

THE EFFECT OF LIGHT INTENSITY, AREA, AND FLICKER FREQUENCY ON THE VISUAL REACTIONS OF THE HONEY BEE

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I

Experimental studies on the visual capacity of the eye of the honey bee have shown that the relative motion of the eye and the object seen plays an important rôle in vision. Bees show an increased sensitivity toward moving objects and flickering visual stimuli based upon the frequency of intermittent stimulation of the elements of the ommatidial mosaic of the retina (Wolf, 1932-33 *a, b*, Wolf, 1933-34; Wolf and Crozier, 1932-33; Wolf, 1933; Zerrahn, 1933). It was found that the bee's reaction depends upon the light intensity, the velocity of motion of the test object or the flicker frequency, and the size of the object. It seemed to be essential to obtain quantitative relationships between these factors. For this investigation the phototropic response of the bee was used.

II

The experimental set-up can be understood with the help of Fig. 1. In a vertical piece of ply-wood 175 cm. long and 50 cm. high two openings 37×37 cm. were cut. The distance between the centers of the two holes is 64 cm. Into each opening opal glass plates are fitted which are illuminated from behind. The areas of the illuminated opal plates can be varied by means of cardboard frames, reducing the original area to $\frac{1}{2}$, $\frac{1}{4}$, $\frac{1}{8}$, and $\frac{1}{16}$. The cardboard frames were constructed so that their lower edges coincided with the lower edge of the opening in the ply-wood so that the illuminated fields were always at "eye level" of the bees.

The vertical wooden wall serves as one side of a cage, triangular in shape in which the bees are allowed to migrate to the illuminated fields. The cage is 170 cm. in length; the bottom consists of cardboard, the sides and top of wire screens, through which the bees can be observed. The bees are admitted through a door at the distal end of the cage; they can after arriving at the illuminated fields be taken out through side doors in the cage.

For illumination of the opal plates in the wall of the cage two 500 watt concentrated-filament lamps are used. To provide an even illumination of both areas the lamps are set back 150 cm. Directly in front of each source a small opal plate is placed which provides a larger and more easily controllable source of uniform illumination than the lamps. The amount of light emitted from these diffusing screens is controlled by diaphragms which permit a variation in brightness over a range of 200 units. The brightness of the large opal plates in the wall of the cage at different diaphragm openings is measured with a Macbeth illuminometer. From the photometric readings calibration curves are drawn from which any desired brightness can be read and the diaphragms adjusted accordingly.

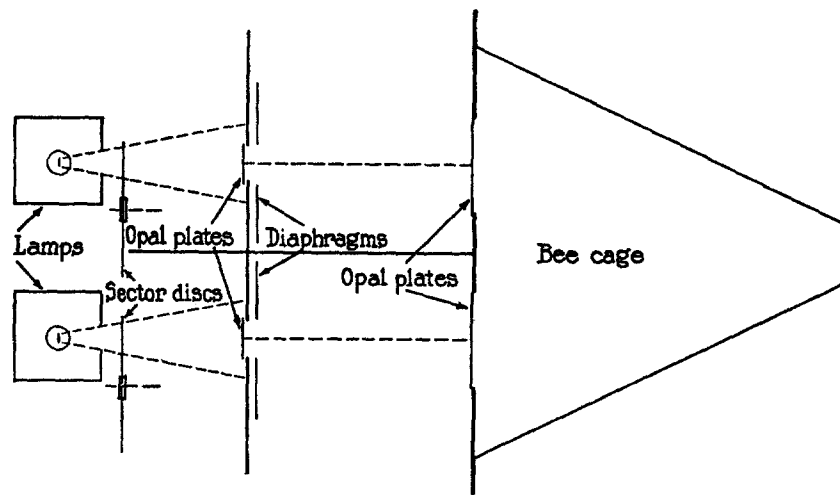


FIG. 1. Apparatus for testing the bee's reaction to two illuminated fields differing in area, intensity, and flicker frequency.

