frequently strong enough to overcome the effect of light. An examination of the cases cited above shows that the phototropism of these animals is not of the unequivocal kind exhibited by *Vanessa*. It seems likely, therefore, that their apparently exceptional behavior was due to contact and not to photic stimulation.

Suppressions of photic circus movements by responses to other stimuli are not surprising, when it is recalled with what facility even the stereotyped circus movements produced through unilateral lesions of the central nervous system may be altered in a similar manner. Thus Bethe ('97 b, p. 507) states that the tendency of bees to circle toward the normal side after the removal of one half of the brain or the severance of one of the oesophageal commissures, may be arrested, and the animal may even be compelled to deviate toward the injured side by stimulating the legs of the normal side. Moreover, in a general statement concerning the several crustaceans and insects subjected to similar operations (p. 541), he says, ". . . nach Aufhebung der Hemmung der gesunden Seite durch angebrachte Reize aber auch spontan bei allen Versuchstieren gerader Gang und Kreisgang nach der operirten Seite eintritt."

Whether the effect of contact stimulation also accounts for certain of the phenomena observed by Axenfeld ('99) is not so clear. Axenfeld reports that nocturnal lepidoptera with one eye blackened turned toward the blackened eye during the day. In the same paper he makes the following general statement: "Enfin on peut observer que ces mêmes animaux photofuges, qui tournent en pleine lumière du soleil du côté de l'oeil couvert, offrent le mouvement contraire au soir ou même de jour, quand ils sont transportés dans une chambre mal éclairée; . . ." It may be that such animals, being attuned to a low intensity, respond positively to it, whereas a stronger intensity evokes a negative reaction, somewhat according to the idea of Davenport ('97, p. 197). Certainly, if the circling of the nocturnal lepidoptera toward the covered eye was a light response, it is not in harmony with the statement of Loeb ('90, p. 51) to the effect that all 'day and night butterflies' are without exception positively phototropic. I am led to suspect, however, that some of the reactions noted by Axenfeld were the results of contact stimulus, for Hess ('13 a, p. 651) has shown that *Coccinella*, which Axenfeld reports as circling toward the blackened eye, is not negative to light. Axenfeld's experiments, therefore, need careful repetition before any final conclusions may be drawn from them.

It seems quite certain, therefore, that what have appeared to be exceptions to the general occurrence of circus movements among phototropic arthropods are not really incompatible with this view. Taken as a whole, the investigations of these reactions demonstrate rather conclusively that, although they may be modified through experience or obscured by responses to other than photic stimuli, they are, nevertheless, to be considered as characteristic of phototropic arthropods. Photic orientation in this group of animals, therefore, cannot be accounted for by any theory which fails to offer a satisfactory explanation of circus movements.

III. APPARATUS AND METHODS

1. *Directive Light*

In the experiments of the present paper, both directive and non-directive light were employed. Those involving directive illumination were carried on in a circular area (fig. 1) 2.44 m. in diameter, which was laid out in black lines on the concrete floor of a dark room. Sixteen centimeters³ above the center of this area, an incandescent lamp was suspended. The lamp employed was a 100-watt, 115-volt, stereopticon, Edison mazda lamp. Of several bulbs used in the course of experimentation, only the last was determined photometrically, its candle-power being approximately 80. These lamps when new are calculated to furnish 100 c.p., but their efficiency decreases considerably with usage.

In making tests in the directive light area, bees were started creeping at the outer circumference. The course of the animal as it traveled toward the light was then traced as accurately as possible on a record bearing a plan similar to that of the light area and drawn to scale. Such a record is shown in figure 1.

2. *Non-directive light*

a. Construction. The apparatus employed to furnish non-directive light consisted essentially of a white-walled, cylindrical chamber. This chamber was illuminated by an incandescent lamp, the light of which was diffused through a thin, white screen, suspended a short distance below the lamp. Bees were admitted to the apparatus through a small, circular opening in the center of the floor, and the course of their creeping was then traced as accurately as possible on a record. The apparatus was especially designed to afford a creeping animal a continuous photic stimulation of uniform intensity over the entire surface of the eye. A more detailed description is presented in the following paragraphs (see figure 2).

³ Distances from lamps to creeping surfaces were measured from the center of the filament in all cases.

The cylindrical chamber, which measured approximately 84 cm. in height by 87 cm. in diameter, was constructed on a light wooden framework covered on the exterior with heavy, corrugated cardboard. On the interior it was lined with a thickness

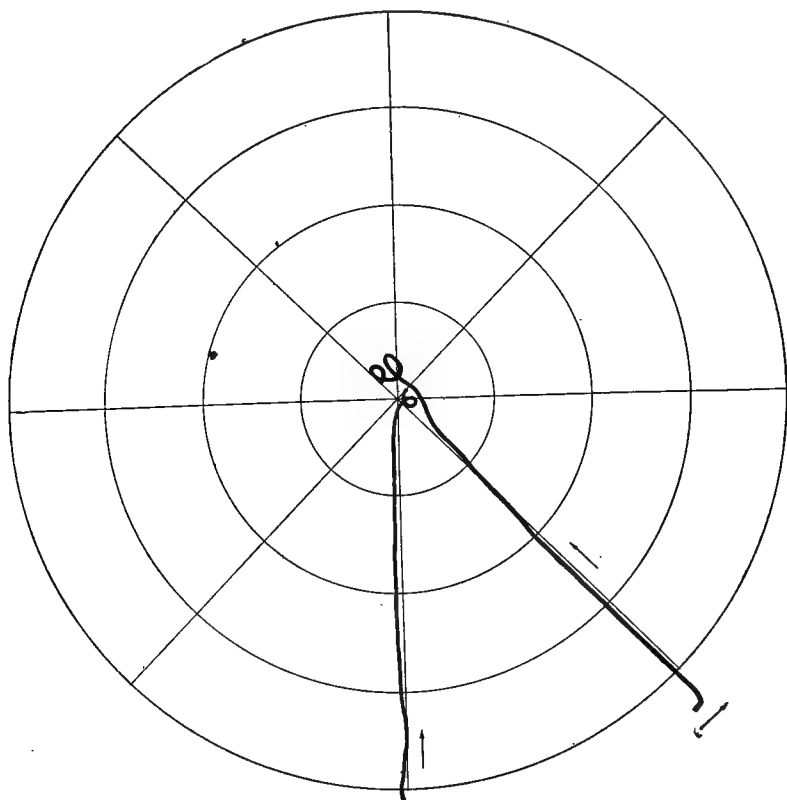


Fig. 1 Plan of directive light area, showing two trails of a normal bee. Note the deflection of the courses in the non-directive region near the lamp and directly beneath it.

of dead white, cotton cloth, backed by a layer of heavy white paper. On one side of the cylinder, and extending from its bottom edge, a rectangular opening 58 cm. high by 32 cm. wide was cut through the cardboard and paper layers. The white cloth lining only closed this opening, and it was here slit from top to bottom, the bottom edges being left free. The two flaps thus

formed allowed free access to the interior of the cylinder. In one of them a small opening (fig. 2, *o*), 3 by 4 cm., was cut for purposes of observation.

The top of the cylinder was similar in construction to the side walls except that the cardboard layer was omitted. Near opposite edges of the top, two circular openings, 8 cm. in diameter,

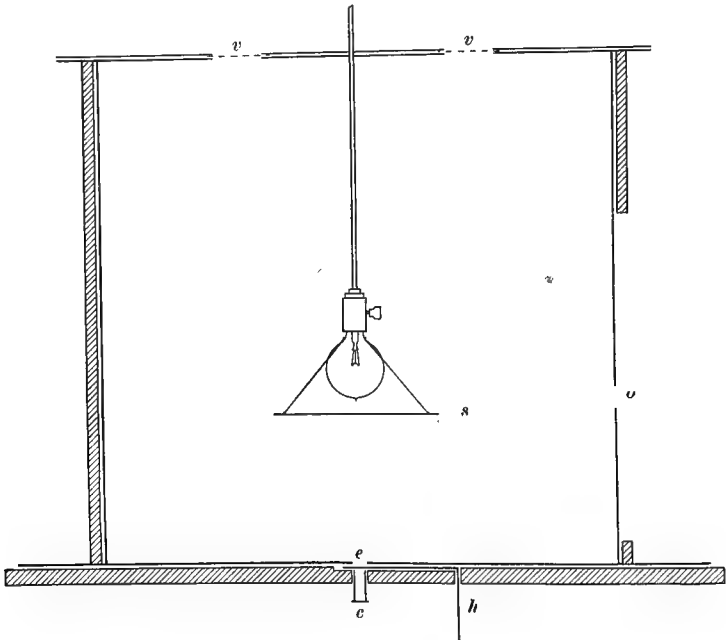


Fig. 2 Diagrammatic section through non-directive light apparatus. *c*, transferring cage; *e*, entrance to light chamber; *h*, handle of slide opening and closing *e*; *o*, opening for observation; *s*, light screen; *v*, ventilators.

were cut (fig. 2, *v*). These were covered with a thin, white gauze of coarse mesh, and served as ventilators, preventing any undue rise of temperature within the apparatus. The bottom of the cylinder was formed by a layer of heavy, dead white paper, which covered the table on which the cylinder stood. This paper was especially selected to afford a good creeping surface. On it was drawn a plan, similar to that shown in figure 3, by means of which the course of a creeping bee could be accurately followed.

The illumination of the apparatus resembled the semi-indirect illumination of a modern house, the light from an incandescent lamp being diffused through a circular screen (fig. 2, s), 22 cm. in diameter, of white bond paper. Two intensities of illumination were employed. The less intense was produced by a carbon filament lamp of approximately 2 c.p.,⁴ 66 cm. above the floor, and the more intense by the 80 c.p. mazda lamp previously described, 33 cm. above the floor. The intensity of illumination in each instance was measured at three different points on the floor of the cylinder. One determination was made at the center; a second at a point 3 cm. from the right side wall, and a third, at a point 3 cm. from the left side wall. The results of these measurements are given in table 1. Hereafter, in referring to the

TABLE 1

A	B	C	D	E	F
CANDLE-POWER OF LAMP	INTENSITY ON FLOOR AT CENTER	INTENSITY ON FLOOR 3 CM. FROM RIGHT SIDE WALL	INTENSITY ON FLOOR 3 CM. FROM LEFT SIDE WALL	AVERAGE OF C AND D	AVERAGE OF B AND E
<i>c.p.</i>	<i>mc.</i> ⁵	<i>mc.</i>	<i>mc.</i>	<i>mc.</i>	<i>mc.</i>
2.36	25.9	17.93	25.25	21.59	23.75
79.45	1051.5	831.37	894.45	862.91	957.21

two intensities of illumination employed, the averages given in the table will be used in round numbers. The less intense will be designated as non-directive light of 24 mc.; the more intense, as non-directive light of 957 mc.

The transference of bees to and from the apparatus was effected by means of a small, cylindrical cage of wire screen, 5 cm. in length by 2 cm. in diameter (fig. 2, c). This cage, one end of which was open, exactly fitted into a circular opening cut through the table top to the center of the chamber floor. By means of a

⁴ The lamp used throughout experimentation was, unfortunately, broken before being determined photometrically. Its candle-power was certainly between 2 and 4.

⁵ Throughout the present paper, the abbreviation mc. will be used to designate meter candles.

slide operated by a handle (fig. 2, *h*), it was possible, after inserting the cage, to open or close the light chamber at will. The difficulties involved in direct manipulation of bees were thus entirely avoided. An individual to be tested in non-directive light was merely allowed to creep into the cage, which was then inserted into the opening in the table top. The slide was then pushed aside and the bee allowed to creep up on to the floor of the apparatus. As soon as the bee had entered the light chamber, the slide was pushed back, closing the entrance and leaving the floor of the apparatus complete.

The ideal apparatus for studying the effects of continuous photic stimulation of a constant intensity would be one so constructed that all the ommatidia of a compound eye would receive equal illumination, irrespective of the direction of locomotion. Such an apparatus is virtually a physical impossibility. However, the apparatus just described is perhaps somewhat of an approximation to it, even if it does not afford an absolutely uniform light intensity over the floor of the light chamber. As table 1 shows, the illumination is more intense toward the center. Some fluctuation will, therefore, occur in the stimulation of the various ommatidia as the animal moves. However, in any position whatever on the floor of such a light chamber, all the ommatidia are receiving some stimulation. Moreover, the amount of stimulation received by those areas of the eye which are minimally affected does not differ vastly from that received by areas of maximal stimulation.

b. Records. The method of recording behavior in non-directive light is illustrated in figures 3 and 4. The animal to be tested was transferred to the light chamber, and its course of creeping, observed through the 'peep hole' in the curtain, was traced as carefully as possible on a record sheet. The record bore a plan similar to that on the floor of the light chamber, drawn on a scale of 1 to 6. The duration of each trial was ascertained by counting the rings of an electric bell, attached to an electric clock regulated to seconds. How long the trial should last was determined by an interval previously decided upon or by the animal encountering the side wall of the chamber and creeping up. On completion of

a trial, the bee was removed, and the remaining data called for on each record were entered. The tracing was marked with arrows to indicate its direction. Observations on the physical condition of the animal and others of importance, which were made from time to time, were also noted on the record. All the records of a single animal were then filed away together, thus affording a permanent record for further reference.

Since it was desired to make a quantitative study of circus movements, it was necessary to adopt some method whereby the amount of turning exhibited by an animal, in a given trial or group of trials, might be expressed as a single value. These values have been stated in terms of average number of degrees turned per centimeter of progress, and were obtained in the following manner. The length of the trail was first measured with a map tracer. Several readings were taken until two were obtained with a difference of less than 0.3 cm. These were then averaged, and the result used in computations. Thus in figure 3, the length of the original tracing is 26.95 cm. Since, however, the records were on a scale of 1 to 6, and these in reproduction have been reduced one half, the length of the text figure tracing must be multiplied by $(6 \times 2 =)$ 12 in order to obtain the distance actually traveled by the animal.

The various turns or angular deflections of the trail were next estimated by reference to the radii of the plan. It is obvious that in traveling a curved course, the direction of locomotion at any given instant is the tangent to the curve at that point. For example, in figure 3 the initial direction of locomotion is shown by the tangent at *a*. This direction is parallel to a radius. From *a*, the tangent to the curve or the direction of locomotion rotates continuously to the left until the point *b* is reached. At *b* the tangent is parallel to a second radius, which makes with the radius of initial parallelism an angle of $\frac{4}{8}$ of 360° or 180° . (Each radius forms angles of 45° or $\frac{1}{8}$ of 360° with its adjacent radii.) In other words, in traveling from *a* to *b* the axis of the animal's body has rotated 180° to the left, or the animal has executed $\frac{1}{2}$ of a complete sinistral loop. Similarly, from *b* to *c* the course of the animal makes $1\frac{3}{4}$ dextral loops; from *c* to *d*, $\frac{1}{8}$ of a sinistral

loop, and finally from *d* to *e*, $1\frac{1}{8}$ dextral loops. The total amount of turning, or angular deflection, toward the right in this trail is, therefore, $1\frac{3}{4} + 1\frac{1}{8}$ or $2\frac{7}{8} \times 360^\circ$, while that to the left is $\frac{1}{2} + \frac{1}{8}$ or $\frac{5}{8} \times 360^\circ$.

Since the honey-bee is positively phototropic and in this case the left eye was blackened, the angular deflection toward the right or functional eye is designated as positive; that toward the left or covered eye, as negative. The algebraic sum of these

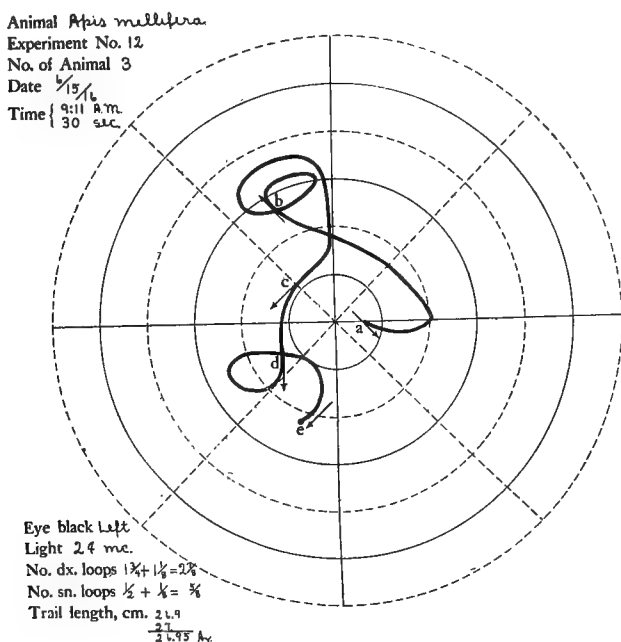


Fig. 3 Record of bee no. 123 in non-directive light.

angular deflections will give a result equivalent to the amount of continuous turning required to carry the animal from the starting point to the end of its course. Thus, in figure 3, the direction of locomotion at *a* makes with the direction at *e* an angle of $2\frac{7}{8} \times 360^\circ - \frac{5}{8} \times 360^\circ$ or $2\frac{1}{4} \times 360^\circ$.

Knowing the distance traveled in centimeters and the amount of turning in degrees, the average degrees turned per centimeter is easily computed. Denoting this average deflection, as I shall call it, by *D*, we have for the trail in figure 3,

$$D = \frac{2\frac{1}{4} \times 360^\circ}{26.95 \text{ cm.} \times 6} = +5.01^\circ/\text{cm.}$$

It is to be emphasized that the value $+5.01^\circ/\text{cm.}$, does not signify that the animal turned only toward the functional eye. It merely shows that the algebraic sum of all its deflections averages $5.01^\circ/\text{cm.}$ toward the functional eye.

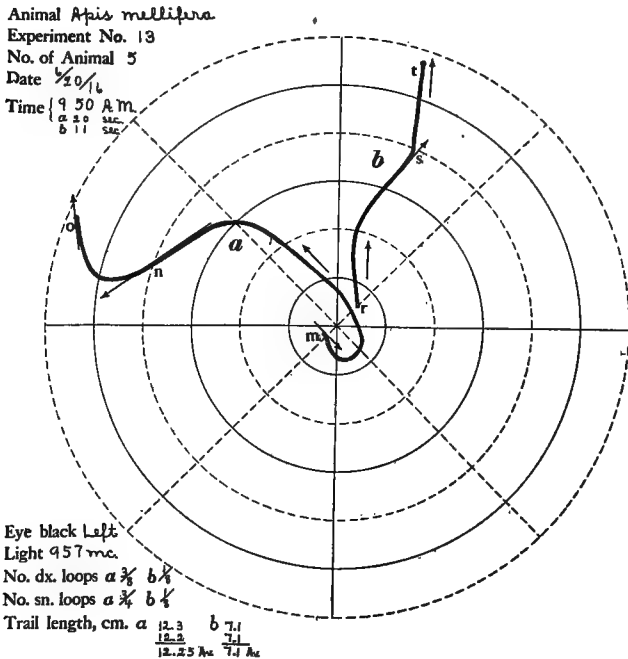


Fig. 4 Two trails of bee no. 135 in non-directive light.

