

FLICKER AND THE REACTIONS OF BEES TO FLOWERS

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The quantitative evidence secured thus far about the visual functions of the eye of the honey bee is based upon the fact that a bee will respond to a displacement of a pattern within its visual field. Whether we are dealing with visual acuity tests (Hecht and Wolf (1928–29)), intensity discrimination (Wolf (1932–33 *a,b*)), dark adaptation (Wolf and Zerrahn-Wolf (1935–36)), or marginal recognition of flicker (Wolf (1933–34)), the reaction of the bee always depends upon the transition of visual elements from one state of excitation into another. Even when confronting a bee with the task of distinguishing patterns of different design and coarseness the same is true. If bees are to choose between a series of patterns of the same area but different in design, the number of choices of each pattern is proportional to the lengths of the contours within each pattern (Zerrahn (1933)). This again indicates that the transitory stimulation produced during the bee's flight over the patterns by reason of the edges separating black from white, arouses the response. A different proof for this kind of reaction to patterns can be given by conditioning bees to flickering fields of equal size but different flicker frequencies. Under such conditions the bee's choices are directly proportional to the flicker frequencies, provided the frequencies are below fusion (Wolf (1933)). At the same time we have evidence that only the numbers of alternating stimuli reaching the ommatidia are responsible for a choice, since patterns different in area and coarseness of design can be combined in such a way that equal numbers of choices are obtained (the number of elements stimulated by transition being equal for the patterns presented for choice) (Wolf and Zerrahn-Wolf (1934–35)). On the other hand, two flickering fields will have the same stimulating effect upon bees if for both the product of flicker frequency \times area is the same (Wolf and Zerrahn-Wolf (1934–35)).

We therefore come to the conclusion that recognition and distinction of patterns by the bee is based upon the transitory stimulation produced by a pattern and that the pattern as such is of no importance. This theory is in disagreement with the experimental evidence and the conclusions of Hertz (1930, 1931, 1933, 1934 *a,b,c*, 1935), who claims that pattern discrimination by the bee is based upon recognition of the pattern as such, upon the distinction of patterns as patterns, and a memory of form.

If we recall the fact that the bee's visual acuity is only about 1/100 of ours, its intensity discrimination only 1/25, we hardly can assume that the bee's vision is *a priori* sufficient for any higher visual perception such as distinction of patterns and forms. In only one respect is the function of the bee's eye equal to the human, namely in the recognition of flicker. For the human eye the maximum critical flicker frequency is between 45 and 53 per second (Hecht, Shlaer, and Verrijp (1933-34)). At very high illuminations the bee will still respond to 55 flickers per second, so that its recognition of flicker is certainly as good as in man, if not even better. It seems generally true that flicker perception in Arthropods is higher than in mammals. So far we know that dragon fly larvae can react to slightly over 60 flickers per second (Sälzle (1932); Crozier, Wolf, and Zerrahn-Wolf (1936-37)), and *Eupagurus* to 56 flickers per second (Bröcker (1935)).

It seems probable therefore that flicker may play an important rôle in the vision of the bee, and the question arises whether reactions to intermittent stimulation might play a part in nature. It was pointed out in earlier papers (Wolf (1933, 1935)) that perhaps flickering effects produced by the relative motion of the bees and flowers while collecting nectar might have an effect upon the bees' settling on the flowers. The finding of small blossoms closely spaced, even if their particulars of flower formation are below threshold visibility, might be facilitated by the relative motion of the flowers in regard to the bee's eye, and thus through the production of flicker cause the bee's reaction to the flower.

We had made the observation that the number of bees settling on particular flower beds on quiet and on windy days is greater when the flowers are slightly moved by the air. There is no question that with an air current odors from the flowers might drift over a greater area

and thus attract more bees. It can be shown, however, that the intermittent optical stimulation has a considerable effect upon the bee's reaction when odors are excluded.

By studying the bee's reaction to natural and artificial flower beds which can be moved, evidence can be brought about for the effect of flicker upon the bee's reaction toward the experimental arrangement.



FIG. 1. Arrangement of 25 flower pots planted with *Phlox sabulata alba*. Any one of the pots can be put on a turntable and rotated. By the increase in flicker produced by the rotation more bees are attracted to the moving flowers.

For test purposes bees from one of our colonies are conditioned to collect a sugar solution from Petri dishes about 50 meters from the hive. The dishes are placed in between an arrangement of 5 x 5 flower pots, making a flower bed one square meter in size, in which there are planted *Phlox sabulata alba*, a flower which has no particular odor, very small white blossoms, and which is rarely visited by bees. After a constant stream of bees visits our flower bed and settles with certainty on the dishes which are frequently shifted around among the pots so as to avoid conditioning to a particular location in the flower bed, the dishes are removed for test and the bees observed. The bees search over the flowers and will gradually settle on the flowers in bunches, in the manner observed when bees spontaneously or after conditioning react to patterns. The arrangement of the

flower pots is such that each one can be placed on a turntable and can thus be rotated at a slow speed. A turntable is attached to a kymograph motor which has been adjusted in such a way that $\frac{1}{2}$ to 1 rotation is obtained per second. We therefore have the possibility of increasing the intermittent stimulation produced by the flower bed by rotating one pot. Under these conditions the bees do not settle at various places over the whole field but follow the rotating pot in a circling cloud. Unfortunately the bees do not settle down on the flowers, but gradually disappear and return to the hive. It would be of great importance to obtain some quantitative measure for the bee's reaction. We therefore changed the