The experiments are carried on with single individuals. They are caught in front of one of our hives, left in the dark a short time for adaptation, and then set free at the narrow end of the cage. Being positively phototropic they move, in part crawling in part flying, toward the lights; and by changing the areas and their brightnesses one can easily recognize the stimulating effect of the two areas from the course of the bees' path. If the two areas are equal in brightness the course of the bees is generally the bisecting line between the two fields, and this is maintained until they almost reach the front wall; then swinging motions occur until the animals finally go to one of the two fields. If the two areas are not equal in their stimulating effect, the course of the bees is slightly turned to the brighter field. The angle of deflection from the vertical can serve as an indication of the difference between the stimulating values of the two fields.

In the first series of experiments both fields were equal in intensity and size (37×37 cm.). In a great number of tests equal numbers of bees travelled to both fields. We now changed the relative areas of the two fields, keeping the intensities the same. Testing in each case 50 bees and decreasing the size of one of the areas to $1/2$, $1/4$, $1/8$, and $1/16$ of the original, we obtained with increasing difference in area

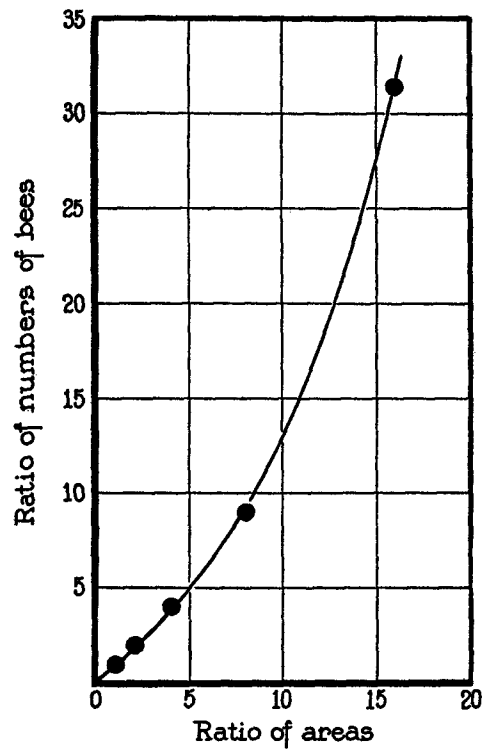


FIG. 2. Relation between the relative numbers of bees seeking two illuminated fields and the relative sizes of the areas.

an increasing proportion of animals going to the larger field. The data are represented in Fig. 2 where the relative numbers seeking the two fields are plotted against the relative areas.

It may be assumed that the stronger response to the larger field at equal intensity is due to the greater number of elements stimulated, and hence the greater total frequency of retinal responses. How

ever, Hartline and Graham (1932) have shown that the total frequency of optic nerve discharges in *Limulus* also increases with intensity. It therefore might be possible to equalize the stimulating effect of two different areas by decreasing the intensity of the larger area, until the total frequency of response from both areas is equal.

To test this point we presented two different areas, then decreased the brightness of the larger field step by step until we obtained in a considerable number of trials equal numbers of bees going to both fields. At this point the product of area and intensity was found to be identical for both sides. The data are given in Table I.

Since the larger area stimulates a greater number of retinal elements weakly, while the smaller area stimulates a smaller number more

TABLE I

Values for areas and intensities of illuminated fields which have the same stimulating effect upon the bee's eye. The products of area and intensity are approximately equal for two fields presented simultaneously.

Area	Intensity, millilamberts	Area × intensity	Area	Intensity, millilamberts	Area × intensity
<i>cm.</i>			<i>cm.</i>		
1354.2	6.42	8696.9	1354.2	6.42	8696.9
681.2		4374.5		3.26	4304.8
338.6		2174.2		1.70	2302.2
169.0		1085.3		0.75	1019.7
86.5		555.4		0.54	578.9

strongly, due to the respective brightnesses, and the net effect is the same for the orientation of the bees, we must assume that it is irrelevant for the processes which control the coordination of motion whether weak impulses travel from a greater number of receptor elements over a greater number of nerve fibers, or whether a smaller number of stronger impulses pass over fewer pathways.