A record is shown in figure 4 which represents two trials taken in rapid succession. This was necessitated by the animal's encountering the side wall of the light chamber so quickly that the first trial was shorter than usual. The deflections in these trails are estimated as previously described. It will be noted, however, that in the trail marked *a*, the angular deflection between *m* and *n* does not amount to quite $\frac{3}{4}$ of a sinistral loop, although it is so counted. In such instances the angle was always estimated

to the nearer $\frac{1}{8}$ of a circumference, no attempt being made to discriminate differences of less than 45° . In this record it is desirable to combine both trails into a single computation. Proceeding as before,

$$D = \frac{(+\frac{3}{8} + \frac{1}{8} - \frac{3}{4} - \frac{1}{8}) 360^\circ}{(12.25 + 7.1 \text{ cm.}) 6} = - 1.16^\circ/\text{cm.}$$

The negative sign of the average deflection here obviously indicates that the bee turned more toward the covered eye than toward the functional eye in these trials.

In the course of experimentation, records of normal bees were also made in non-directive light. Since in such individuals neither eye was blackened, the positive sign was arbitrarily applied to the direction of greater angular deflection in each set of trials. Otherwise the computations for normal bees were performed in the same manner as those for bees with one eye blackened.

These various examples will illustrate the method employed in all quantitative determinations. Upon the results thus obtained the chief conclusions of the present paper are based.

IV. MATERIAL

1. *General care of animals*

The bees used in all quantitative experiments were thoroughly active workers taken from the flowers of a near-by garden, and were, for the most part, individuals from a single large hive situated there. The animals were trapped by simply inverting a long glass tumbler over the flower, and then transferring them to a small screen fly-trap. In some experiments, however, which were performed too late in the fall to obtain bees in this way, animals were used from a single comb of workers confined in an observation hive. The exit of the hive was kept securely screened, for such a colony quickly disintegrates if its members are permitted to leave the hive freely. Bees kept in this way remained in reasonably good condition, for at least a month.

Bees destined to undergo experimentation were first subjected to having their wings clipped, an operation easily executed when

the animals were feeding. Each wingless individual was then confined in a small cylindrical cage of screen wire, the bottom of which was formed by a layer of tissue-paper over cotton to prevent injury in case of falling. In the same cage were also placed two friendly winged workers to counteract any possible effects of isolation. The cages of bees were kept in a darkened box when not directly under experimentation, since the influence of light often caused the animals to maintain a restless activity which appeared, in some cases, to shorten life considerably. In the dark, however, they usually remained more quiet.

Each cage was supplied with water by a small wad of saturated cotton placed on its top. Small quantities of honey were also supplied on short wooden sticks stuck to the side of the cage. Early in the morning, at noon, and in the evening the cages were cleaned by removing excess honey, etc., and fresh honey and water were provided. Such operations were carried out at least a half-hour before any trials were made on the animals.

The temperature of the laboratory in most of the experiments was kept above 20° to 21°C. This was found to be an important consideration, since at lower temperatures bees became torpid and inactive. In collecting the animals even, an attempt was made to take them on warm, sunny days which had, in general, been preceded by warm weather. It was found that bees brought in after a brief period of cold, wet weather were apt to be either unresponsive or extremely variable in their behavior.

2. Blackening the eye

Any technic for blackening the eye of a wingless bee requires, of course, the use of an anaesthetic. In the present experiments ether was used exclusively. Care was taken to administer it rather slowly and in minimal doses. When completely anaesthetized, the bee was placed on one side, on a small cork pinning board. Here it was fastened down securely by the use of insect pins, with which the thorax, abdomen, and legs were securely braced against the cork. The blackening was then applied to the eye, the entire surface being covered with as thick a coat as pos-

sible. Two kinds of blackening material were used, viz., lamp-black in shellac and a dead black paint known commercially as 'Jap-a-lac.' The latter proved the more satisfactory and was used throughout the majority of experiments.

Although bees under ether often began to recover in five to ten minutes, they were not removed from the pinning board for twenty to twenty-five minutes, when the covering of the eye was well hardened. Recovery from anaesthesia was usually complete in an hour and often much less. As a rule, however, operations were carried out in the evening, and the bees were not subjected to further experiment until the following day. Ample time was thus allowed for the animals to recover as much as possible from the effects of the operation.

V. BEHAVIOR OF NORMAL BEES

1. *Kinetic effect of light*

The remarkable sensitivity of the honey-bee to photic stimulation must have long been patent to students of its behavior. Bethe ('98, p. 83) says, "Das Licht ist bei diesen Tagthieren [bees, flies, etc.] der auslösende Reiz zum Fliegen; in einer dunklen Schachtel fliegt keine Biene auf, auch nicht, wenn man sie reizt. Das Licht gibt die Regulirung beim Fluge ab." This observation was repeatedly confirmed in the present experiments. When collecting bees from flowers, fifteen to twenty individuals were confined in a single cage, which was then placed in a closed box. Although at the height of activity when captured, a few minutes in the darkness of the box seldom failed to reduce these animals to a state of quiescence. If a little light was admitted to the box, however, by even partially removing the lid, there was a sudden resumption of activity.

Precisely the same behavior was exhibited by wingless bees. If confined in a dark box, they were, as a rule, reduced to comparative inactivity. A brief exposure to light, however, was usually sufficient to excite vigorous locomotion, and continued exposure not infrequently resulted in the maintenance of an intense activity for extended intervals of time.

Individuals which had been subjected to operations of removing the wings and blackening the eye frequently responded somewhat more slowly to this photic activation than did normal bees. In the former, locomotion was preceded by a more or less prolonged sequence of cleaning operations. The proboscis was extended and stroked with the fore legs. The eyes, particularly the covered one, were the objects of repeated and vigorous scrapings, responses no doubt largely attributable to the irritation of the blackening material. The abdomen was meanwhile bent from side to side, while the middle or hind legs were rubbed together, or the hind legs assiduously stroked the dorsum of the abdomen. These movements became more and more intense until at length they culminated in active creeping.

Light, then, exerts a strong activating or kinetic influence upon the honey-bee, while darkness has the opposite effect. Essentially similar phenomena have been reported by Loeb ('90) for the plant louse, Carpenter ('05) for the pomace fly, and Turner ('12) for the mason wasp. Stockard ('08) has reported the case of *Aplopus*, the 'walking-stick,' which also falls into this category of behavior. In *Aplopus*, however, light inhibits activity, while darkness induces it. Hence the 'walking-stick' is nocturnal, whereas the plant louse, the pomace fly, the mason wasp, and the hive bee are diurnal.

In diurnal animals this response is apparently due to the continued action of light rather than a sudden change in it. Thus, while many bees respond almost, if not quite, at once to the presence of light, others may respond only after some minutes of exposure. According to Turner ('12, p. 360), the same is true of the mason wasp.

2. *Directive light*

Not only does light induce locomotion in the honey-bee, but directive light regulates the course of locomotion. Bees brought into the laboratory direct from their foraging activities out of doors seldom failed to exhibit a most striking phototropism. Such insects when liberated in the laboratory flew almost immediately to the nearest window, where they remained fluttering

against the glass. Or, if escaping in a darkened room, they not infrequently flew directly into the flame of the nearest gas jet.

Observations of this sort were long ago reported by Lubbock ('82, pp. 278, 279, 284). A few years later, Graber ('84) demonstrated the same thing experimentally by confining forty to sixty bees in a small box, one half of which was illuminated by direct sunlight, the other half being shaded, with the result that the majority of the bees soon collected in the illuminated end. More recently, Hess ('13 a, '13 b, '17) has repeated this and a variety of other experiments. As a result of these he has been able to show that in the presence of several sources of photic stimulation, which differ in color and intensity, bees always orient toward the one which to a totally color-blind person appears brightest. The positive phototropism of the honey-bee is thus demonstrable in a variety of ways.

In the experiments just cited, winged bees were used exclusively. My own experiments, on the contrary, were confined entirely to workers from which the wings had been clipped. Such bees when creeping in the directive light area exhibited an orientation which was striking in three respects, viz., its rapidity, its precision, and its constancy.

An individual to be tested was removed from the dark box and exposed to light for a few minutes until it was thoroughly active. It was then allowed to creep from its screen cage to a small, rectangular piece of black paper, and on this it was transferred to the edge of the directive light area. An effort was made to start the animal creeping at a right angle to the direction of the light rays by turning the paper just before it crept off. The rapidity of orientation was so great, however, that the intervening centimeter or so was frequently sufficient to allow the animal to reorient perfectly. Since the velocity at which bees creep averages 3 to 6 cm. per second, orientation in these cases occurred in considerably less than one second. I have also tried leading a bee by moving the light, now in this direction, now in that, with varying degrees of curvature. Always the animal followed, orienting rapidly to even slight movements of the lamp.

The precision with which orientation was maintained was no less conspicuous. Once oriented, the animal generally moved in a nearly straight line toward the source of light. In figure 5 are shown two records of each of six bees in the directive light area. Of a large number of animals tested in the course of experimentation, considerably over 25 per cent maintained their orientation as precisely as did bee no. 66. The deviations of

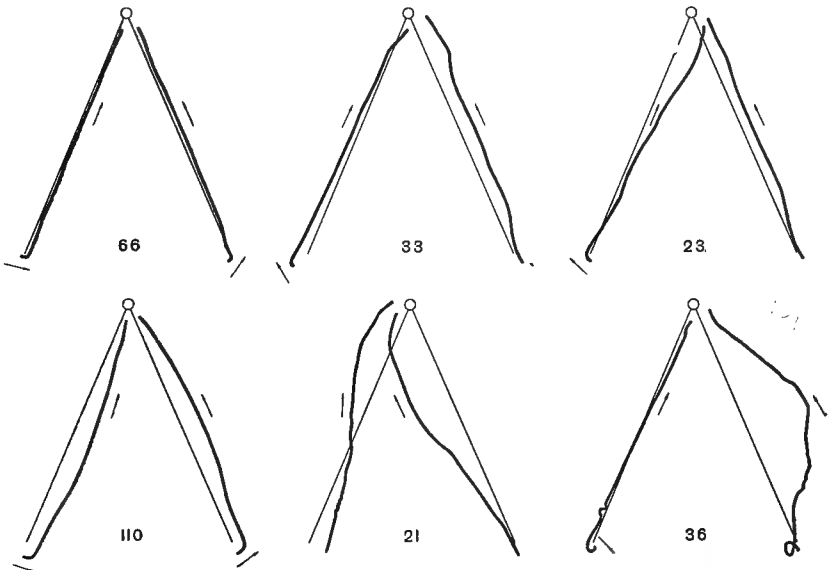


Fig. 5 Two trails of each of six normal bees in directive light. In this, as in subsequent figures of records in directive light, the clear circle represents the light source, and the straight lines from it, the direction of the rays.

most of the animals would, moreover, easily fall within the latitude of that exhibited by bees nos. 66, 33, and 23. Results similar to those shown for animals nos. 110 and 21 were, on the contrary, less frequently encountered, while trails such as those of bee no. 36 were seldom or never found among normal, healthy bees.

The response to directive light is very constant in the bee. The oncoming of death itself seems often to intensify rather than to weaken this phase of its behavior. Bees occasionally escaped

in the laboratory. Such individuals rarely survived the lack of food for more than a day or so. Yet it was not an infrequent occurrence to observe one of these starved animals, so weak that it was barely able to creep, slowly emerging from a hidden corner in a final struggle toward the light.

Nevertheless, bees were discovered which in a few instances failed to exhibit the usual positive reaction to directive light. Such cases, however, are not to be construed as a total absence

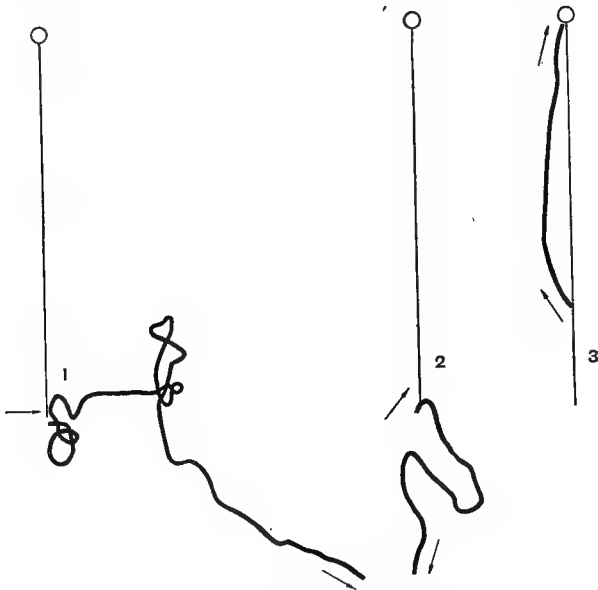


Fig. 6 Three successive records of a normal bee in directive light, showing a failure to orient in two cases.

of phototropism, but rather its momentary suppression by other factors of behavior. This is well illustrated by the following example. Seven cages of bees were prepared from the stock in the observation hive, Oct. 30, at 2:45 P.M. When tested about an hour later in the directive light area, six of the seven animals exhibited the usual positive response. One animal, however, gave the records reproduced in figure 6.

This bee when given its first trial at 4:06 (fig. 6, 1) did not orient toward the light source. Instead it pursued a devious course

looping now to the right, now to the left, and finally turning almost directly away from the light. In a second trial at 4:14, it exhibited a somewhat similar response (fig. 6, 2). One minute later, the animal was subjected to still a third trial, being started on this occasion some 30 cm. nearer the light. This time it oriented and moved in a fairly direct course toward the source of illumination (fig. 6, 3). What the temporary, inhibiting factors were which produced these very atypical responses could not be ascertained. In all other respects this bee was quite indistinguishable from the other individuals in the experiment. This example, however, shows that even the constant response of the bee to directive illumination is not free from abrupt and apparently inexplicable departures.

3. *Non-directive light*

The behavior of bees in non-directive light is no less characteristic than that in directive illumination. Since all quantitative experiments on circus movements were conducted in non-directive light, an intimate acquaintance with the behavior of normal animals under the same conditions was necessary. Every bee was, therefore, subjected to several trials in non-directive light before having one eye blackened.

It was a matter of continual observation that a bee creeping in the directive light area ceased to move in a straight course upon reaching the area near and immediately beneath the lamp. Here, where the illumination was essentially non-directive, the animal deflected from its former, precise path and began to loop in a constant or varying direction (fig. 1). In other words, the bee was trapped; for directly it crept away sufficiently for the light to become directive again, it was forced to turn back. Thus the animal continued to creep round and round in a limited area, occasionally rearing on its hind legs in an abortive attempt at flight, or finally ceasing locomotion to begin cleaning operations.

In the non-directive light apparatus (fig. 2), the same tendency to loop was manifested, only on a much more extensive scale. Here the bee seldom crept in a straight line for any great

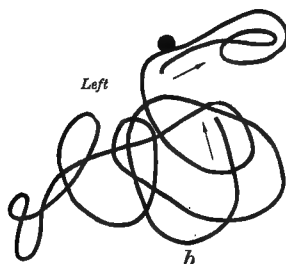
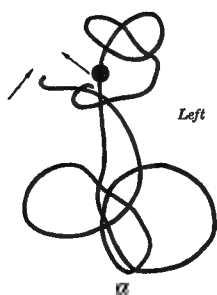
distance. Each animal was subjected to two sets of trials, an hour or so apart. Usually a single trial only constituted a set. In case the bee quickly encountered the side wall of the light chamber, however, or exhibited unusual variability in its behavior, additional trials were made. The aggregate duration of the trials of each set varied considerably, even in the same animal. Sometimes they were as short as thirty seconds; again, as long as two minutes. The average was in the neighborhood of thirty to sixty seconds. Preliminary to each trial, the bee was exposed to light until aroused to active creeping. The illumination used throughout in experimenting with normal bees was 957 mc.⁵

The average deflection to the right or to the left has been computed for each set of records thus obtained, and the results of these computations presented in table 2 (appendix), columns B and C. On the basis of these data, the fifty-two bees experimented upon may be classified into three groups:

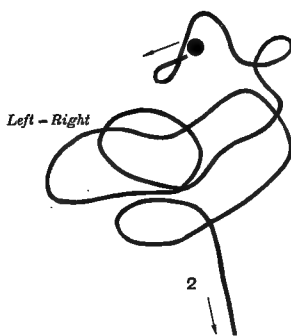
1. Bees whose average deflection in both sets of trials was over $2^{\circ}/\text{cm.}$ and in the same direction.
2. Bees whose average deflection in both sets of trials was small.
3. Bees whose average deflection in the two sets of trials varied widely, either in magnitude or direction, or in both.

The first class is composed of animals which exhibited a more or less pronounced tendency to turn in a constant direction (right or left). These animals, 29 in number, comprised 56 per cent of the total 52 bees. Fourteen of these were chiefly right-handed in their turns; 15, left-handed. In 14 of the 29 bees, or 27 per cent of the total number, the average deflections exceeded $4^{\circ}/\text{cm.}$, while in 6 individuals, or 12 per cent, it rose to over $8^{\circ}/\text{cm.}$ Similar right and left-handed tendencies of locomotion in non-directive light have been reported by Walter ('07) for planarians and by Patten ('14) for the blowfly larva. A typical example of this behavior in bees is illustrated in figure 7, bee no. 101. In its first trial (fig. 7, 101, *a*), this animal showed an average deflection of $7.11^{\circ}/\text{cm.}$ to the left, and in the second trial (fig. 7, 101, *b*), a similar deflection of $6.10^{\circ}/\text{cm.}$ Since these records were made nearly an hour apart the left-handed tendency was not the result of a

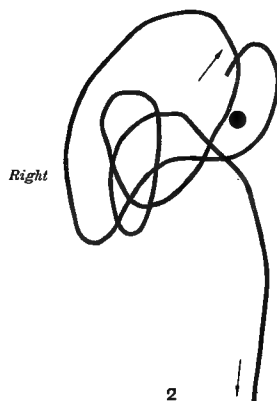
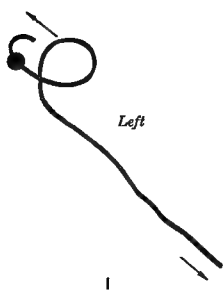
101



36



a



b

Fig. 7 Records of normal bees in non-directive light. In this, as in subsequent figures of records in non-directive light, a solid circle is used to indicate the center of the floor of the non-directive light apparatus. *a*, records of the first set of trials; *b*, records of the second set of trials. Bee no. 101 deflected constantly toward the left. Bee no. 36 varied its deflection in the course of single trials.

brief, temporary condition, but was probably a more or less permanent feature of this animal's behavior.