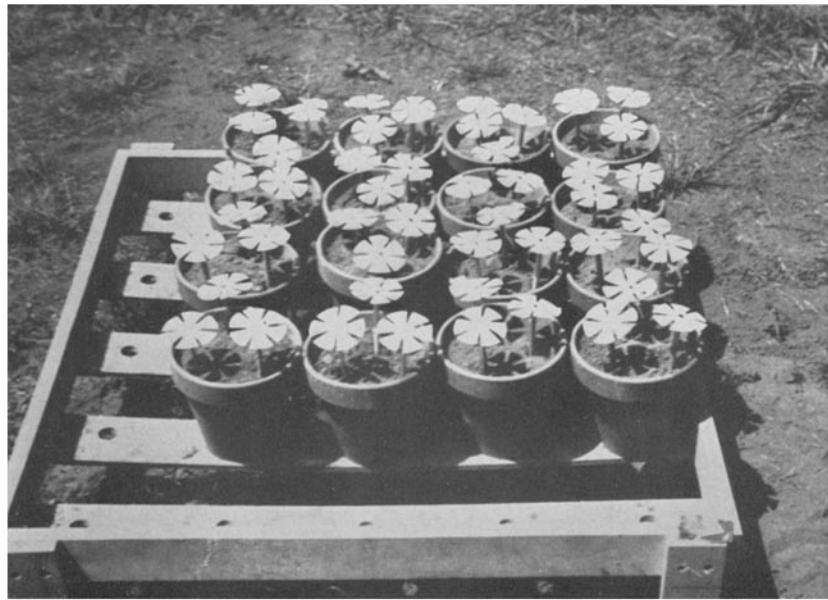


FIG. 2. Artificial flowers arranged in flower pots. Each pot can be rotated to increase the flicker effect produced by the flowers.

arrangement by covering the whole bed with a glass plate on which the bees are fed. This arrangement has great advantages since the glass plate can be washed before test so that all traces of odors which might cause reactions are removed, and the food can be spread over the whole surface of the glass plate so as to avoid conditioning to a certain place. Then under these conditions, after removing the food and cleaning the covering glass plate, one of the flower pots is rotated. A slight reaction to the rotating section can be observed, but it is not as clear as in the previous case. It seemed that the reflection of light from the glass greatly disturbed the bees and that possibly the distance of the flowers from the bee's eye reduced the visibility to a degree which interfered with a proper reaction.

In another test we employed artificial flowers instead of the small white blossoms of *Phlox*. The flowers were cut out of white cardboard 7 cm. in diameter and with 6 flower leaves, leaving spaces of about 8 mm. between them at the margin. These artificial flowers were fixed on top of thin wooden sticks and 3 of them were placed in each of 16 flower pots. The whole arrangement was covered with a glass plate on which the bees were fed. One of the pots can be rotated. During test, when the food is removed and a section of 3 blossoms is in motion, the bees during their search for food react to the motion, but again the precision of the reaction is not very great. Much better results are obtained if during test

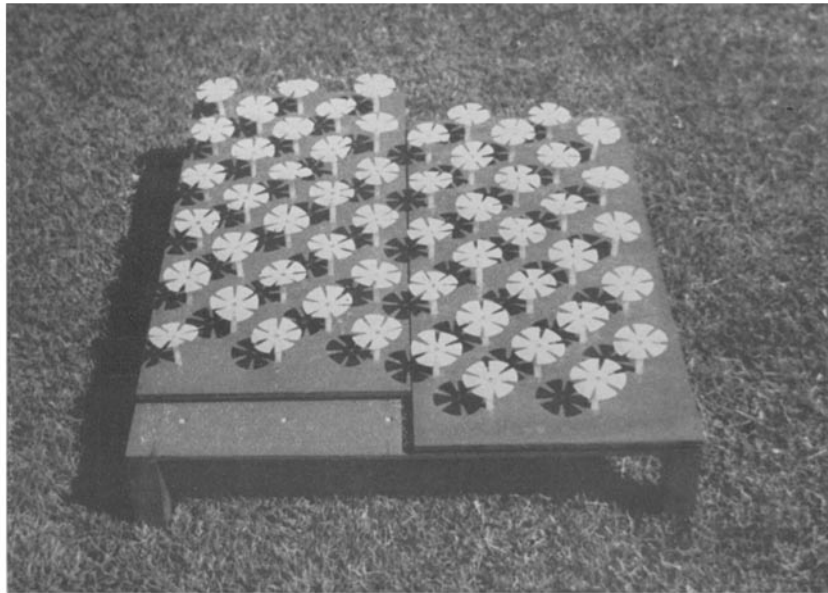


FIG. 3. Artificial flower bed on which bees are fed. One half can be moved back and forth. By the increase in flicker produced by the motion the number of bees visiting the moving section is increased.

the glass plate is removed. The bees then follow the rotation in a cloud, and occasionally settle down. The reaction in general is clearer than with the *Phlox*, but is not yet satisfactory. It seemed that for clear results a close association between flowers and food was desirable.