III

In the experiments just mentioned continuous lights were used. The peculiar effect of intermittent light can be demonstrated by presenting to the bees simultaneously a stationary and a flickering field of the same objective intensity. If bees are exposed to two such

fields they practically always travel to the flickering field, provided that the flicker frequency is below fusion. Even if the light intensity or the frequency of the flickering field is decreased considerably it always shows a pronounced predominance (Wolf, 1933).

To obtain quantitative data upon the effect of flicker on the orienting reaction of bees with fields of different areas we placed in front of our light sources sector discs which were slowly rotated by a motor and gave flicker frequencies between 2 and 16 per second. One field was flickered at a constant frequency, the other at an integral multiple of this frequency. The question was whether such fields can be made equal in their stimulating effects by adjusting their areas accordingly.

In the first experiment both fields were made equal in intensity and size (37×37 cm.), the flicker frequency of one being twice that of the other. The bees now migrated to the field of higher frequency. We then decreased the size of this field and observed that as soon as its area was reduced to one-half equal numbers of bees travelled to both fields. We then changed to different sizes of areas and flicker frequencies and found that under all circumstances a ratio of 1:2 in flicker frequency can be balanced by a reciprocal ratio of 2:1 in area. If flicker frequencies are produced in the ratio 1:4 balancing occurs when the relative areas are as 4:1 and so on. In all such tests it can be shown that to produce equal photic stimulation by flickering fields the flicker frequencies must be inversely proportional to the field areas. For phototropic orientation of bees we therefore have to assume that it is irrelevant whether a great number of photic receptors is stimulated at a low frequency or a smaller number more often per unit time.

IV

Since it was shown that the frequency of alternate stimulation of the elements of the ommatidial mosaic of the bee's eye is the basis for reaction to flickering fields, evidence has been brought forward that the same holds true for the bee's reaction toward patterns of different design in free choice experiments (Zerrahn, 1933; Wolf, 1933). When conditioning bees for patterns we are not dealing with any visual impressions (learning) and recognition of known forms but with a forced reaction to the pattern. The reaction depends upon the

stimulation given by the contours of a pattern which cause transitions of the retinal elements from one state of excitation to another during the bee's flight over the pattern.

From some unpublished experiments by Zerrahn we know that the choice is always in favor of a pattern greater in area, if two patterns of the same degree of coarseness are presented to the bees. We can deduce from this that for the bee's reaction not a single retinal element but the total number which undergo changes in their state of excitation has to be taken into account. Thus the question arises whether two patterns different in area can be made equal in their stimulating effects by adjusting the "grain" of the patterns, since by this means both might give the same number of alternating stimuli, causing the bees to go to one pattern just as often as to the other.

To test this we used a method which was applied previously by Zerrahn. Bees are conditioned to come to a table, covered with a glass plate on which they are fed with a sugar solution. Underneath the glass plate is a white surface on which can be placed patterns for choice. During feeding no patterns are shown because all choices are supposed to occur without previous conditioning but spontaneously. After a large number of bees comes regularly to the table, the food is removed and two patterns presented. The bees then settle down on one of the two patterns in a big bunch. By means of a feather they are brushed off the glass plate. The glass is cleaned quickly with a moist cloth to remove odors, then the figures are shifted in relative position to each other to avoid conditioning to any particular location on the table. Then the bees are given a new chance to choose. This can be repeated half a dozen times. As soon as the number of searching bees decreases, sugar solution has to be given anew.

For patterns, checkerboards and stripes were used. Patterns of concentric design such as sectors, *etc.* were not taken into consideration since they are complicated by the greater density of contour toward the center, which can hardly be treated analytically.

A checkerboard pattern with checkers 1 cm. square and a total area of 10×10 cm. (A) is presented with other patterns of coarser grain. First we present our pattern (A) together with a checkerboard with 2 cm. squares and 10×10 cm. area (B). In 51 tests the finer pattern is chosen 31 times, the rough pattern 11 times, and in 9 cases we obtained

collections of bees on both patterns. The relation of choices of the finer to the coarser pattern is 2.8:1.