The second class of animals includes those whose average deflections were small in both directions. The results obtained here are attributable to either of two causes:

a. The bee varied its turning from right to left, so that on an average, one tendency nearly or quite balanced the other.

b. The bee exhibited little or no tendency to turn either to the right or to the left.

An example of the first type is seen in the records of bee no. 36, figure 7. In its first set of trials (*a*, 1, 2) this animal turned sometimes to the left, sometimes to the right, so that the resultant average deflection was but $0.79^\circ/\text{cm.}$ to the left. Similarly in the second set of trails (*b*, 1, 2), the average deflection amounted to only $1.94^\circ/\text{cm.}$ to the right. The second type of this class is illustrated by bee no. 134, figure 8. This animal showed no pronounced tendency to turn either to the right or left. The average deflection for each set of records was, therefore, small, being only $1.52^\circ/\text{cm.}$ to the left for the first set (*a*, 1, 2, 3) and $1.22^\circ/\text{cm.}$ to the left for the second set (*b*, 1, 2, 3, 4).

In the third class of bees are to be found those which, although they exhibited fairly uniform behavior in a single set of trials, varied widely in different sets. For example, bee no. 82, in its first record (fig. 8, 82, *a*) showed a pronounced deflection which averaged $5.81^\circ/\text{cm.}$ to the left. In its second set of trials (fig. 8, 82, *b*, 1, 2, 3, 4), on the contrary, it showed little tendency to turn, and the average deflection was but $0.65^\circ/\text{cm.}$ to the left. An even more striking case of variation, however, was afforded by bee no. 63. In a single record of fifty-three seconds' duration (fig. 8, 63, *a*) this animal deflected, on the average, $5.58^\circ/\text{cm.}$ to the left. Approximately two hours later, in a record of sixty seconds' duration (fig. 8, 63, *b*), the same animal exhibited an even greater average deflection in the opposite direction, viz., $7.50^\circ/\text{cm.}$ to the right. The range of variation presented by these two records is no less than $13.08^\circ/\text{cm.}$

In a uniform, non-directive light field, therefore, many bees exhibit a fairly constant tendency to turn toward a given side,

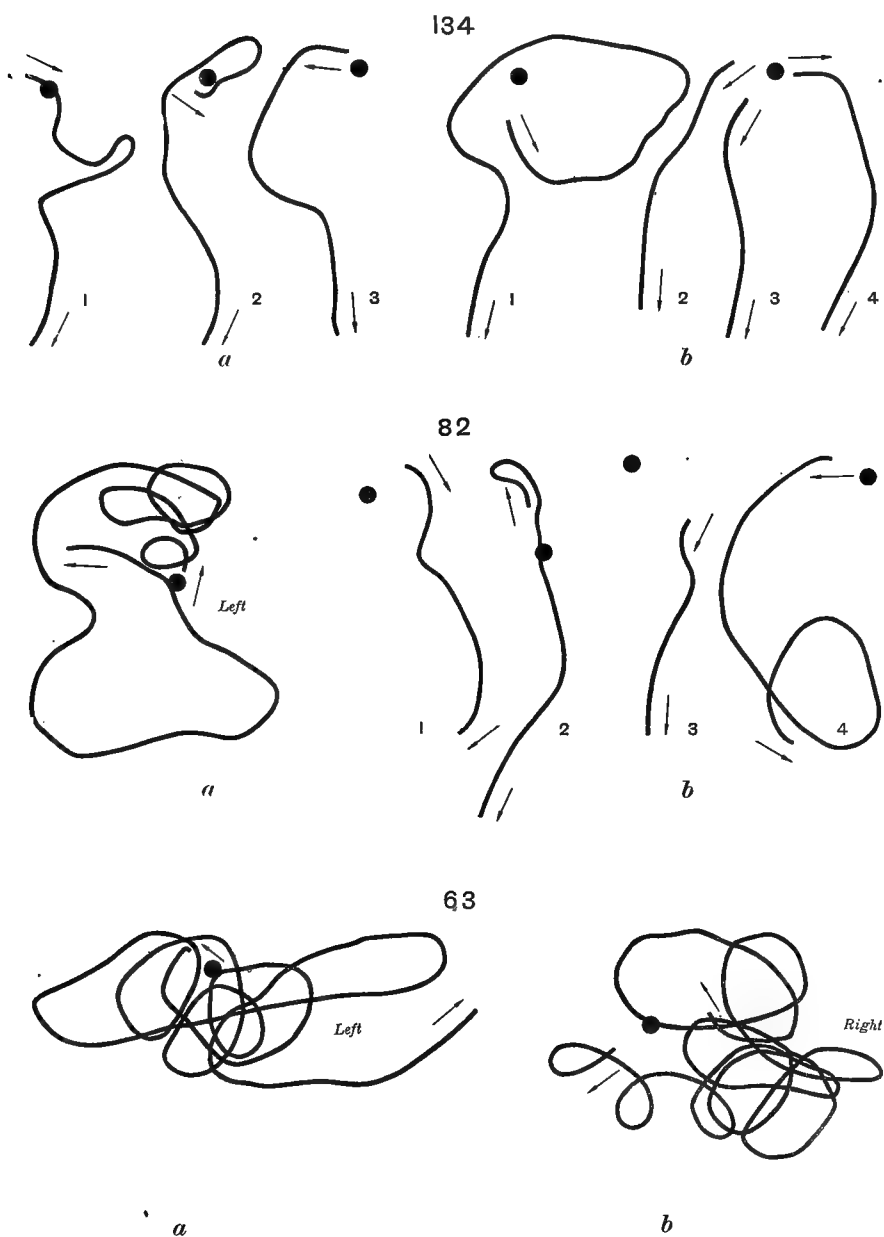


Fig. 8 Records of normal bees in non-directive light. *a*, records of the first set of trials; *b*, records of the second set of trials. Bee no. 134 exhibited little tendency to deflect in either direction. Bees nos. 82 and 63 varied widely in their average deflections in the two sets of trials.

others display little or no such tendency, while still others vary widely in their deflections from time to time. Since the animal moves in a uniform environment, the conspicuous asymmetry of response so frequently noted must be attributed to internal factors. Such factors are, for the most part, probably quite independent of light. A more detailed discussion of these will be presented in a subsequent section of this paper.

4. *Total darkness*

If internal factors are responsible for the asymmetric responses of bees in non-directive illumination, a similar behavior should be exhibited in the total absence of photic stimulation. Such was indeed the case. Animals creeping on smoked paper, in total darkness, showed the same conspicuous tendencies to loop and turn as did animals in non-directive light (fig. 16). The data here referred to were taken in connection with experiments conducted for a different purpose. They are, therefore, not sufficiently extensive to establish more than a similarity to the behavior exhibited in non-directive light.

Responses essentially like those of bees in total darkness have also been described by Pouchet ('72) for the larvae of *Lucilia caesar*, Davenport ('97) for the amoeba, and Frandsen ('01) for the garden slug *Limax*. Frandsen's observations in particular bear a striking resemblance to those which I have just described for the honey-bee in non-directive light. Thus he found that while most of his animals looped in a fairly constant fashion to the right or left, a few were extremely variable, while still a few others moved in rather straight courses. The responses of creeping bees in the total absence of photic stimulation are, therefore, very similar to those observed for other animals under the same conditions.

5. *Summary*

In the preceding pages certain responses of normal bees have been described in considerable detail, but only as a prerequisite to an adequate understanding of the behavior of the animals

when one eye is blackened. The features of behavior which are important in this connection may be summarized as follows:

1. In the honey-bee, light tends to induce activity; darkness, to inhibit it. This response is dependent upon the continuous action of photic stimulation.

2. Isolated worker bees in an active condition exhibit strong positive phototropism when flying or creeping. Temporary suppressions of this response may occur, however.

3. Normal bees when creeping in non-directive light usually exhibit pronounced asymmetrical responses of constant or variable index. Since essentially the same responses occur in total darkness they are not fundamentally dependent upon photic stimulation. They are probably, therefore, conditioned largely by internal factors.

VI. BEHAVIOR OF BEES WITH ONE EYE BLACKENED

1. *Directive light*

The previous investigations of circus movements have pointed unmistakably to the generality of these responses among phototropic arthropods. Positive animals with one eye covered tend to circle toward the functional eye; negative animals, under the same conditions, tend to circle away from the functional eye. The honey-bee exhibits a striking positive phototropism. When one eye is blackened, therefore, we should expect the bee to circle toward the remaining functional eye. Such is indeed the case, as Axenfeld ('99, p. 374) has previously shown.

In my own experiments, bees thus operated upon were no longer able to creep in a straight course toward a source of illumination. Instead, their progress thither was marked by repeated loops. If the right eye was blackened, the bee looped to the left; if the left eye was blackened, it looped to the right. Moreover, it was possible by blackening one eye, then removing the black and blacking the other eye, to cause a single individual to perform circus movements first in one direction, then in the opposite direction.

The above experiment was carried out on five bees. In general, all of these animals looped more or less markedly toward the functional eye as they crept toward the light source. This tendency, moreover, was not confined to the period immediately subsequent to the operation of blackening the eye, as the experiment clearly demonstrates. The first records of these bees with their left eyes blackened were taken in the evening between 6 and 7 P.M. No further tests were made until the following day at 11:30 A.M. Yet the behavior at the end of this seventeen-hour period was practically the same as it had been before. One bee, it is true, showed considerable improvement. In the other four animals, however, the two sets of records were indistinguishable. In the absence of experience, therefore, the performance of circus movements remains a permanent feature of behavior.

Of the five bees tested, the most pronounced and uniform exhibition of circus movements was displayed by bee no. 5. Its records are almost diagrammatic in their close approximation to the theoretical expectation. Records of this animal are reproduced in figure 9.

Not all of these animals, however, yielded such striking results. Some individuals were found which manifested little or no tendency to deviate toward the functional eye, except in the area immediately beneath the lamp, where the illumination was essentially non-directive. Thus, bee no. 4, with its right eye blackened, circled toward the left in the usual manner. But a few hours later, when the black had been removed from the right eye and the left eye painted over, it exhibited little or no tendency to circle toward the right (fig. 10, *B*). The explanation at once suggests itself, that in such cases the eye was imperfectly covered, and hence not absolutely free from stimulation. This may be correct. As will be shown later, however, there are also a variety of other circumstances which might account for such behavior.

The tendency to circle toward the blackened eye was not frequently encountered in the reactions of bees to directive light. No instance of it occurred in the experiment described above, although it was occasionally met with in other experiments. A

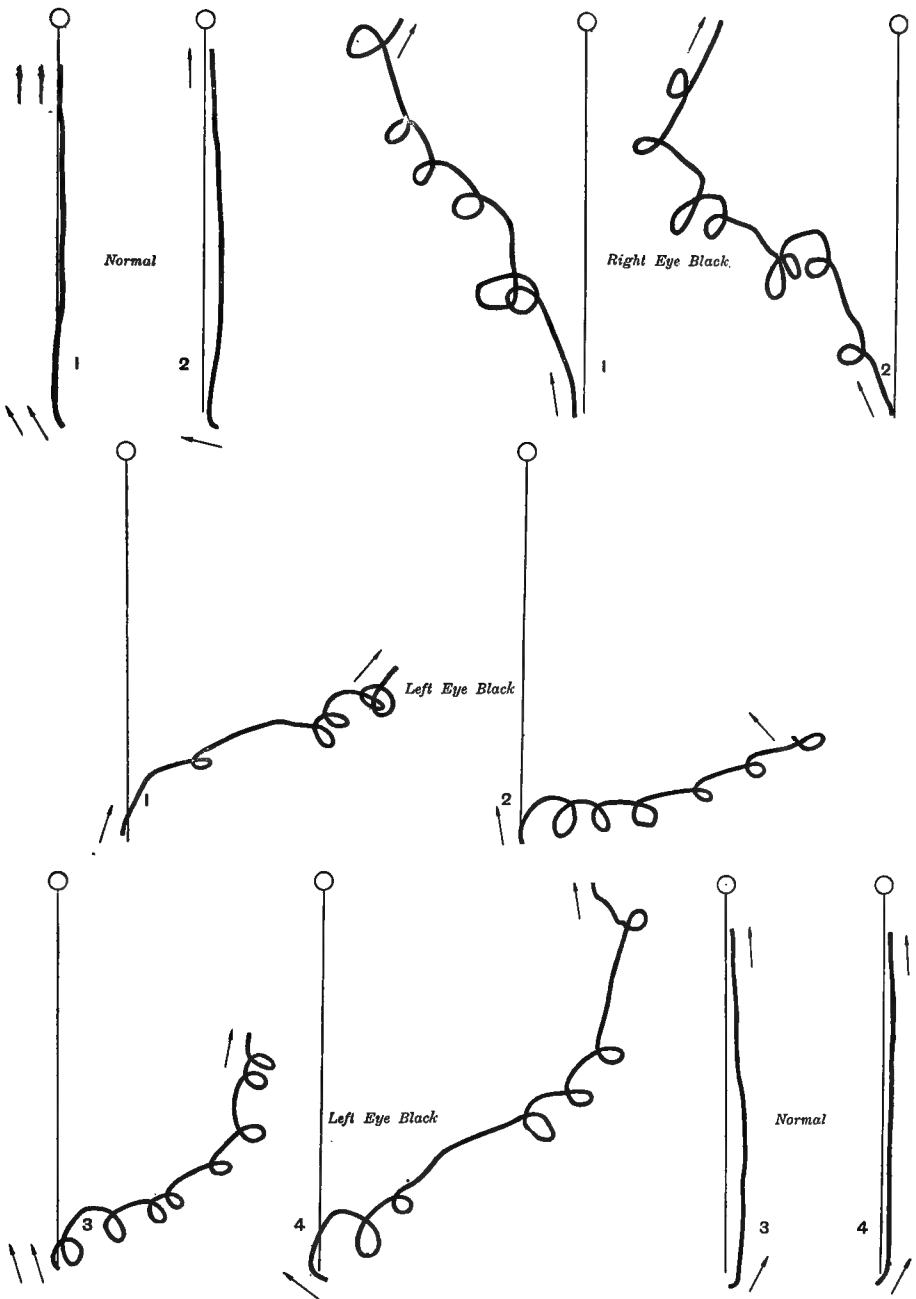


Fig. 9 Consecutive records of a bee in directive light, showing the effect of blackening first one eye, then the other.

single record of this kind is shown in figure 10, *A*. This was obtained from an animal which subsequently became wholly unreactive. Its aberrant tendencies may, therefore, have been due to an abnormal condition. In any case it is significant that, although the bee looped toward the covered eye, yet it progressed toward the light source. Consequently, this was not a case of reversal of phototropism.

Instances somewhat similar to the one last mentioned have been described by Dolley ('16, p. 373) for the butterfly *Vanessa*.

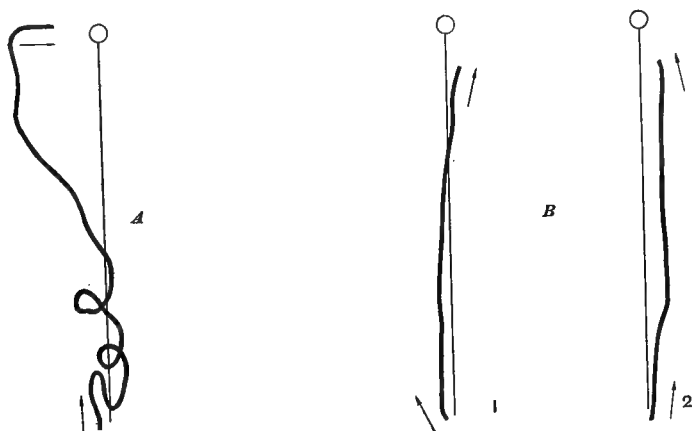


Fig. 10 *A*. Record of a bee in directive light, showing loops toward the blackened eye. *B*. Two records of a bee in directive light which showed no deflection, although the left eye was blackened.

Although positive to light, this insect with one eye blackened occasionally turned toward the covered eye instead of toward the functional eye. Possibly results of this sort are to be attributed to the effect of contact stimulus afforded by the covering of the eye, as indicated by Dolley ('16, pp. 394-399). This will be discussed more fully in a subsequent portion of the paper.

2. *Non-directive light*

a. Amount of turning. In non-directive light, bees with one eye blackened tended, in general, to turn more or less pronouncedly toward the functional eye. As was to be expected, the course

taken by the animals under these conditions assumed no specific direction. They either continued to circle in a fairly limited area or proceeded in a looping fashion in any direction whatever. The variability of this response, moreover, was much greater than in the case of the response to directive light. Thus, a number of animals circled almost continuously toward the covered eye in non-directive light, while still others varied, circling sometimes toward the covered eye, sometimes toward the functional eye. This was doubtless true for much the same reasons that normal bees also exhibited a greater variability of response in non-directive light.

Circus movements attendant upon the elimination of one photoreceptor undoubtedly represent the orienting process of an asymmetric animal. The specific photic stimulus, therefore, which produces these reactions must be identical with that which effects orientation in the normal animal. Whatever the nature of this stimulus be, moreover, it is afforded by both directive and non-directive light, since circus movements occur in either situation. What is the nature of this orienting stimulus? Perhaps the best method of demonstrating the dependence of a particular response upon a certain stimulus is to show that the intensity of the response varies with the intensity of the stimulus in question. It seemed possible to attack this problem, therefore, through a study of the relationship existent between the amount of turning displayed by an animal with one eye blackened and the intensity of the illumination to which it was subjected.

Non-directive illumination was chosen in preference to directive illumination because of the simpler experimental conditions which the former affords. In directive light, every movement of the entire animal is accompanied by more or less complicated changes not only in the intensity of the stimulation received, but also in the area of the eye stimulated. As an animal with one eye covered moves toward a light source, the stimulation of the functional eye steadily increases. As it loops toward this eye, however, this steadily increasing stimulus is subjected to rapid and transitory fluctuations. When the animal begins to loop, the functional eye is first turned away from the light, resulting

in a rapid decrease of photic stimulation. As the loop is completed, the photoreceptor in turn experiences an increase in stimulation. In non-directive illumination such as was employed in the present experiments, however, these complications are largely avoided. Photic stimulation here is maintained at a fairly uniform and constant intensity over the entire surface of the compound eye.