In a further experiment we made use of an artificial flower bed 1 x 1 meter in size, on which there were placed 10 rows of artificial flowers evenly spaced. The flower bed is divided into two halves, one of which rests on rails so that it can be moved forward and backward over a length of 20 cm. The speed of movement is such that a forward motion takes 1 second, then the section stays quiet for

1 second, then the backward motion takes 1 second again. The flowers on the bed consist of glass tubes 6 cm. high, 8 mm. in diameter, around the upper end of which the flower leaves (7 cm. in diameter) are fitted. The flowers are set into holes in the base of the bed so that they stay rigid during the motion. Each tube is filled two thirds full with paraffin so as to prevent the collecting bees from creeping too deeply into the tubes. For conditioning the bees all the flowers are filled with a sugar solution. The bees which come to the bed spread rather evenly over the whole surface of the bed and take the sugar solution. The bees show a tendency to cross over the field in a certain direction, which is due to the location of the hive and the easiest way of access to the feeding place. If,

TABLE I

Data on the visits of bees in a 5 minute period to a flower bed consisting of two sections, one of which stays quiet (*q*) while the other is moving (*m*). In the top row the relative positions of the quiet and the moving sections are shown. The arrow indicates the direction in which the bees from the hive approach the artificial flower bed.

| No. of test | | | | | | | | |
|-------------|----------|----------|----------|----------|----------|----------|----------|----------|
| | <i>m</i> | <i>q</i> | <i>m</i> | <i>q</i> | <i>m</i> | <i>q</i> | <i>m</i> | <i>q</i> |
| 1 | 129 | 80 | 123 | 73 | 130 | 73 | 110 | 77 |
| 2 | 142 | 67 | 119 | 69 | 106 | 69 | 107 | 67 |
| 3 | 160 | 89 | 173 | 87 | 194 | 81 | 175 | 89 |
| 4 | 158 | 102 | 139 | 84 | 133 | 60 | 160 | 86 |
| 5 | 164 | 97 | 189 | 83 | 168 | 98 | 176 | 97 |
| Total . . . | 753 | 435 | 743 | 396 | 731 | 381 | 728 | 416 |
| Mean . . . | 151 | 87 | 149 | 79 | 146 | 76 | 146 | 83 |
| Ratio . . . | 1.7:1 | | 1.9:1 | | 1.9:1 | | 1.8:1 | |

however, one of the flowers is occupied by one or two bees, the newcomer goes on searching until it finds a proper place for feeding. The evenness of the distribution permits a quantitative study of the bees collecting if one section of the flower bed is moved.

For test we filled all tubes up to the margin with sugar solution. During this process the bees are kept away from the flowers. We then set one half of the bed into constant motion for 5 minutes. During that time the bees settling on either half are counted, one observer watching the moving section, the other the quiet one. Since we observed that there was a certain direction in which the bees crossed the field, for each new test we turned our arrangement through 90°, so

that the bees would meet the quiet and moving parts at different angles. By going through the whole cycle five times a picture of the bee's reactions can be given (Table I).

The data show that without doubt the number of bees is greater on the moving half of the flower bed compared with the quiet half. The ratios are almost 2:1. One might expect that the frequency of visits to the moving section should even be higher, on account of the flicker effect. If we consider, however, that the moving section as a whole is shifted and thus the distance between the flowers stays the same, the flicker effect is not very great. One should expect a greater number of bees to collect on the moving flowers if one could introduce an irregularity of motion such that each row of flowers is moved independently. Since this procedure would involve great technical difficulties, we have to rely on the data as they are presented here. There is one striking fact, which permits the assumption that the relative shift of the flowers within a certain area of the field induces more bees to settle down. The two rows at the dividing line between the quiet and moving sections are more frequently visited than the rest of our arrangement, and the row on the moving and on the quiet part obtain about equal numbers of bees. Due to this fact a great many bees are counted in favor of the quiet section, even while their reaction has been induced by the shifting of the flowers, and thus the observed ratio of visits to the two halves of the field is not greater than 2:1.

With these results it seems justifiable to assume that flicker plays a rôle in nature while bees are visiting flowers. With a reaction to flicker the finding of flowers by the bee can be understood easily, whereas the low visual acuity and intensity discrimination could not support an adequate interpretation (Wolf (1933, 1935)).

SUMMARY

Bees were conditioned to collect food on natural and artificial flower beds, parts of which could be set into rotation or side to side movement. Through the relative motion of the flowers the number of alternating stimuli upon the bee's eye is increased. Due to the fact that bees show a strong reaction to intermittent optical stimulation, the proportion of bees settling on the moving section of the flower bed is increased. It seems probable therefore that the visual reaction of bees to flowers in nature is largely due to the flicker effect produced through the motion of the bees relative to the flowers.

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