The question now arises how much the size of the coarser pattern has to be increased until we obtain a 1:1 relationship of choices. In analogy to our darkroom experiments we double the area and obtain a pattern (C) 14×14 cm. in size and find that the relation in choices of (A):(C) becomes 1:1. In 54 trials pattern (A) is chosen 21 times, (B) 21 times, and in 12 cases we obtain choices of both patterns at the same time. By increasing the size of the coarser pattern still further, using a pattern (D) 20×20 cm. in size, the relation of choices is shifted in favor of the coarse pattern. In 53 tests (A) is chosen 14 times, (D) 30 times, and in 9 cases bees collect above both patterns. The relationship (A):(D) is now 1:2.1.

In a second series of tests we combine pattern (A) with checkerboards with 1.5 cm. squares. First this is tried in an area of 10×10 cm. (E). Since the areas of both patterns are the same we should expect from our previous results that the finer design takes predominance. We obtain in fact in 54 tests 29 choices of pattern (A) and 18 of pattern (E). In 7 cases both are visited by bees. In order to obtain a 1:1 relationship in choice with a pattern which has 1.5 cm. squares we must use a pattern (F) which is 12×12 cm. in size. Then among 53 choices 26 are in favor of (A), 26 in favor of (F), and one remains undecided.

Finally we present together with pattern (A) a still coarser design with 4 cm. squares. First we use a 10×10 cm. field of this pattern (G). (A) now has a very pronounced overweight. In 75 tests (A) is chosen 53 times, (G) 16 times, and in 6 cases (A) and (G) at the same time. The relation (A):(G) now is 3.3:1. Increasing the size of (G) until we obtain a 1:1 relationship of choices we have to use a pattern 20×20 cm. in size (H). In 60 tests we obtained 27 choices of (A), 27 choices of (H), and 6 choices of both together.

The results of these experiments show that coarseness of design and area can be successfully combined to obtain equal stimulating values for different patterns. The increase in area of the coarser pattern necessary for equal stimulating effect is directly proportional to the increase in size of the squares: with 1.5 cm. squares the area is 1.5 times that of pattern (A), with 2 cm. squares twice that of (A), and

with 4 cm. squares 4 times that of (A). The necessitated increase in size can be explained with help of our statement made previously, namely, that the length of contours of the pattern is decisive for the bee's reaction, providing a measure of the number of elements undergoing changes in their state of excitation. We thus ought to expect that in all cases in which we obtain a 1:1 ratio in choice the lengths of contours of the patterns used are approximately identical (Table II).

Thus by two patterns presented simultaneously the same numbers of retinal elements must have experienced changes in their state of excitation. When the pattern is small and has a fine design, the elements stimulated within the eye during transition lie close together.

TABLE II

Patterns which are different in area and coarseness of design but have the same stimulating effect upon the bee's eye. All patterns have about the same lengths of contours.

Pattern	Area	Length of contours
	<i>cm.</i>	<i>cm.</i>
(A) 1 cm. ²	10 x 10	200
(B) 2 cm. ²	14 x 14	200
(F) 1.5 cm. ²	12 x 12	192
(H) 4 cm. ²	20 x 20	208

When the pattern is larger in area and coarser in design the elements stimulated lie further apart, covering a greater retinal area.

Checkerboards must without any doubt give most easily the results theoretically asked for, since because of their structure they produce a very regular alternate stimulation of the retinal elements, regardless of the direction in which the patterns are crossed during flight. Conditions might be less favorable when using stripes, but in a great number of tests the chances must become even that the bees cross the patterns in the direction of the stripes or at 90° to them, as our experimental results show.