Two slightly different types of experiment were performed. The procedure in the first type was as follows. Bees were collected from flowers in the morning between 8 and 10 o'clock, brought into the laboratory and prepared for experimentation. One and two hours later, respectively, they were given single trials in the directive light area. On a basis of these records, individuals of abnormal tendencies were discarded, and those evincing the greatest accuracy of orientation were selected.

An hour or so later, the selected bees were tested in non-directive light of 957 mc. Two sets of records, about one hour apart, were made of each animal. Each set was composed of one to several records, the aggregate duration of which, in general, was between thirty and sixty seconds. An examination of the records showed clearly whether the individual was normally right-handed, left-handed, or variable in its deflection in non-directive light. These results determined which eye should be blackened. If, for example, a bee normally circled to the right, the right eye was covered. Whatever influence was exerted by photic stimulation, therefore, would tend to force the animal toward the left. In this manner, responses which might otherwise have been mistakenly attributed to photic stimulation were to some extent eliminated.

The operations of blackening the eye were carried out in the late afternoon of the first day of experimentation, in accordance with the technic previously described. On the following morning, before resuming experimentation, it was not infrequently necessary to discard a few additional animals either because of extreme weakness or occasionally death as a result of the operation.

The majority of bees usually appeared quite normal, however, and were subjected to several series of trials in non-directive

light. Throughout a single series of consecutive trials, or, as I shall call it, a determination, one intensity of light only was employed. But in the total number of determinations the more intense illumination of 957 mc. and the less intense of 24 mc. were used an equal number of times. The animal to be tested was first removed from the dark box and exposed from half a minute to several minutes in the intensity of light in which it was to be tried. This was usually sufficient to activate the animal thoroughly, and several records were then made in the non-directive light chamber. In case the bee failed to respond to photic activation, recourse was had to mechanical stimulation. The cage was tapped or even shaken fairly vigorously until locomotion was induced. This procedure seldom failed to elicit activity. When it did fail, it was usually necessary to discard the animal altogether.

The number and duration of the records comprising a single series or determination varied widely even in the same animal. If the bee quickly encountered the side wall of the light chamber, records were short, and a number had to be taken. If, on the contrary, the animal kept well toward the center of the floor of the apparatus, one or two records were quite sufficient. In cases of great variability of response or unusual departures from the general, expected behavior, additional trials were made, on the assumption that a greater number would more accurately express the average tendency of the animal. Single trials seldom exceeded thirty seconds, and were often much shorter. Occasionally, however, records of forty-five seconds, sixty seconds, or even slightly greater durations were taken. The aggregate duration of the trials comprising a single determination, for one intensity of light, was usually in the neighborhood of thirty or sixty or ninety seconds. The adoption of any more uniform period for all animals, at all times, was quite impossible.

Upon completion of a series of trials in one intensity of light, the bee was returned to the dark box. Here it was allowed to remain for a period of about fifteen minutes to one hour. In the earlier experiments the longer period was practiced; in subsequent experiments, the shorter. After this period in the dark, the ani-

mal was subjected to a second set of trials of the same aggregate duration as the first, but in the other of the two light intensities. The order in which the two intensities of illumination were employed was varied from time to time. Sometimes the first determination was made in the more intense light; the second, in the less intense. Sometimes the reverse order was observed.

A single series of records in one intensity of non-directive light together with the corresponding series in the other intensity constitute what I shall term a pair of determinations. The protocol of such a pair of determinations on bee no. 42 is given in table 3. Four or five pairs of determinations were usually made on each individual of an experiment in the course of a day, beginning

TABLE 3

DETERMINATION FOR NON-DIRECTIVE LIGHT OF 24 MC.			DETERMINATION FOR NON-DIRECTIVE LIGHT OF 957 MC.		
Number of record	Hour of record	Duration of record	Number of record	Hour of record	Duration of record
		<i>seconds</i>			<i>seconds</i>
4	1:47 p.m.	30	1	1:32 p.m.	31
5	1:47½ p.m.	30	2	1:32¾ p.m.	30
6	1:48 p.m.	30	3	1:33¼ p.m.	30
Totals		90			91

between 8 and 9 o'clock in the morning and concluding between 4 and 5 in the afternoon. The bees often seemed to become sluggish in the late afternoon. Whether this was due to fatigue or a natural rhythm of activity from day to night, I am unable to say. This phenomenon, however, led me to abandon any attempt to continue experimentation much after 5 o'clock.

On the third and concluding day of the experiment, the scheme of the second day was again carried out as far as possible. Bees usually survived the first two days of experimentation, and in case they did not, the data on them were discarded. A number of individuals, however, failed to survive in fit condition for the trials of the third day, and still others had to be discarded in the course of the day, although in both cases the results were counted.

Some of the more vigorous animals survived not only a third day of experimentation, but lived on for three or four days, and in a few instances even longer. Although no further trials were made with such bees, they were kept and, as far as possible, records of their subsequent longevity taken.

Having described the first type of non-directive light experiment in considerable detail, the second type may be described very briefly. It differed from the first only in the method of making pairs of determinations. In this case, the two determinations of a pair were made during the same period of time,

TABLE 4

DETERMINATION FOR NON-DIRECTIVE LIGHT OF 24 MC.			DETERMINATION FOR NON-DIRECTIVE LIGHT OF 957 MC.		
Number of record	Hour of record	Duration of record	Number of record	Hour of record	Duration of record
		<i>seconds</i>			<i>seconds</i>
2	1:43 p.m.	11	1	1:41 p.m.	30
4	1:51 p.m.	23	3	1:48 p.m.	44
5	1:53 p.m.	40			
7	1:59 p.m.	30	6	1:56 p.m.	30
Totals		104			104

instead of an appreciable interval apart. The bee was first tested in one intensity of light, then within a minute or so in the other intensity, then again in the first, and so on until a series of one to five records had been completed for each intensity. Care was exercised, however, even with this rapid alternation of intensities, always to expose the animal for thirty to sixty seconds in a given intensity before subjecting it to a trial in the same. The following protocol from bee no. 83 (table 4) will illustrate this method of making determinations.

In both types of experiment, there were obtained for each bee a number of pairs of determinations, usually four to ten, depending upon the longevity of the individual. The records of each

determination have been computed collectively in the manner already described. Single values have thus been derived which express the average deflection, or tendency to turn, exhibited by the animal in each determination. When the turning was chiefly toward the blackened eye, the sign of these values is negative; when chiefly toward the functional eye, it is positive. If, now, the value of each determination in 24 mc. light be subtracted from the corresponding one in 957 mc. light, differences will be obtained which should answer conclusively the question of relationship between the amount of turning and the intensity of photic stimulation.

The differences obtained in the manner just described I shall designate as *d*. A given value of *d* may be negative or positive. If it be negative, it signifies one of the two following possibilities:

1. The bee turned *more toward the blackened eye in an illumination of 957 mc. than it did in one of 24 mc.*

For example, in the second pair of determinations on bee no. 32 (table 2),

$$\begin{array}{r} 957 \text{ mc.} \qquad 24 \text{ mc.} \\ -13.28^\circ/\text{cm.} - (-9.22^\circ/\text{cm.}) = -4.06^\circ/\text{cm.} \end{array}$$

2. The bee turned *less toward the functional eye in an illumination of 957 mc. than it did in one of 24 mc.*

For example in the second pair of determinations on bee no. 23,

$$\begin{array}{r} 957 \text{ mc.} \qquad 24 \text{ mc.} \\ +6.44^\circ/\text{cm.} - (+8.92^\circ/\text{cm.}) = -2.48^\circ/\text{cm.} \end{array}$$

If, however, the value of *d* be positive, it signifies one of the two following possibilities:

1. The bee turned *less toward the blackened eye in an illumination of 957 mc. than it did in one of 24 mc.*

For example, in the first pair of determinations on bee no. 31,

$$\begin{array}{r} 957 \text{ mc.} \qquad 24 \text{ mc.} \\ -3.87^\circ/\text{cm.} - (-7.14^\circ/\text{cm.}) = +3.27^\circ/\text{cm.} \end{array}$$

2. The bee turned *more toward the functional eye in an illumination of 957 mc. than in one of 24 mc.*

For example, in the first pair of determinations on bee no. 21,

$$\begin{array}{r} 957 \text{ mc.} \\ +29.41^\circ/\text{cm.} \end{array} - \begin{array}{r} 24 \text{ mc.} \\ +15.84^\circ/\text{cm.} \end{array} = +13.57^\circ/\text{cm.}$$

If the great majority of *d* values are of the first category, viz., negative, we may conclude that the animal experiences a greater impulse to turn toward the functional eye in an illumination of 24 mc. than it does in one of 957 mc. If equal numbers of negative and positive values occur, there is no relation between the intensities of photic stimulation employed and the amount of turning. If, however, *d* is generally positive, we may conclude that the tendency to turn toward the functional eye increases if the intensity of photic stimulation is sufficiently increased.

Experimentation soon demonstrated that the only satisfactory solution of the problem was to be had through a statistical treatment of large numbers of data. Even the more constant animals often varied widely from one pair of determinations to another without any apparent external cause. Therefore, a large number of bees were experimented upon and each individual was subjected to many tests, the averages of which were relied upon to indicate the general trend of behavior. In table 2 (appendix) are presented the results obtained from a careful measurement and computation of over two thousand records taken on fifty-two bees. On some individuals as few as sixteen records were taken; on others as many as seventy-four. This difference was due in part to varying longevity of individuals and in part to the fact that more favorable animals were frequently experimented with longer than less favorable ones. The determinations of approximately the first half of the animals were made on the plan of the first type of experiment, while the remainder were carried out according to the scheme used in the second type.

From the figures presented in columns F and G of table 2, it is evident at once that there is a marked preponderance of the positive *d* values over the negative. The ratio of the two is strikingly shown in the frequency polygon (fig. 11). Since the number of *d* values varied considerably with the individual, due

to the causes noted above, I have included in the polygon only the first four values for each bee, thus giving equal weight to every animal. Of the total two hundred and seven⁶ values represented in the polygon, 81.16 per cent are positive, whereas only 18.84 per cent are negative, a ratio of over 4 to 1.

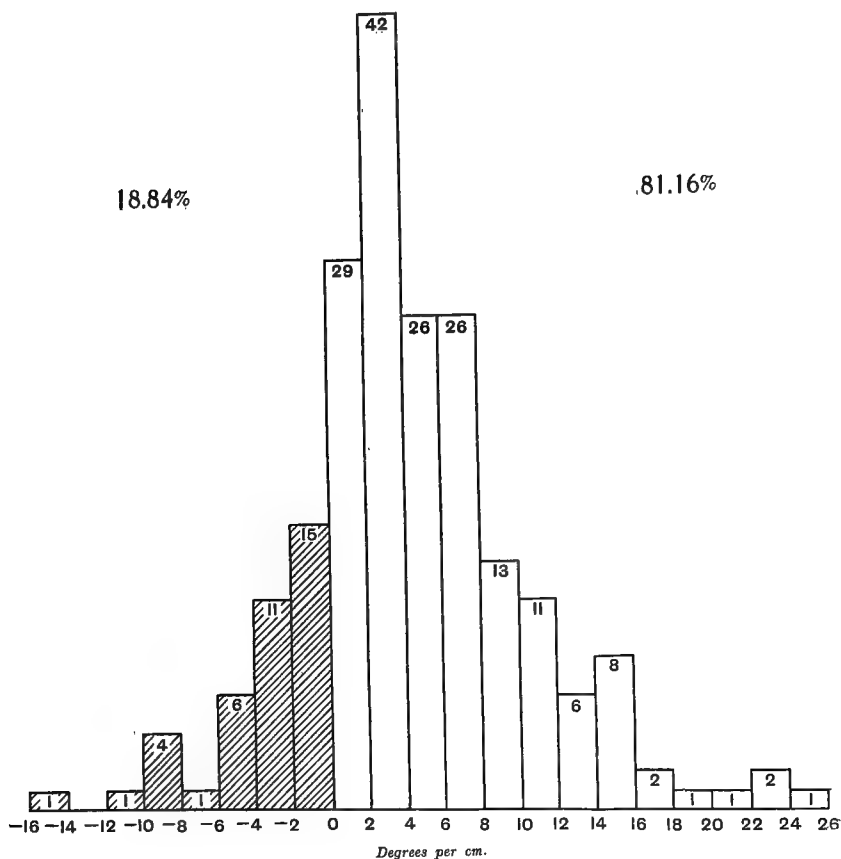


Fig. 11 Frequency polygon of the first four *d* values of fifty-two bees. The negative values are represented by the shaded areas; the positive values, by the clear areas.

⁶ In the case of one bee it was possible to include only three values for *d*, because of a missing record. See Table 2. (Appendix), bee no. 45.

The objection might be raised that although the majority of values of d are positive, a number of them are too small to be of any significance. It is true that differences of the order of $1^\circ/\text{cm.}$ or less might easily be attributed to slight errors in tracing the course of a bee. Errors in recording, however, are as likely to occur in one direction as the other. Such is not the case with these small values. The class of d values between 0 and $-2^\circ/\text{cm.}$ contains but fifteen, while the class of 0 to $+2^\circ/\text{cm.}$ numbers twenty-nine—nearly twice as many.

Moreover, the mode of the curve, $+2^\circ/\text{cm.}$ to $+4^\circ/\text{cm.}$, lies well beyond these small values. Differences of this magnitude are readily detected in the records of bees which circled constantly toward the functional eye, as the pair of determinations in figure 12 demonstrate. Each record shown in the figure was of exactly thirty seconds' duration. The first two were taken three minutes apart in 24 mc. illumination, while the third and fourth were taken about twenty minutes later in 957 mc. illumination, one minute apart. The value of d in this case is $+2.98^\circ/\text{cm.}$ —about the average modal value.

In bees exhibiting considerable variation in their deflections, however, d values, or of the modal class of even greater magnitude, are not so easily recognized without the accompanying figures. To illustrate this, I have selected a pair of determinations (fig. 13) approximating the mean value of the frequency polygon, which is $+4.35^\circ/\text{cm.}$ As attested by the data given in connection with the figure, this animal was extremely variable in its direction of turning. All four records were taken in the brief period of eight minutes, nos. 1 and 2 being of twenty-eight seconds' duration each; nos. 3 and 4, of thirty seconds. The value of d is $+4.09^\circ/\text{cm.}$ —a fact which does not become apparent until the records are submitted to a careful scrutiny.

The data presented in table 2 and figure 11 show clearly that bees with one eye blackened tend to turn more toward the functional eye in a non-directive illumination of 957 mc. than they do in one of 24 mc. The validity of this conclusion is confirmed by still another line of evidence. A certain number of animals were found to exhibit a very constant tendency to turn toward

the functional eye, which was always much more pronounced in the intense than in the weak illumination. In other words, these individuals always yielded positive values of d of rather high magnitude. Bees nos. 73, 83, 95, 105, and to a lesser extent numerous others afforded striking examples of such behavior. These

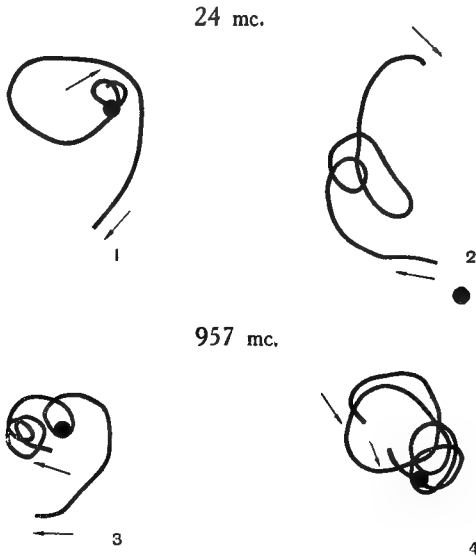


Fig. 12 A pair of determinations of bee no. 42, left eye black, non-directive light. The records are numbered in the order in which they were taken.

Number of record	24 mc. Light		Number of record	957 mc. Light	
	+Degrees turned	-Degrees turned		+Degrees turned	-Degrees turned
1	900	0	3	1440	0
2	945	0	4	1485	0
Average deflection, $+9.49^\circ/\text{cm}$.			Average deflection, $+12.47^\circ/\text{cm}$.		
$d = +2.98^\circ/\text{cm}$.					

animals were all thoroughly vigorous individuals, surviving not only the three days of experimentation, but living on for at least two days thereafter. Two of these bees, in fact, survived no less than four days after the conclusion of the experiment.

In figures 14 and 15 are shown pairs of determinations from two of these animals. The eight records of bee no. 73 (fig. 14) were taken in the course of $28\frac{1}{4}$ minutes, while the six records of

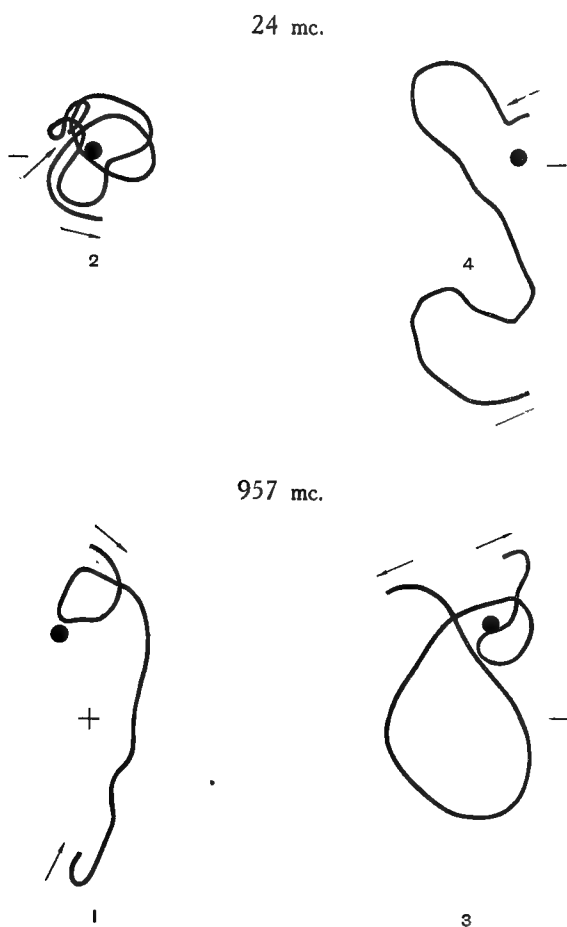


Fig. 13 A pair of determinations of bee no. 123, left eye black, non-directive light. The records are numbered in the order in which they were taken.

Number of record	24 mc. Light		Number of record	957 mc. Light	
	+Degrees turned	-Degrees turned		+Degrees turned	-Degrees turned
2	495	1170	1	630	0
4	270	450	3	225	720
Average deflection, $-3.53^\circ/\text{cm}$.			Average deflection, $+0.56^\circ/\text{cm}$.		
$d = +4.09^\circ/\text{cm}$.					

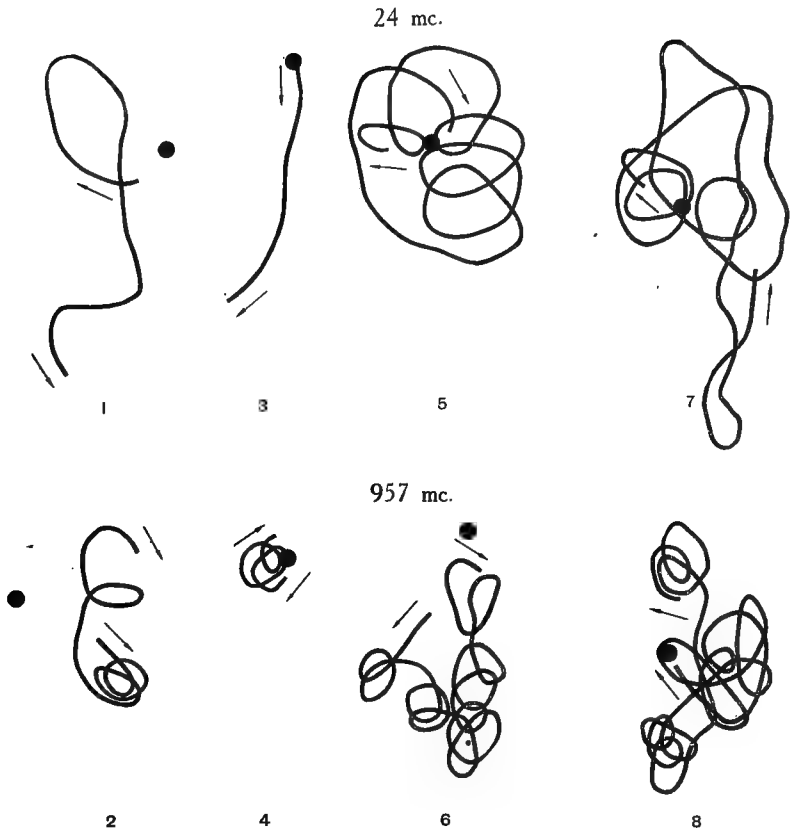


Fig. 14 A pair of determinations of bee no. 73, left eye black, non-directive light. The records are numbered in the order in which they were taken.

Number of record	24 mc. Light		Number of record	957 mc. Light	
	+Degrees turned	-Degrees turned		+Degrees turned	-Degrees turned
1	360	90	2	1485	0
3	45	0	4	990	0
5	2115	0	6	3510	0
7	2070	225	8	4005	0
Average deflection, $+6.07^\circ/\text{cm}$.			Average deflection, $+13.82^\circ/\text{cm}$.		
$d = +7.75^\circ/\text{cm}$.					

bee no. 105 (fig. 15) required only fifteen minutes. In both figures, each record of the top row is of exactly the same duration as the corresponding one of the lower row, except records 1 and 2 of bee no. 73, which differ by one second. It would be difficult to

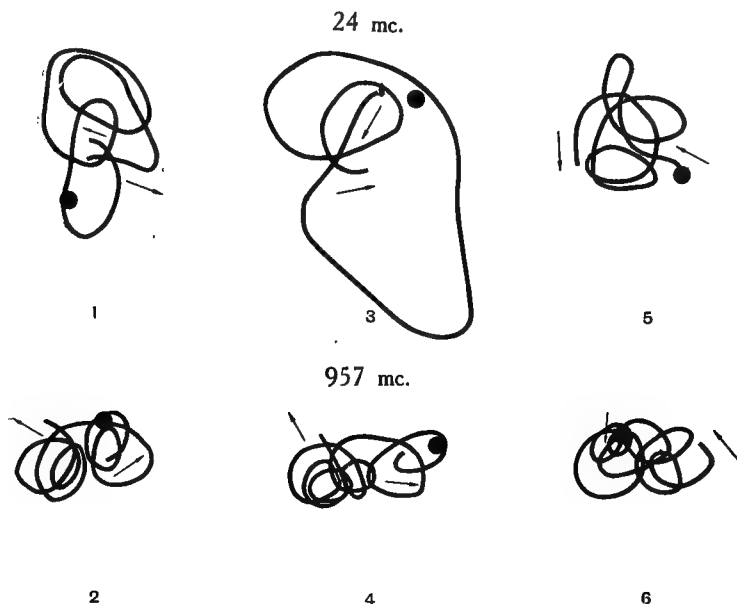


Fig. 15 A pair of determinations of bee no. 105, right eye black, non-directive light. The records are numbered in the order in which they were taken.

Number of record	24 mc. Light		Number of record	957 mc. Light	
	+Degrees turned	-Degrees turned		+Degrees turned	-Degrees turned
1	1260	45	2	1935	0
3	855	0	4	2430	0
5	1305	90	6	2520	0
Average deflection, $+6.74^{\circ}/\text{cm}$.			Average deflection, $+14.83^{\circ}/\text{cm}$.		
$d = +8.09^{\circ}/\text{cm}$.					

imagine more conclusive results than those afforded by these two bees.

It might be supposed that animals would be found which would exhibit the opposite of the condition just described. Such, however, was not the case. I failed to find any individuals which continually circled more toward the functional eye in an illumi-

nation of 24 mc. than they did in one of 957 mc. Bees presenting a number of negative d values, such as nos. 22, 25, 34, 41, 43, 55, 56, 62, 66, 85, 126, and 135, with one exception, showed an equal or greater number of positive values. The exception noted was bee no. 56. Three of the four pairs of determinations obtained on this animal not only yielded negative differences, but differences of large magnitude as well. Bee no. 56, like a number of other individuals presenting a considerable number of negative d values, varied considerably in its behavior and turned chiefly toward the blackened eye. How far the disturbing factors thus evidenced account for the results is not absolutely certain, since a number of bees of apparently similar tendencies yielded positive values of d . Certainly, however, there are a number of factors, particularly in the type of experiment under consideration, which do interfere with the effect of photic stimulation. Some of these serve to intensify the response, while others tend to counteract or even completely annul it. Without attempting to minimize the significance of these negative data in the least, I believe some of them, probably all of them, find their explanation in such factors. If this be correct, the negative results obtained lie well within the range of variation which might be expected in experimental work of this sort. A more extended discussion of the factors responsible for variability of behavior in the present experiments is presented in the next section of this paper.

The evidence in general, therefore, seems to warrant the conclusion that bees with one eye blackened tend to turn more toward the functional eye in an illumination of 957 mc. than in one of 24 mc. This tendency may result in the animal's actually turning more toward the functional eye, or in its turning less toward the covered eye, depending upon the idiosyncrasies of the individual. In either case, however, with increased photic stimulation, there is an increased tendency toward the functional eye. The nature of the stimulus afforded by the apparatus employed was continuous and of almost uniform intensity, and since the circus movements of the honey-bee vary with the intensity of such stimulation, they must be dependent upon it. These con-

clusions are the exact antitheses of those reached by Dolley ('16) in his work on Vanessa. He says (p. 417): "Vanessas with one eye blackened do not move in smaller circles in strong light than they do in weak light, unless it is extremely low. On the contrary, the evidence seems to indicate that the stronger the light is the larger the circles are. These results also are not in harmony with those demanded by the 'continuous action theory.'" I shall return later to a more complete consideration of the theoretical significance of the results afforded by the honey-bee.

b. Rate of locomotion. Although bees with one eye blackened tend to turn more toward the functional eye in a non-directive light of 957 mc. than they do in one of 24 mc., there is no difference in the rate of locomotion in the two intensities. In table 5 are given the average velocities of thirty-four bees for each of the two light intensities employed. These figures show a considerable range of individual variation, from as low as 3.49 cm. per second to as high as 6.77 cm. per second. There is, however, no consistent difference which might be attributed to the effect of light. Eighteen of the animals showed a greater velocity in 957 mc. illumination; sixteen, in 24 mc. illumination. Unilateral photic stimulation of the intensities employed is, therefore, without effect upon the rate of locomotion.

3. Summary

1. Bees with one eye blackened usually loop toward the functional eye as they creep toward a source of light. Some individuals are encountered however, which display little tendency to loop, and occasionally an animal will be found which loops toward the covered eye. In the absence of experience, the tendency to loop toward the functional eye remains a permanent feature of behavior.

2. In non-directive light, bees with one eye blackened generally circle toward the functional eye, although a number are found which circle more or less toward the covered eye.

3. In a uniform non-directive illumination of 957 mc., the tendency to turn toward the functional eye is greater than it is in a similar illumination of 24 mc.

4. Since the amount of turning varies directly with the intensity of continuous photic stimulation, the turning is produced by this stimulus.

5. Unilateral photic stimulation of the intensities employed has no effect upon the rate of locomotion.

TABLE 5

A NUMBER OF BEE	B VELOCITY CM. PER SEC. 24 MC. LIGHT	C VELOCITY CM. PER SEC. 957 MC. LIGHT	D C-B
21	6.10	6.22	+0.12
22	5.10	5.12	+0.02
23	5.02	5.03	+0.01
24	4.95	5.18	+0.23
25	4.67	4.53	-0.14
31	3.77	4.23	+0.46
32	4.20	4.74	+0.54
33	5.27	5.19	-0.08
34	4.78	4.99	+0.21
36	3.49	3.63	+0.14
41	4.45	4.29	-0.16
42	4.76	4.30	-0.46
43	5.59	5.76	+0.17
44	4.94	4.90	-0.04
45	4.36	4.99	+0.63
51	4.51	4.40	-0.11
52	5.09	5.08	-0.01
53	6.77	6.53	-0.24
54	5.53	5.17	-0.36
55	6.09	5.21	-0.88
56	5.32	5.53	+0.21
62	4.82	4.59	-0.23
63	5.80	5.72	-0.08
66	5.10	5.15	+0.05
68	5.14	5.34	+0.20
72	4.69	4.87	+0.18
73	4.97	5.44	+0.47
77	4.26	3.99	-0.27
81	4.41	4.32	-0.09
82	5.25	5.29	+0.04
83	5.22	4.93	-0.29
85	4.91	4.79	-0.12
91	4.48	4.64	+0.16
92	4.49	4.51	+0.02

VII. VARIABILITY OF PHOTIC RESPONSE

The honey-bee is remarkably constant in the strong positive phototropism which it evinces. The course of individuals creeping in directive light is a straight path toward the source. Yet, as has been shown, occasional departures from this behavior do occur. In non-directive light, moreover, the responses of normal bees are frequently extremely variable. The animal may turn markedly toward a given side in one trial, and in the next, turn quite as markedly toward the opposite side. Again, the direction of turning may be completely changed several times in the course of a single trial.

It is not surprising, therefore, that bees with one eye blackened also exhibit considerable variability of response in both directive and non-directive illumination. In non-directive light particularly, there were a number of cases in which animals turned little or not at all toward the functional eye, while there were still others in which they circled chiefly toward the covered eye. In fact, over 25 per cent of the first four pairs of determinations on the fifty-two bees, when averaged, gave negative values. These departures from the more usual tendency, to turn toward the functional eye, sometimes characterized the entire behavior of an individual; again, they appeared only spasmodically.

Thinking that some of the results above mentioned might be attributed to a loss of phototropism, either permanent or extending over a considerable interval of time, I frequently subjected the animals exhibiting them to one or more immediate trials in directive light. This, however, failed to show anything which might be construed as a loss of phototropism. The variations of response noted, therefore, must be referred to external and internal factors which are capable of modifying, in a more or less profound way, the dominating effect of unilateral photic stimulation. Such factors are of two sorts, those which are continuously effective and those which are not continuously effective, but fluctuate from time to time. Both types played so considerable a rôle in the experiments previously described, that I have felt they merited the somewhat extended analysis presented in the following pages.

1. Continuous factors

a. Temperature and humidity. Of the continuously operative factors, none are more important than the general conditions of temperature and humidity. These profoundly affect the activity of bees. McIndoo ('14, p. 279) says: "Climatic conditions perceptibly affect the activity of bees. When it is extremely warm, they are most active and are rarely quiet even for a few seconds. When it is moderately warm, they are less restless, and when rather cool, bees do not move freely." Again he says: "During cool weather their movements are quite sluggish, and when the humidity is high they are much less active and respond to various odors more slowly than when there is low humidity."

Precisely the same effects were noted in the present experiments. So serious did they become on several occasions that the experiment had to be abandoned. On cool, damp days bees were apt to be quite unreactive, and prolonged exposure to light often failed to induce locomotion. Considerable mechanical stimulation might call forth creeping, but it was of desultory kind and was apparently unaffected by photic stimulation. There can be no doubt, therefore, that general weather conditions considerably affect the behavior of bees toward light. Since some experiments were continued under less favorable weather conditions, it is quite probable that they account for some of the aberrancies observed.

b. After-effects. In making quantitative determinations in non-directive light, trials were frequently made in the two intensities in rapid succession. Although the bee was always exposed for at least thirty seconds to a given intensity before making a test, there still existed the possibility that an after effect of the first intensity might influence the behavior of the animal in the second. Thus Herms ('11, p. 215) has demonstrated an after-effect of photic stimulation in the blow-fly larva, which may manifest itself in the continued orientation of the animal for as much as fifteen to twenty seconds after the cessation of the stimulus. That such is not the case for bees, however, is very clearly demonstrated by the following experiment.

Normal bees were allowed to creep on a strip of smoked paper toward the 80-c.p. incandescent lamp. When, after creeping a distance of about 60 cm., the bee reached a point 40 cm. from the source of light, the lamp was extinguished. Not only was the current turned off, but a screen was simultaneously placed before the lamp, so that even the slight after-glow of the filaments was eliminated. After ten seconds of total darkness the light was turned on and the bee removed. Two to four records were made of each of eleven animals in this manner. In not one case did the bee fail to lose its orientation within at most a couple of seconds after the extinction of the light. Often the loss of orientation was almost, if not quite, simultaneous with the cessation of the stimulus. The deviation from the former orientation was sometimes marked by a pronounced tendency to turn toward one side, with the result that the animal crept in circles in the dark. At other times the bee merely wandered, turning first in one direction, then another. Typical records of two animals are reproduced in figure 16. There is, therefore, no after-effect of photic stimulation in the honey-bee, and this does not account for any of the irregularities observed.

c. Failure to eliminate photoreceptor. The difficulties in manipulating bees necessitate relying upon a single operation to eliminate completely the function of the compound eye. Although in this operation great care was exercised to cover the eye completely with a heavy coat of paint, there is a possibility that in a few cases this was not accomplished. Moreover, from the moment the animal began to recover from the anaesthetic, the covered eye was repeatedly subjected to vigorous scrapings by the front leg of the same side. While the examination of a number of animals after experimentation showed that this seldom resulted in a removal of any of the eye covering, it probably succeeded in doing so in a few cases. Occasionally, also, the varnish cracked somewhat on drying. These unavoidable failures to keep the compound eye entirely free of light, undoubtedly modified, to a greater or less extent, not a few of the results obtained.

Beside the failure to cover the eye, there is the possibility that the three ocelli of the honey-bee are concerned in its photic

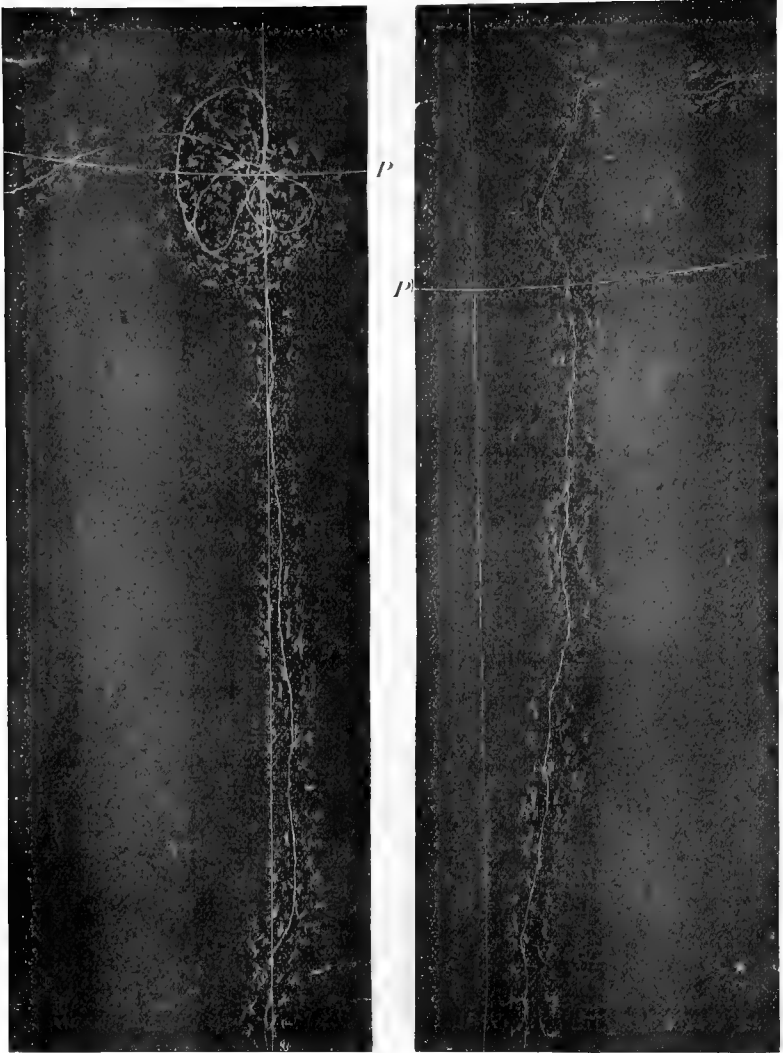


Fig. 16 Smoked-paper records of two normal bees creeping toward a light source (upward in the figure). As the animals reached the line indicated by the letter *P* the light was extinguished. Note the extremely rapid loss of orientation.

behavior. In blackening the compound eye I made no attempt to cover the ocelli, but afterward in examining the specimens used, I found that sometimes all, sometimes only one or two, at other times none of these organs had been covered. If the ocelli do exercise any considerable function, therefore, there was involved here a variable of no small magnitude.

It is also possible that in bees other portions of the body, or even the entire integument, may be photosensitive. Photodermatic sensitivity is not unknown among arthropods. It has been reported by Graber ('84) for the cockroach, by Plateau ('87) for two species of blind myriapods, and by Stockard ('08) for the walking-stick.

In order to find out if these several possibilities were affecting results, I conducted several experiments with bees both eyes of which had been carefully covered with a thick coat of 'Jap-a-lac.' On the morning after the operation, each bee was placed in a separate cage in non-directive illumination of 957 mc. Although with one or two exceptions the bees were quiet when first exposed to the light, within fifteen minutes all had become thoroughly active, showing clearly that they were not free from the activating effect of the light.