For the test we combine a pattern (I), having stripes 1 cm. in width, an area of 10 × 10 cm., and a length of contours of 110 cm. with patterns having stripes 2 cm. wide but different in area. First we combine (I) with a pattern (K, 2 cm. stripes) which has an area of

10 × 10 cm. In 53 tests (I) is chosen 31 times, (K) 17 times, and both patterns at the same time in 5 cases. The relation of (I):(K) is 1.8:1, the relation of the lengths of contours is 110:72 cm. We then increase the area of the coarser pattern until its length of contours corresponds to that of (I). The new pattern (L) has an area of 12.5 × 14 cm. and a length of contours of 116 cm. (I) and (L) are presented to the bees 50 times. (I) is chosen 23 times, (L) 23 times, and in 4 cases bees collect above both patterns. The ratio of choices is 1:1 which was

TABLE III

Summary of the Results of the Bees' Choices among Patterns Different in Area and Coarseness of Design

Exp. No.	No. of tests	Pattern	Area	Length of contours	No. of choices	Pattern	Area	Length of contours	No. of choices	Choices of both patterns	Ratio fine:coarse
		Checker-boards				Checker-boards					
I	51	1 cm. ² (A)	10 x 10	200	31	2 cm. ² (B)	10 x 10	104	11	9	2.8:1
II	54	1 cm. ² (A)	10 x 10	200	21	2 cm. ² (C)	14 x 14	200	21	12	1:1
III	53	1 cm. ² (A)	10 x 10	200	14	2 cm. ² (D)	20 x 20	400	30	9	1:2.1
IV	54	1 cm. ² (A)	10 x 10	200	29	1.5 cm. ² (E)	10 x 10	142	18	7	1.6:1
V	53	1 cm. ² (A)	10 x 10	200	26	1.5 cm. ² (F)	12 x 12	192	26	1	1:1
VI	75	1 cm. ² (A)	10 x 10	200	53	4 cm. ² (G)	10 x 10	64	16	6	3.3:1
VII	60	1 cm. ² (A)	10 x 10	200	27	4 cm. ² (H)	20 x 20	208	27	6	1:1
		Stripes				Stripes					
VIII	53	1 cm. (F)	10 x 10	110	31	2 cm. (K)	10 x 10	72	17	5	1.8:1
IX	50	1 cm. (F)	10 x 10	110	23	2 cm. (L)	12.5 x 14	116	23	4	1:1
X	52	1 cm. (F)	10 x 10	110	15	2 cm. (M)	20 x 20	220	32	5	1:2.1

to be expected from our considerations. In one further experiment we combine (I) with a pattern (M) having an area of 20 × 20 cm. and a length of contours of 220 cm. Since for pattern (M) the length of contours has become the double of (I), its stimulating value should be increased. Of the 52 tests made 15 are in favor of (I), 32 in favor of (M), and in 5 cases both patterns are chosen. The ratio (I):(M) is 1:2.1.

For comparison all the data for the experiments with patterns are brought together in Table III.

V

A picture of the effect of the alternate stimulation upon the bee's eye during motion when looking at a pattern can be provided by mapping out on a sheet of translucent coordinate paper the points of intersection of the axes of the ommatidia with a plane whose distance from the eye corresponds to the distance of the pattern at the moment of choice. This distance is in our case approximately 15 cm. Such a system of coordinates can be obtained from a figure given by Baumgärtner (1928) in his paper where he gives a schematic picture of the resolving power of the bee's eye. His coordinates only need to be replotted for our distance. By placing our patterns underneath the map of the eye one can count the number of elements which are covered by the white and by the black parts of the pattern. If now the pattern is moved over a unit length of distance in any direction the number of elements undergoing transition during the shift may be counted. For any coarser pattern which does not provide as many transitions as a fine one of the same area when moved over the same distance, the increase in size can be estimated which would give it a stimulating value corresponding to that of the fine pattern. Our investigations, in fact, began by studying the effect of patterns upon the elements of this model of the bee's eye and the calculations made were justified by the results of our experimental tests.

SUMMARY

1. For the phototropic reaction of bees, the stimulating effects of two illuminated fields differing in intensity and area become equal when the product of area and intensity is the same for both fields.
2. The effect of two areas differing in size and flicker frequency is the same for the bee, when the product of area and flicker frequency is equal for both fields.
3. If two patterns of the same character but varying in size and coarseness are presented to bees for free choice, a 1:1 ratio of choices is obtained when both patterns stimulate equal numbers of retinal elements alternately by transition from one state of excitation to another.

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