At the conclusion of the above test the same bees were individually subjected to trials in the directive light area. Here they looped and turned in a variety of ways, some circling more or less constantly toward a given side, not unlike bees with only one eye blackened. Despite most devious courses, however, they sooner or later managed to work their way to the general region of the source of light. It is quite clear, therefore, that photoreception had not been entirely abolished, although both compound eyes had been covered as carefully as possible.

Which of the several explanations advanced accounts for these results, is not certain. I am disposed to believe that the failure to eliminate the compound eyes completely was chiefly, perhaps solely, responsible. However that may be, it is certain that in this, as well as in other experiments, the incomplete suppression of photic stimulation was the source of a large amount of variation in the results obtained.

d. *Effect of contact stimulus.* The effect of the contact stimulus afforded by the blackening material on the eye and the adjacent parts of the head must also be recognized as a considerable factor in modification of photic behavior. The influence of this stimulus has been clearly demonstrated by Dolley ('16, pp. 394-397) on *Vanessa antiopa*. With one eye blackened, this butterfly, when creeping in total darkness, turned, with few exceptions, continuously toward the blinded eye. The tendency to circle was often quite pronounced, and showed little or no modification from day to day. The effect of contact stimulus on the covered eye was, therefore, antagonistic to that produced by light on the opposite, functional eye.

I tried experiments with the honey-bee similar to those carried out by Dolley on *Vanessa*. Bees with one eye blackened were allowed to creep on smoked paper in total darkness. Unfortunately, the trials were of such duration that the bee recrossed its course many times. This made it quite impossible to decipher the records, and I have not since had an opportunity to repeat the experiments. It is not unlikely, however, that the effect of contact stimulus on the eye of the bee is similar to that demonstrated for *Vanessa*. If such be the case, it probably accounts for much of the circling toward the covered eye, which was evinced by numerous individuals particularly in non-directive light.

e. *Asymmetry of the animal.* As was previously pointed out, normal bees frequently exhibited a marked tendency to turn more or less constantly toward the right or left when creeping in non-directive light. Such tendencies are doubtless due to a lack of perfect symmetry on the part of the animal. The asymmetry may be physiological; it may be anatomical. It may consist of a differential sensitivity of the photoreceptors on the two sides of the body, as Patten ('14, p. 259) has suggested, or it may be due to an inequality of any two symmetrically located elements of the neuromuscular mechanism. Under the influence of directive light, these idiosyncracies are, as a rule, continually corrected. In non-directive illumination or total darkness, however, they at once assert themselves. Since the eye to be blackened was always chosen so that the effect of photic stimulation would be opposite

to that exerted by natural asymmetry, many failures to turn toward the functional eye are probably thus accounted for.

f. Modifiability through experience. The work of Axenfeld, Holmes, Brundin, and Dolley has shown that a number of arthropods are able to modify their photic behavior through experience. The same is true of the honey-bee, at least in directive light, as the following experiment shows. Each of a number of normal bees, selected on the basis of the accuracy with which they oriented to directive light, had one eye blackened. On the following day those animals which exhibited a more or less pronounced tendency to loop toward the functional eye were subjected to trials (twenty to twenty-five in number) in the directive light area.

Bees which displayed little or no tendency to loop were given several trials to ascertain if their behavior was constant, and then discarded. These animals may have been able to modify their behavior almost immediately, or their failure to exhibit circus movements may have been due to an imperfect covering of the eye, or to the effect of contact stimulus.

Of those bees which did perform circus movements, records were taken about every ten to twenty minutes from 9 A.M. to 5 P.M., with the exception of about an hour at noon. Ten bees were thus tested. Four of these animals displayed a steady and marked improvement in the course of the trials. Two others showed some improvement, although considerably less than the first four. Two more of the ten improved for a time, only to regress again, so that while a number of trials near the middle of the series were somewhat modified, those at either end were much alike in the number of loops performed. The last two bees showed practically no improvement, although in one of the animals the tendency to circle was at no time very pronounced. It is quite certain, therefore, that at least some bees are able to modify their responses to directive light through experience.

The records shown in figure 17 afford a striking example of this modifiability. Although in its first trials the animal looped repeatedly as it crept toward the light, it was subsequently able to reach the light by a nearly straight course. This animal, how-

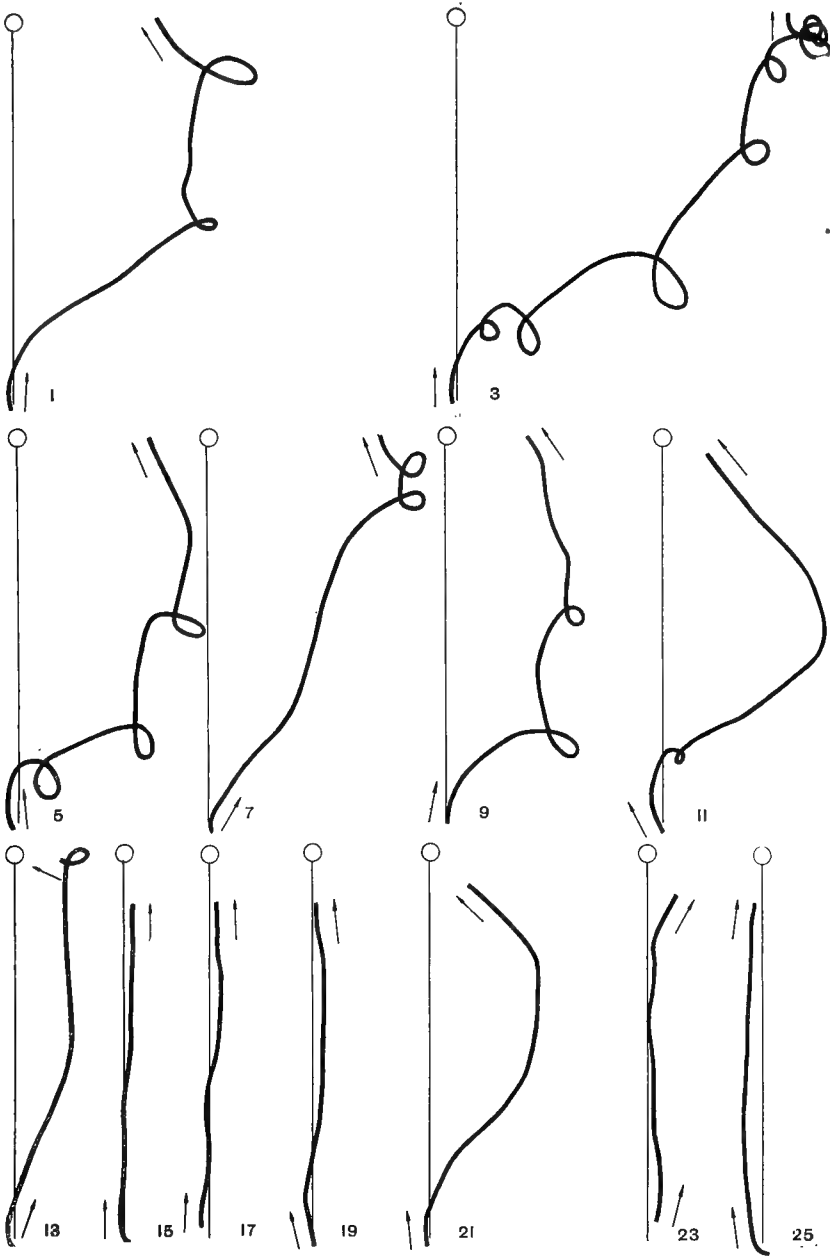


Fig. 17 Records of a bee with the left eye blackened, in directive light, showing modifiability of behavior through experience. Alternate records from a series of twenty-six are shown in the figure.

ever, as well as the others, usually circled again toward the functional eye upon reaching the non-directive region near and directly beneath the lamp. The records shown in the figure do not include this region.

Dolley ('16, p. 402) states that he observed some modification from day to day in the behavior of *Vanessa* in non-directive light. The following evidence seems to indicate that the same is true, to at least some extent, for the honey-bee also. In directive light, individuals with one eye covered were sometimes observed to begin to swerve toward the functional eye, only to check themselves by a sharp turn in the opposite direction. Correcting movements of this sort sometimes occurred repeatedly in a single trial, with the result that the animal reached the source of light by a much more direct course than it would have otherwise been able to follow. Precisely the same sharp turns away from the functional eye were occasionally seen in non-directive light also. It seems probable, therefore, that modifiability through experience affects the behavior of bees in non-directive as well as in directive light.

2. Fluctuating factors

The variables which have thus far been discussed are those which continuously or progressively affect the behavior of bees throughout an experiment. They probably account in a large measure for such phenomena as the persistent turning toward the covered eye in certain individuals or the apparent lack of any tendency to turn at all in still others. They do not, however, explain the many sudden changes of behavior which were observed. Such variations are dependent upon factors of behavior which fluctuate from time to time. A few of these factors result from environmental changes. The majority, however, arise from changes within the organism itself.

a. External. In quantitative experiments every possible precaution was exercised to keep all external factors uniform, except the intensity of the light which was changed from trial to trial. This, of course, was possible to a limited extent only. The manipulation of the bees introduced varying mechanical stim-

uli which were quite unavoidable. An animal was accidentally pressed slightly in changing it from one cage to another, or, failing to react to photic stimulation, the cage had to be shaken. Again, in transferring a bee from the light to which it was subjected for activation to the center of the non-directive light chamber, it was subjected to increases and decreases of light intensity. All of these details and endless others, collectively and individually, were undoubtedly responsible for many of the sudden variations of behavior which occurred.

b. Internal. The chief causes of irregular variations, however, are internal. When under constant external conditions, a bee varies the direction of its turning several times in the course of a single trial, the behavior must be attributed to changes within the animal itself, the physiological states of Jennings ('06). Generally speaking, the analysis of these changing physiological states is difficult or impossible. In several instances, however, I was able to make a fairly certain diagnosis. I may cite several examples.

Bee no. 147 was subjected to the usual quantitative experiment in non-directive light. From the beginning this animal exhibited a rapid, uneasy locomotion. Its entire behavior may best be described by the word 'excitable.' In the course of the first day after the eye was blackened, five pairs of determinations were made. In 24 mc. light, the animal circled chiefly toward the covered eye, while in 957 mc., its behavior varied from one set of records to another.

On the following morning, the first pair of determinations was begun at 9:49. The bee circled markedly toward the covered eye in both intensities of light. At 12:14, a second pair of determinations was begun. In making the first trial, the bee rushed about its cage for some minutes before finally creeping up into the non-directive light chamber. When it did appear, it seemed greatly excited and crept very rapidly. As the series of records progressed, the animal circled more and more pronouncedly toward the functional eye, the locomotion grew more rapid, and a continuous buzzing began. The performance of small circles toward the functional eye in 24 mc. light was surprising, for in

all previous record sets for this intensity, the animal had shown a more or less pronounced tendency to circle toward the covered eye. In the course of the fourth trial in 957 mc. light, the bee had reached a state of intense excitation. Its turning became so rapid, and the consequent circles so small, that at length the animal tumbled over on its back. Defaecation occurred. Meanwhile it continued buzzing loudly, and, though lying on its back, managed to whirl round and round toward the functional eye.

After the trial just described, the animal was allowed to rest for two hours. At 2:44 and 4:10, respectively, two more pairs of determinations were made. The bee continued to circle markedly toward the functional eye in 957 mc. light, and more or less toward the functional eye in 24 mc. light. The 'excitement' which had characterized the previous trials, however, was absent, and the animal manifested signs of weakness and exhaustion.

In the behavior of this animal there was a sudden—even violent—increase of phototropism. This was probably due to an unusual intensification of activity. I have repeatedly observed the close correlation between these two features of behavior in bees. As a rule, the greater the activity, the more pronounced is the manifestation of phototropism. The increase of activity in this animal was produced by a state of metabolism, entailed by a collection of faeces in the intestine. That such a condition may affect the activity of bees to a marked degree is evidenced by the following statement made by Phillips and Demuth ('14, p. 12) in connection with a study of certain hive conditions in winter. "It therefore appears that the accumulation of feces (in the intestine) acts as an irritant, causing the bees to become more active and consequently to maintain a higher temperature."

In several other animals defaecation occurred in the course of a trial without being preceded by any conspicuous change of behavior. Neither the amount voided nor the force of expulsion, however, gave any evidence of long accumulation or intestinal irritation in these cases. It seems reasonably certain, therefore, that the sudden increase of phototropism exhibited by bee no. 147 was due to the accumulation of faeces in the intestine.

There were likewise certain other physiological conditions which seemed to intensify photic reactions. Thus bees, upon first recovering from anaesthesia, were frequently observed to creep in very small circles toward the functional eye. Bees, which throughout an experiment appeared physically weak, were also apt to be more intense in their positive deflections. Examples of this latter behavior were afforded by bees nos. 77 and 92. Again, individuals which appeared vigorous at the beginning of an experiment, but became weak and moribund toward the end, generally showed a progressive increase in their circus movements. For example, bee no. 91 circled rather strongly toward the covered eye at first. In the course of the experiment, the animal became weak. Correspondingly, its average deflections became more and more positive until, just before being discarded, it was turning at the rate of $+23.82^\circ/\text{cm.}$ in 957 mc. light.

These instances demonstrate the profound manner in which internal factors are capable of modifying photic behavior. As a rule, only the change in behavior is noted. The recognition of the internal state which conditions this outward expression is possible only in extreme cases. Nevertheless, I believe that these internal factors were directly responsible for most of the sudden variations which characterized the behavior of so many bees.

Thus far we have tacitly assumed that the honey-bee is a purely reflex organism. It is not the purpose of the present paper to discuss the mooted question of psychic powers in this animal. It may be said, however, that the opinion advanced by Bethe ('98), that the behavior of bees affords no evidence of psychical attributes, has not met with extensive approbation. Forel ('07) and v. Buttell-Reepen ('07), in particular, have presented considerable evidence to show that bees are something more than mere reflex machines.

v. Buttell-Reepen ('07, p. 23) has shown that after bees have been deadened with chloroform, ether, saltpeter, puffball, etc., their memory for location entirely disappears. Subsequently they may again 'learn' the position of the hive, etc., but for the time at least, "they have forgotten everything previously known." My own observations have shown that during recovery from an

anaesthetic and in weakened or moribund conditions the photic responses of bees become more intense. Photic behavior, however, is probably largely reflex in character. It would appear, therefore, that the same conditions which occasion a loss of 'memory' or other central function and the like cause the reflex phases of behavior to appear more boldly. In other words bees, though fundamentally reflex, may possess certain rudiments of higher behavior. Under the influence of narcotics and anaesthetics or in moribund conditions, these factors cease to affect behavior, and the animal is reduced to a simple reflex condition. If this be correct, we have here an important variable to account for modifications of photic behavior.

3. Summary

The variability of response displayed by bees with one eye blackened when creeping in non-directive light is never due to a permanent loss of phototropism or to after-effects of one intensity upon trials in a second intensity. It is attributable to the following causes:

- a. Conditions of temperature and humidity.
- b. Failure to eliminate completely the photoreceptors on one side of the body.
- c. Effect of contact stimulus afforded by the eye covering.
- d. Natural asymmetry of individuals.
- e. Modifiability through experience.
- f. Mechanical stimuli attendant upon manipulation.
- g. Internal factors which affect behavior variously from time to time.

VIII. NATURE OF PHOTIC ORIENTATION

1. Theories

In recent years the photic behavior of lower animals has been the subject of two theories, respectively known as the 'continuous action theory' and the 'change of intensity theory.' The 'continuous action theory,' as its name implies, postulates a continuous action of light upon the organism, orientation resulting when

such action is equal on the symmetrical photoreceptors of opposite sides of the body. In its present form this theory is perhaps best summed up by Loeb ('16, p. 259). "If a positively heliotropic animal is struck by light from one side, the effect on tension or energy production of muscles connected with this eye will be such that an automatic turning of the head and the whole animal towards the source of light takes place; as soon as both eyes are illuminated equally the photochemical reaction velocity will be the same in both eyes, the symmetrical muscles of the body will work equally, and the animal will continue to move in this direction. In the case of the negatively heliotropic animal the picture is the same except that if only one eye is illuminated the muscles connected with this eye will work less energetically."

The 'change of intensity theory,' however, accounts for orientation in an entirely different manner. According to it, the process depends not upon the continuous action of light, but upon the intermittent action of rapid changes in its intensity (Jennings '04, '06, '09; Mast, '11). In positive organisms the effective stimulus is assumed to be a sudden decrease of intensity on the photoreceptor; in negative organisms, a sudden increase. A photopositive animal, such as the honey-bee, for example, orients and maintains its orientation through sudden swervings away from the side experiencing a decrease of illumination, and orientation is attained when neither eye is undergoing such a decrease. A similar explanation is applied to photonegative organisms except that the effective stimulus for them is assumed to be an increase of intensity.

There is thus a wide diversity in the explanations of orientation offered by these two theories. In the concluding pages of this paper, therefore, I propose to discuss the evidence afforded by my own experiments, as well as that afforded by the observations on circus movements in general, with a view to ascertaining which of the two theories more correctly applies to the orientation of arthropods.

2. Orientation in the honey-bee

As has been previously stated, the process involved in circus movements must be regarded as identical in every respect with that involved in normal orientation. The circus movement is the orienting process. A normal creeping bee may be caused to perform circus movements without having one eye blackened, if the light is merely moved so as to keep it constantly to one side of the animal. Whether the eye be blackened or the light be moved, the case is the same. The orienting process is merely prolonged, and the final attainment of orientation prevented.

The experimental data detailed in the present paper show conclusively that when one eye of a bee is blackened, the resulting circus movements are produced by the continuous action of the light upon the functional photoreceptor. In the experiments in non-directive light, the only photic stimulation afforded was one of constant, almost uniform intensity over the entire surface of the eye. Under such conditions, the animals not only performed circus movements toward the functional eye, but the amount of turning increased with an increase in the stimulus. It is clear, therefore, that the process of normal orientation, which is identical with that involved in the circus movement, must also be dependent upon the continuous action of light.

The impulses arising from this stimulation are, at least in part, transmitted to the musculature of the opposite side of the body, since upon hemisecting the brain, the bee suffers a complete loss of phototropism (Holmes, '01, p. 227). Although his experiments were not conclusive on the point, Holmes believed that the result obtained was not entirely due to "the effect of the shock of the operation, or of incidental injury to other paths of photic impulses." It must, therefore, have been due to the severance of crossed tracts or commissures which served in the transmission of such impulses. There are present in the dorsocerebrum of the bee at least three commissures in more or less intimate connection with the optic tracts (Kenyon, '96), and it is possible that these are the elements concerned. There is thus neurological as well as physiological evidence for the crossed transmission of photic impulses.

The resultant effect of these impulses on the opposite side of the body is most probably an increase in the tonus of the extensor muscles. I have no direct evidence on this point in the case of the honey-bee. However, Holmes ('05) and Holmes and McGraw ('13), in experiments dealing with unilateral stimulation of photopositive insects, frequently observed that the legs on the side away from the stimulated eye were strongly extended, while those on the same side exhibited a pronounced flexion. Recently, Garrey ('17) has published an account of numerous experiments in which the same phenomenon was observed. In such animals it is clear that orientation is effected through a difference in the posture and not through a difference in the speed of the legs on the two sides of the body. This conclusion is further substantiated by the results obtained by Dolley ('17) on Vanessa. Careful measurement of the velocity of these butterflies showed that they did not creep faster in a very intense illumination than they did in a fairly weak one. From the above observations, therefore, it is clear that in many insects orientation is effected through changes of tension in the leg muscles. As previously stated, I have not been able to observe any constant and pronounced difference in the muscular tension on the two sides of the body in the honey-bee, although I have made only casual observations in this direction. I do believe that orientation is produced in this manner, however, and that the failure to detect it was due to the slight degree of the tensions together with the extreme rapidity of their execution.

This attempt to analyze the process of orientation in the honey-bee is, of course, far from complete. Certain features of it, however, may be defined with reasonable certainty. Thus it is clear that the stimulus regulating photic orientation is continuous and not intermittent. Furthermore, it appears to be essential that at least some of the impulses arising in the eye be transmitted to the opposite side of the body, where they probably regulate the tonus of the extensor muscles. As far as it is known, therefore, the process of orientation in the honey-bee is in strict conformity with the 'continuous action theory.'

3. *General evidence*

In experimenting with locomotor organisms, it is not an easy matter to regulate absolutely the conditions of photic stimulation. Thus, a photopositive animal as it moves toward the light is acted upon continuously by the light. But it is also subjected not only to a gradual increase of intensity with every forward movement, but also to sudden decreases and increases with every lateral deviation, however slight. Whether the orientation of the organism, therefore, is effected through a continuous action of the stimulus or only through sudden changes in its intensity from time to time, is frequently difficult to determine with certainty. This difficulty in separating the two conditions experimentally has led to much confusion in solving the problem of orientation. Among arthropods, however, there is a growing body of evidence tending to show that orientation is produced by continuous photic stimulation and not by intermittent changes of intensity.

No stronger evidence is to be found in this connection than that afforded by the general phenomenon of circus movements. The importance of this evidence has been repeatedly emphasized by Parker ('03, '07), Loeb ('06, '13), Bohn ('09 a, b), Holmes and McGraw ('13), Garrey ('17), and others. Parker ('07, p. 548), in reviewing one of the earlier expositions of the 'change of intensity theory' (Jennings, '06), states the case clearly when he says, "If the modern tropism theory were as weak as Jennings would have us believe, the experimental evidence upon which it rests ought easily to be explained away. Yet it has always seemed to the reviewer that the characteristic circus movements performed by animals immersed in a homogeneous stimulant, but with sense organs unilaterally obstructed, are explainable only on the basis of this theory."

This statement is certainly justified by the facts. Circus movements seem quite incapable of explanation in terms of the 'change of intensity theory' of orientation. Let us examine the case of a photopositive arthropod, with the right eye blackened, as it creeps toward a source of light. From experiment we know

that such an individual usually loops to the left. As it does so, however, the functional eye experiences a pronounced decrease of stimulation during the first half of each loop. According to the 'change of intensity theory,' such decreases should result in swerves toward the opposite side. Such, however, do not occur, as a rule. The animal, instead, completes the loop. It, therefore, does not respond very strongly to a decrease of intensity. If it did, the performance of circus movements would be quite impossible. If we assume, however, that the looping is produced by the continuous inequality in the stimulation received by the two eyes, the asymmetry of response becomes intelligible at once. For, in an animal with one eye blackened, the functional eye, even when turned farthest from the light, is the recipient of some stimulation, whereas the covered eye receives none whatever.

It may be objected, however, that many positive arthropods with one eye blackened are able to overcome their tendency to circle in directive light, and that this is a response to the decrease of intensity on the functional eye at the beginning of each loop. Such may well be the case, as Holmes ('05, p. 345) has suggested. This is a matter for further experiment to decide. In any case, however, circus movements must be regarded as an established phenomenon of general occurrence among this group of animals. The significant thing, therefore, to an understanding of orientation is to discover what is effective in producing these reactions rather than what is effective in modifying them.

The evidence afforded by circus movements in directive light as to the nature of the stimulus concerned in their production is thoroughly corroborated by the results obtained in non-directive light. Under the conditions of non-directive illumination employed by Holmes and McGraw ('13) and by myself, an animal is absolutely free from any pronounced or consistent changes in the intensity of the stimulus to which it is subjected. Moreover, the experiments of Dubois ('86) on the beetle *Pyrophorus* furnish a case in which there is no possibility whatever of intensity changes playing a significant rôle in orientation, since the source of light is within the animal itself. Yet in all these cases the elimination of one eye was usually followed by typical circus

movements toward the functional eye. In the absence of significant intensity changes, these responses must have been produced through the continuous action of light. The correctness of this conclusion is further attested by the fact that bees with one eye blackened tend to circle more toward the functional eye in a non-directive light of high intensity than in one of low intensity. The response may thus be made to vary with the intensity of a constantly acting stimulus.

Bohn ('09, a, '09 b) has suggested circus movements as a criterion for tropisms. Certainly, if the photic orientation of an animal is the result of a continuous action of the light on both eyes, as the tropism hypothesis postulates, the elimination of one eye should produce circus movements. The form of response will, of course, be subject to the peculiarities of locomotion. However, the elimination of the photoreceptors on one side of the body should result in a more or less asymmetrical response toward or away from that side, depending upon the index of phototropism. A failure to obtain such responses means either that the orienting stimulus does not consist in the continuous action of light or that modifying factors are present which interfere with the expected response. As stated in the introductory pages of this paper, the failures to obtain circus movements which have thus far been reported, are, I believe, to be attributed to the latter rather than to the former cause.

In conclusion, we may say that circus movements, both in directive and non-directive illumination, are produced by the continuous action of light and not by intermittent changes in its intensity. This, together with the general occurrence of circus movements among arthropods and the close relationship of such responses to normal orientation afford strong evidence that in this group of animals photic orientation is normally produced through the continuous action of light. This does not mean that photosensitive arthropods do not respond to sudden changes in illumination. They undoubtedly do. The orientation of the body toward or away from a source of light, however, cannot be fundamentally the result of such responses.

IX. GENERAL SUMMARY AND CONCLUSIONS

1. Light exerts a kinetic influence upon the honey-bee; that is, it tends to induce activity. In its absence, on the other hand, activity is either greatly reduced or entirely lacking.

2. Isolated worker bees, in an active condition, exhibit strong positive phototropism when flying or creeping. Temporary suppressions of this response may occur, however.

3. Normal bees when creeping in non-directive light usually exhibit pronounced asymmetrical responses of constant or variable index. Since essentially the same responses occur in total darkness, they are not fundamentally dependent upon photic stimulation. They are probably, therefore, conditioned largely by internal factors.

4. Bees with one eye blackened usually loop toward the functional eye as they creep toward a source of light. Some individuals are found, however, which display little tendency to loop, and occasionally an animal loops toward the covered eye. In the absence of experience, the tendency to loop toward the functional eye remains a permanent feature of behavior.

5. In non-directive light, bees with one eye blackened generally circle toward the functional eye, although a number are found which circle more or less toward the covered eye.

6. Although subject to considerable variation, bees with one eye blackened tend, in general, to circle more toward the functional eye in non-directive light of 957 mc. than in one of 24 mc. This tendency may be manifested in:

a. A lesser amount of turning toward the covered eye in the intense light than in the less intense one.

b. A greater amount of turning toward the functional eye in the more intense light than in the less intense one.

7. Since circus movements not only occur in a uniform, non-directive light field, but also vary in amount with the intensity of the light, they are produced by continuous unilateral stimulation.

8. In bees with one eye blackened, the rate of locomotion, unlike the amount of turning, is not dependent upon the intensity of photic stimulation.

9. The variability of response displayed by bees with one eye blackened, when creeping in non-directive light, is never due to a loss of phototropism or to after-effects of one intensity upon trials in a second intensity. It is attributable to the following causes:

- a. Conditions of temperature and humidity.
- b. Failure to eliminate completely the photoreceptors on one side of the body.
- c. Effect of contact stimulus afforded by the covering of eye.
- d. Natural asymmetry of individuals.
- e. Modifiability through experience.
- f. Mechanical stimuli attendant upon manipulation.
- g. Internal factors which may affect behavior from time to time, but not necessarily continuously.

10. Photic orientation in the normal honey-bee is effected through the continuous action of light on both photoreceptors.

11. The following considerations afford strong evidence that among arthropods generally, orientation to light is effected through the continuous action of the stimulus rather than intermittent changes of its intensity.

- a. Circus movements are of general occurrence among phototropic arthropods.
- b. The process involved in circus movements is identical with that involved in normal orientation.
- c. Circus movements in directive light are explainable only on the assumption of continuous photic stimulation.
- d. Circus movements are performed under conditions of non-directive illumination where the only stimulus afforded is one of approximately constant intensity.

12. Circus movements, as Bohn has suggested, furnish a criterion for testing the 'continuous action theory' of orientation. The failure of the test, however, does not necessarily invalidate the theory.

Postscript. The preparation of this paper has been much retarded by the absence of the author, who is still in government service in France. Hence it has not been possible to include in the discussion Garrey's recent paper (*Jour. Gen. Physiol.*, vol. 1,

p. 118), in which he has shown that the diameter of the circle in circus movements varies with changes in light intensity, nor Loeb's most recent volume on "Forced Movements, Tropisms, and Animal Conduct."

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XI. APPENDIX (TABLE 2)

A	B	C	D	E	F	G	H	I
NUMBER OF BEE	NORMAL BEE AV. PER CM. TO RIGHT 957 MC. LIGHT	NORMAL BEE AV. PER CM. TO LEFT 957 MC. LIGHT	ONE EYE BLACK AV. PER CM. TURNED 24 MC. LIGHT	ONE EYE BLACK AV. PER CM. TURNED 957 MC. LIGHT	+ VALUES OF E - D OR d	- VALUES OF E - D OR d	DURATION OF RECORDS IN SECONDS IN 24 MC. LIGHT	DURATION OF RECORDS IN SECONDS IN 957 MC. LIGHT
21		8.02 10.63	+15.84	+29.41	13.57	7.38	30	30
			- 3.00	+19.33	22.33		30	30
			- 3.22	+ 2.91	6.13		60	60
			- 2.35	+ 3.34	5.69		52	60
			+ 6.96	+13.59	6.63		60	60
			+ 5.06	- 2.32			58	60
			- 0.59	+ 2.70	3.29		90	80
			- 3.62	+14.72	18.34		49	47
			- 1.58	+ 0.53	2.11		70	80
			22	0.19 3.00			- 7.83	- 0.74
+ 0.96	- 3.08					20	22	
- 5.51	+ 0.40	5.91				30	21	
- 4.41	0.00	4.41				16	16	
- 3.65	- 6.37					60	60	
- 0.72	- 1.54					42	42	
- 5.92	- 7.32					76	60	
- 0.32	+ 1.45	1.77				27	33	
23	10.88	2.22	+ 9.72	+13.50	3.78	2.48 2.72	30	30
			+ 8.92	+ 6.44			60	60
			+10.59	+ 7.87			30	22
			+ 5.10	+22.65	17.55		63	60
			+ 0.32	+11.24	10.92		60	48
			- 1.18	+ 9.49	10.67		38	29
			+ 5.71	+16.33	10.62		60	60
			+ 9.96	+25.12	15.16		68	47
24		12.45 25.58	+ 7.19	+17.86	10.67		30	30
			+12.80	+27.01	14.21		30	30
			+ 2.17	+12.11	9.94		55	60
			+ 1.77	+17.73	15.96		30	30
			- 2.03	+ 4.36	6.39		60	60
			- 7.02	0.00	7.02		60	60
			-11.80	- 6.37	5.43		60	60
- 7.08	- 5.66	1.42	60	60				
25		8.34 10.09	+13.49	+ 5.32	12.07	8.17	30	30
			- 5.51	+ 6.56			30	21

XI. APPENDIX (TABLE 2)—Continued

A	B	C	D	E	F	G	H	I
NUMBER OF BEE	NORMAL BEE AV.° PER CM. TO RIGHT 957 MC. LIGHT	NORMAL BEE AV.° PER CM. TO LEFT 957 MC. LIGHT	ONE EYE BLACK AV.° PER CM. TURNED 24 MC. LIGHT	ONE EYE BLACK AV.° PER CM. TURNED 957 MC. LIGHT	+ VALUES OF E - D OR d	- VALUES OF E - D OR d	DURATION OF RECORDS IN SECONDS 24 MC. LIGHT	DURATION OF RECORDS IN SECONDS 957 MC. LIGHT
25			+ 1.63	- 7.24			22	28
			- 9.75	- 3.76	5.99	8.87	60	55
			- 2.81	- 6.57		3.76	60	70
			- 7.27	- 3.25	4.02		30	30
			- 6.90	- 6.63	0.27		60	70
				- 3.68	No reaction		36	
31	5.05		- 7.14	- 3.87	3.27		63	48
	5.04		0.00	+ 3.02	3.02		50	45
			+ 3.53	+ 1.05		2.48	71	74
			- 3.35	+ 1.73	5.08		37	45
32	9.34		-13.71	-12.92	0.79		60	60
	12.55		- 9.22	-13.28		4.06	30	30
			-12.17	- 8.86	3.31		60	60
			-14.12	- 8.85	5.27		60	60
33	5.31		+ 1.92	- 1.80		3.72	78	70
		8.59	+ 5.08	+ 7.25	2.17		60	64
			- 2.12	+ 5.08	7.20		58	58
			- 6.89	+ 1.50	8.39		33	29
34	2.34		-19.36	-21.92		2.56	60	60
	7.66		-24.85	-16.82	8.03		50	60
			-18.49	-16.84	1.65		60	60
			-22.05	-23.68		1.63	60	60
36		0.79	+ 3.08	+ 6.29	3.21		90	90
	1.94		0.00	+11.35	11.35		30	35
			+ 2.04	+ 8.85	6.81		66	70
			- 0.66	+ 2.05	2.71		68	79
41	3.92		+ 6.46	+ 5.48		0.98	62	60
		0.51	+ 9.77	+12.34	2.57		56	57
			- 2.41	+ 4.63	7.04		49	49
			+ 7.53	+ 7.30		0.23	75	69
42	0.92		+ 6.01	+12.24	6.23		76	70
		5.66	+ 4.21	+13.32	9.11		57	60

XI. APPENDIX (TABLE 2)—Continued

A	B	C	D	E	F.	G	H	I
NUMBER OF BEE	NORMAL BEE AV.° PER CM. IN RIGHT 957 MC. LIGHT	NORMAL BEE AV.° PER CM. TO LEFT 957 MC. LIGHT	ONE EYE BLACK AV.° PER CM. TURNED 24 MC. LIGHT	ONE EYE BLACK AV.° PER CM. TURNED 957 MC. LIGHT	+ VALUES OF E - D OR d	- VALUES OF E - D OR d	DURATION OF RECORDS IN SECONDS 24 MC. LIGHT	DURATION OF RECORDS IN SECONDS 957 MC. LIGHT
42			+ 8.71	+11.20	2.49	0.95	90	91
			+ 8.45	+10.47	2.02		88	90
			+ 9.49	+12.47	2.98		60	60
			+ 7.73	+18.95	11.22		57	60
			+ 9.03	+13.70	4.67		86	90
			+11.18	+10.23			90	90
			+ 9.34	+13.48	4.14		90	90
43	2.05 3.17		- 9.99	- 2.55	7.44	8.17	60	57
			- 4.44	-12.61			76	90
			- 8.48	- 8.43	0.05		90	106
			- 9.57	-11.06			70	60
44	0.00	0.57	+ 2.04	+16.10	14.06		61	76
			+ 1.43	+13.73	12.30		60	45
			+ 4.53	+10.36	5.83		73	70
			+ 2.05	+ 8.76	6.71		72	70
45	5.20 8.01		+ 1.97	+ 2.39	0.42	4.08	48	60
			+ 1.03	+ 3.80	2.77		62	69
			No record	-11.17				84
			- 4.68	- 8.76			59	60
51		3.41 3.75	- 4.49	+ 1.43	5.92		50	53
			- 3.96	- 0.44	3.52		42	48
			+ 2.87	+ 5.05	2.18		60	55
			- 8.30	- 5.05	3.25		71	70
52	2.35	5.00	+ 6.22	+ 9.06	2.84	0.87	91	99
			+ 2.37	+ 4.59	2.22		66	74
			+ 3.30	+ 5.02	1.72		97	111
			+ 8.44	+ 7.57			75	76
			+ 6.94	+11.07	4.13		71	78
53		2.08 2.61	- 5.65	- 3.41	2.24	5.00	59	65
			- 9.92	- 3.79	6.13		73	59
			- 1.19	- 6.19			55	50
			- 9.72	- 3.63	6.09		30	32
54	6.91		- 0.79	+ 8.23	9.02		85	90

XI. APPENDIX (TABLE 2)—Continued

A	B	C	D	E	F	G	H	I	
NUMBER OF BEE	NORMAL BEE AV. PER CM. TO RIGHT 957 MC. LIGHT	NORMAL BEE AV. PER CM. TO LEFT 957 MC. LIGHT	ONE EYE BLACK AV. PER CM. TURNED 24 MC. LIGHT	ONE EYE BLACK AV. PER CM. TURNED 957 MC. LIGHT	+ VALUES OF E - D OR d	- VALUES OF E - D OR d	DURATION OF RECORDS IN SECONDS 24 MC. LIGHT	DURATION OF RECORDS IN SECONDS 957 MC. LIGHT	
54	3.11		+ 5.77	+ 8.25	2.48	1.57	51	59	
			+ 8.20	+ 6.63			50	31	
			+ 3.37	+ 3.54	0.17		76	67	
			+ 1.70	+ 3.71	2.01		112	105	
55		7.69	- 0.35	+ 4.36	4.71	1.99	66	55	
		4.17	+ 8.14	+ 8.89	0.75		72	64	
			+ 9.88	+ 7.89			84	119	
			+ 8.64	+ 6.78			80	76	
56		0.32	+ 1.50	-12.86	5.56	14.36	61	64	
		1.45	+ 1.14	-10.27		11.41	35	30	
			- 3.73	+ 1.83			73	69	
			-10.56	-18.47		7.91	100	115	
62	1.38	2.05	+ 1.55	+ 1.36	7.30	0.19	83	73	
			+ 4.54	+ 2.98			1.56	133	122
			+ 1.88	+ 9.18				98	99
			+ 4.42	+ 8.71			4.29	84	80
			+10.73	+11.61			0.88	77	63
			+ 6.05	+ 6.33			0.28	110	110
			+ 5.79	+10.79			5.00	42	40
			+ 5.58	+ 5.87			0.29	112	113
			+ 7.59	+ 7.45				116	120
			+ 4.50	+ 4.47				103	99
63	7.50	5.58	+ 0.48	+11.83	11.35	9.03	52	49	
			+ 3.94	+ 8.56	4.62		78	72	
			+11.64	+ 2.61			35	38	
			+10.69	+ 8.45			48	50	
			+ 4.13	+ 4.50	0.37		87	74	
			+ 3.04	+ 3.41	0.37		48	61	
			+ 3.59	+12.00	8.41		41	30	
			+ 0.18	+ 8.74	8.56		56	60	
			+ 2.99	+ 9.21	6.22		50	48	
			+ 7.00	+ 9.87	2.87		46	50	
			+12.58	+14.74	2.16		60	54	
+ 5.59	+ 7.79	2.20	80	85					
66		1.82	+ 6.78	+ 6.48		0.30	46	46	

XI. APPENDIX (TABLE 2)—Continued

A	B	C	D	E	F	G	H	I
NUMBER OF BEE	NORMAL BEE AV.° PER CM. TO RIGHT 957 MC. LIGHT	NORMAL BEE AV.° PER CM. TO LEFT 957 MC. LIGHT	ONE EYE BLACK AV.° PER CM. TURNED 24 MC. LIGHT	ONE EYE BLACK AV.° PER CM. TURNED 957 MC. LIGHT	+ VALUES OF E - D OR d	-- VALUES OF E - D OR d	DURATION OF RECORDS IN SECONDS 24 MC. LIGHT	DURATION OF RECORDS IN SECONDS 957 MC. LIGHT
66		0.18	+ 6.46	+ 4.07			85	93
			+ 1.73	+ 4.27	2.54		68	68
			+ 4.36	+ 8.27	3.91		54	55
			+ 7.40	+ 8.68	1.28		96	86
			+ 9.45	+ 5.87		3.58	60	60
			+ 5.23	+ 4.93		0.30	142	136
			+ 4.98	+ 4.60		0.38	100	104
			+ 3.02	+11.09	8.07		83	80
			+ 5.59	+10.32	4.73		101	122
			68	6.08 1.94		+ 4.35	+13.12	8.77
+11.65	+16.40	4.75					66	67
+ 5.56	+14.91	9.35					54	59
+ 8.97	+11.23	2.26					60	69
+ 8.83	+ 9.82	0.99					87	100
+10.57	+12.21	1.64					53	63
+ 5.62	+12.06	6.44					75	60
+10.48	+13.52	3.04					75	87
+ 5.32	+11.79	6.47					91	99
+ 4.37	+ 4.76	0.39					100	104
72	5.73 7.30		+ 7.13	+ 9.11	1.98		60	60
			+ 1.02	+24.35	23.33		20	35
			+ 2.65	- 0.29		2.94	77	58
			+ 0.87	+ 3.13	2.26		87	86
			- 3.92	- 0.66	3.26		103	100
			+ 6.77	+ 6.22		0.55	120	120
			+10.17	+12.94	2.77		100	91
73	4.94 2.24		+ 0.92	+ 8.27	7.35		39	40
			+ 1.53	+ 4.22	2.69		34	34
			- 1.42	+13.04	14.46		60	65
			+ 2.45	+10.89	8.44		100	100
			+ 2.00	+12.55	10.55		61	75
			+ 3.29	+13.79	10.50		93	101
			+ 2.88	+ 9.49	6.61		104	87
			- 0.12	- 8.89	9.01		147	147
			+ 6.07	+13.82	7.75		135	136
- 1.69	+15.55	17.24		110	110			

XI. APPENDIX (TABLE 2)—Continued

A	B	C	D	E	F	G	H	I
NUMBER OF BEE	NORMAL BEE AV.° PER CM. TO RIGHT 957 MC. LIGHT	NORMAL BEE AV.° PER CM. TO LEFT 957 MC. LIGHT	ONE EYE BLACK AV.° PER CM. TURNED 24 MC. LIGHT	ONE EYE BLACK AV.° PER CM. TURNED 957 MC. LIGHT	+ VALUES OF E - D OR d	- VALUES OF E - D OR d	DURATION OF RECORDS IN SECONDS 24 MC. LIGHT	DURATION OF RECORDS IN SECONDS 957 MC. LIGHT
77	4.22 7.46		+10.71	+14.43	3.72		57	75
			+ 9.62	+16.59	6.97		88	65
			+13.53	+18.39	4.86		48	40
			+12.43	+14.74	2.31		104	80
			+ 8.45	+14.92	6.47		90	80
			+11.64	+16.89	5.25		120	130
			+12.60	+15.38	2.78		75	70
			+15.29	+17.98	2.69		40	35
			+11.57	+18.36	6.79		80	80
81	2.09 2.59		+ 4.21	+10.60	6.39		114	117
			+ 1.03	+ 3.98	2.95		53	53
			+ 6.03	+ 7.78	1.75		116	106
			+ 5.76	+ 5.86	0.10		108	101
			+ 3.30	+ 8.35	5.05		70	65
			+ 4.59	+ 9.89	5.30		56	61
			+ 5.03	+ 7.49	2.46		63	63
			+ 4.81	+13.52	8.71		57	80
			+ 2.76	+ 8.21	5.45		110	122
+ 3.71	+12.60	8.89		67	67			
82		5.81 0.65	- 3.94	- 2.33	1.61		124	119
			- 5.37	- 5.01	0.36		110	123
			-10.30	- 6.43	3.87		60	60
			- 6.95	- 4.88	2.07		59	59
			- 2.59	+ 1.42	4.01		66	64
			- 3.29	- 0.57	2.72		74	85
			- 7.06	+ 2.46	9.52		54	56
			- 6.40	- 5.29	1.11		70	80
			- 0.80	- 5.47		4.67	108	105
83	3.59 5.85		+ 5.62	+15.93	10.31		81	76
			+ 8.37	+15.73	7.36		90	90
			+ 8.89	+10.53	1.64		104	104
			+ 6.93	+11.49	4.56		71	71
			+12.84	+21.53	8.69		58	60
			+ 9.39	+17.47	8.08		60	60
			+ 4.93	+16.39	11.46		94	90
			+ 4.53	+12.50	7.97		41	33
			+ 3.52	+14.42	10.90		133	128

XI. APPENDIX (TABLE 2)—Continued

A	B	C	D	E	F	G	H	I	
NUMBER OF BEE	NORMAL BEE AV.° PER CM. TO RIGHT 957 MC. LIGHT	NORMAL BEE AV.° PER CM. TO LEFT 957 MC. LIGHT	ONE EYE BLACK AV.° PER CM. TURNED 24 MC. LIGHT	ONE EYE BLACK AV.° PER CM. TURNED 957 MC. LIGHT	+ VALUES OF E - D OR d	- VALUES OF E - D OR d	DURATION OF RECORDS IN SECONDS 24 MC. LIGHT	DURATION OF RECORDS IN SECONDS 957 MC. LIGHT	
85		0.84	+ 6.46	+12.52	6.06		47	46	
		0.93	+ 1.41	+ 7.78	6.37		113	117	
			+ 7.08	+ 3.74			3.34	75	82
			+ 6.87	+ 6.42			0.45	80	108
			+ 4.34	+ 3.54			0.80	126	123
			+ 1.73	+ 3.63	1.90			64	74
			+ 4.61	+ 8.19	3.58			137	123
			+ 6.13	+ 7.45	1.32			94	94
			+ 4.68	+ 7.99	3.31			71	58
91	0.48 6.99		- 2.42	- 4.98		2.56	125	125	
			-10.05	- 4.00	6.05		85	80	
			- 6.44	- 6.05	0.39		95	95	
			- 7.33	- 3.05	4.28		81	81	
			+ 2.18	+ 3.52	1.34		110	131	
			+ 0.73	+ 6.69	5.96		64	64	
	+10.19	+27.54	17.35		30	30			
92		10.66	+ 4.42	+ 5.77	1.35		113	104	
		8.67	+ 4.28	+ 9.86	5.58		58	62	
			+ 7.41	+ 9.19	1.78		94	85	
			+ 9.64	+ 7.64		2.00	63	61	
			+ 7.49	+17.34	9.85		52	52	
			+14.19	+23.82	9.63		60	60	
93	2.44	0.21	+ 1.61	+ 6.48	4.87		120	120	
			+ 0.19	+ 1.42	1.23		99	99	
			+ 2.87	- 0.46		3.33	63	63	
			+ 2.37	+ 2.92	0.55		98	87	
95		2.29	+ 2.14	+ 4.89	2.75		118	123	
		6.52	+ 1.13	+ 3.07	1.94		100	109	
			0.00	+ 5.67	5.67		58	46	
			+ 0.32	+ 6.58	6.26		71	80	
			+ 1.29	+ 4.82	3.53		70	78	
			+ 0.93	+11.94	11.01		34	30	
			+ 2.39	+ 7.18	4.79		69	74	
			+ 3.67	+ 7.11	3.44		66	67	
			+ 0.85	+ 6.35	5.50		82	75	
	+ 0.21	+ 1.93	1.72		61	60			

XI. APPENDIX (TABLE 2)—Continued

A	B	C	D	E	F	G	H	I
NUMBER OF BEE	NORMAL BEE AV.° PER CM. TO RIGHT 957 MC. LIGHT	NORMAL BEE AV.° PER CM. TO LEFT 957 MC. LIGHT	ONE EYE BLACK AV.° PER CM. TURNED 24 MC. LIGHT	ONE EYE BLACK AV.° PER CM. TURNED 957 MC. LIGHT	+ VALUES OF E - D OR d	-- VALUES OF E - D OR d	DURATION OF RECORDS IN SECONDS 24 MC. LIGHT	DURATION OF RECORDS IN SECONDS 957 MC. LIGHT
96	5.54	2.76	+10.46	+19.08	8.62	0.79	90	92
			+ 9.29	+ 8.50			195	192
			+11.89	+15.99	4.10		60	60
			+14.09	+17.84	3.75		60	60
			+ 5.33	+10.15	4.82		35	29
101		7.11 6.10	- 5.47	- 2.55	2.92	0.40	62	63
			- 1.67	- 2.07			88	79
			- 2.09	- 0.61	1.48		60	59
			- 1.02	- 1.00	0.02		67	70
			- 3.34	- 1.58	1.76		46	49
102	3.67 5.30		- 1.58	+14.37	15.95		49	49
			+ 2.98	+15.02	12.04		50	54
			+ 3.75	+11.08	7.33		71	78
			- 2.23	+ 1.45	3.68		62	66
			- 0.32	+ 6.46	6.78		64	53
			- 3.38	+11.11	14.49		57	58
			- 1.98	+ 4.52	6.50		41	60
			- 2.23	+10.19	12.42		88	88
			+ 3.55	+13.35	9.80		95	95
			- 1.28	+12.23	13.51		70	60
103	0.00 6.34		- 2.46	+13.48	15.94		57	57
			- 4.29	+11.25	15.54		77	60
			+ 0.16	+ 8.49	8.33		60	69
			- 1.26	+11.36	12.62		61	61
			- 0.44	+ 2.15	2.59		84	84
			- 3.75	+11.04	14.79		60	60
			+ 3.89	+ 6.47	2.58		60	65
			+ 2.27	+ 6.99	4.72		63	68
			- 0.18	+ 0.22	0.40		105	104
			+ 0.86	+ 4.22	3.36		62	64
105	5.93 8.81		+ 8.46	+14.64	6.18		68	60
			+ 9.19	+13.78	4.59		50	60
			+ 6.89	+14.10	7.21		80	80
			+ 6.55	+15.20	8.65		60	60
			+ 6.74	+14.83	8.09		93	93
			+ 6.21	+12.73	6.52		60	60
			+10.34	+16.05	5.71		60	60

XI. APPENDIX (TABLE 2)—Continued

A NUMBER OF BEE	B NORMAL BEE AV. PER CM. TO RIGHT 957 MC. LIGHT	C NORMAL BEE AV. PER CM. TO LEFT 957 MC. LIGHT	D ONE EYE BLACK AV. PER CM. TURNED 24 MC. LIGHT	E ONE EYE BLACK AV. PER CM. TURNED 957 MC. LIGHT	F + VALUES OF E - D OR d	G - VALUES OF E - D OR d	H DURATION OF REC- ORDS IN SECONDS 24 MC. LIGHT	I DURATION OF REC- ORDS IN SECONDS 957 MC. LIGHT
105			+10.03 + 9.04 + 7.46	+17.05 +11.01 +12.68	7.02 1.97 5.22		60 100 163	60 100 163
106	6.43 1.71		- 1.18 + 0.44 + 2.79 - 1.49 + 0.59 + 0.53	+ 1.49 + 3.22 + 6.72 + 5.19 - 5.49 + 5.33	2.67 2.78 3.93 6.68 4.90 4.80		70 81 41 35 77 103	68 79 41 35 77 115
121	1.61	6.87	+ 2.96 +11.57 + 3.13 + 1.91 - 4.71	+24.04 +19.71 +15.11 +12.12 +17.50	21.08 8.14 11.98 10.21 22.21		60 60 92 87 60	60 60 88 91 60
122	2.31 2.93		+ 1.88 + 3.65 + 3.25 - 4.39	+ 8.96 + 3.77 + 1.99 + 6.50	7.08 0.12 10.89	1.26	69 118 90 56	73 111 85 55
123		17.86 3.60	+ 7.16 + 1.79 -10.76 - 8.08 - 7.61 - 3.46 - 3.25 - 3.53 - 2.21	+18.55 - 1.21 + 0.59 + 2.29 - 2.14 + 1.12 + 5.69 + 0.56 + 1.97	11.39 11.35 10.37 5.47 4.58 8.94 4.09 4.18	4.00	54 65 69 79 60 140 60 58 90	60 69 67 79 60 135 58 58 101
124		2.59 3.00	+ 3.88 + 3.94 + 2.54 +10.36 +11.04 +10.39 + 5.81 + 6.55 + 7.67	+11.18 + 6.45 + 8.38 +11.19 +17.61 +17.41 +12.54 + 8.95 +10.19	7.30 2.51 5.84 0.83 6.57 7.02 6.73 2.40 2.52		73 53 79 80 90 60 58 74 60	68 59 71 80 90 60 58 60 60

XI. APPENDIX (TABLE 2)—Continued

A	B	C	D	E	F	G	H	I
NUMBER OF BEE	NORMAL BEE AV.° PER CM. TO RIGHT 957 MC. LIGHT	NORMAL BEE AV.° PER CM. TO LEFT 957 MC. LIGHT	ONE EYE BLACK AV.° PER CM. TURNED 24 MC. LIGHT	ONE EYE BLACK AV.° PER CM. TURNED 957 MC. LIGHT	+ VALUES OF E - D OR D	- VALUES OF E - D OR D	DURATION OF RECORDS IN SECONDS 24 MC. LIGHT	DURATION OF RECORDS IN SECONDS 957 MC. LIGHT
126		6.51	- 1.39	+ 3.11	4.50		105	100
		1.19	+ 4.51	- 2.89		7.40	48	50
			+ 3.73	+ 6.14	2.41		78	77
			- 1.44	+23.37	24.81		45	45
			+ 1.83	+ 4.41	2.58		107	107
			+ 4.57	+ 3.65		0.92	148	153
			+ 5.51	+ 4.32		1.19	72	72
			- 2.98	- 2.26	0.72		83	83
			- 1.49	+ 3.73	5.22		25	28
	133	2.82		+ 2.39	+ 3.18	0.79		70
5.86			+ 1.98	+ 3.26	1.28		69	68
			+ 1.54	+ 4.31	2.77		60	61
			+ 4.79	+ 9.29	4.50		60	60
			+ 1.76	+ 4.92	3.16		82	76
			+ 3.30	+11.54	8.24		38	40
			+ 3.35	+ 7.77	4.42		64	68
134		1.52	+ 8.29	+19.62	11.33		69	69
		1.22	+ 9.94	+19.60	9.66		57	57
			+ 5.67	+18.19	12.52		80	80
			+ 0.22	+18.93	18.71		60	60
			+ 3.83	+12.53	8.70		58	58
135		10.77	- 3.25	- 0.54	2.71		63	61
		10.88	+ 0.74	+ 2.03	1.29		95	89
			+ 1.29	+ 3.35	2.06		109	109
			- 9.49	- 5.85	3.64		58	59
			+ 2.28	- 1.37		4.65	71	71
			- 1.05	- 3.03		1.98	94	94
			- 0.33	- 7.67		7.34	79	76
			+ 0.44	- 6.66		7.10	58	59
137		5.99	+11.73	+19.09	17.36		60	60
		2.94	+15.82	+16.09	0.27		49	49
			+10.59	+16.45	5.86		70	70
			+15.78	+16.57	0.79		60	60
			+14.31	+15.40	1.09		78	78
			+14.71	+22.57	7.86		60	60
			+14.69	+17.02	2.33		70	70

XI. APPENDIX (TABLE 2)—*Concluded*

A	B	C	D	E	F	G	H	I
NUMBER OF BEE	NORMAL BEE AV.° PER CM. TO RIGHT 957 MC. LIGHT	NORMAL BEE AV.° PER CM. TO LEFT 957 MC. LIGHT	ONE EYE BLACK AV.° PER CM. TURNED 24 MC. LIGHT	ONE EYE BLACK AV.° PER CM. TURNED 957 MC. LIGHT	+ VALUES OF E - D OR d	- VALUES OF E - D OR d	DURATION OF RECORDS IN SECONDS 24 MC. LIGHT	DURATION OF RECORDS IN SECONDS 957 MC. LIGHT
137			+13.38 + 8.43 +15.92	+15.64 +16.71 +18.08	2.26 8.28 2.16		60 60 60	60 60 60
138		6.55 8.37	- 0.18 - 0.37 - 1.12 - 9.00 - 3.07 - 1.97 - 6.19	- 4.67 + 0.13 +13.52 - 3.52 + 1.60 + 2.57 - 1.08	0.50 14.64 5.48 4.67 4.54 5.11	4.49	129 62 65 70 115 77 69	129 58 60 70 115 74 69

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