The Homing Instinct of the Honey Bee, *Apis mellifica*[1]

By

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(*With 1 Text-figure*)

Introduction

Despite the long history of investigation concerning the analysis of the homing instinct of the honey bee, the problem remains still largely wrapped by the cloud of mystery on account of the complexity of the phenomenon. A. Bethe (1898, 1902), who worked first in this field scientifically, came to the conclusion, that the homing bees find their way home, affected by an unknown force which leads the bees not to the hive itself but to the space where the hive is standing. On the other hand, K. v. Frisch (1913, 1920) who intended to investigate the sensation of the honey bee by means of the learning method, succeeded for the first time for the bees in making associate a certain definite colour or scent in the artificial feeding place with the food and therefore the bees came to be able to utilize those sensory materials as the sensory cue for finding food. In 1925 E. Wolf found otherwise that the optical marks in front of the hive or on the ground just before the entrance of the hive play an important role as sensory cues for the orientation of homing bees.

Though it has been confirmed from the results of these experimental investigations that the visual characters or the scent of the hive and most possibly of the surrounding landmarks, as cottages, trees etc, are working as the important sensory cues in the homing of the bees, there is a remarkable fact that if the hive is displaced to a short distance, for instance 20 cm, the bees just returned gradually form a dense crowd at the very position where the hive was formerly situated, regardless of the presence of the hive near by. This phenomenon occurs no matter how the hive is characterized pronouncedly. We must assume therefore other

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sorts of factors working more intensely in the orientation of the honey bee. Concerning those factors the experimental investigations were made by E. Wolf. (1925, 1927) and the results obtained are as follows: 1) The direction of the sunbeams can be utilized by the bees as a sensory cue, 2) the distance they have flown over can be in any way impressed in memory by bees, 3) by means of an unknown function of the antennae successive changes of the flying direction can be somehow recorded in memory.

Thus it has been gradually obvious that the homing instinct of the honey bee is not organized of a series of the simple reflexes, but it must be rather attributable to the result of the dynamic balance of powers in a field in which a large number of sensory cues are acting simultaneously on a single bee. Under such circumstances, it seems the most available for us to analyze the field, which acts to the homing bees following the "Gestalt" psychology. This is the first work to solve the orientation problem and concerns to the distance-limit of the orientation. The result of the experiments will be summarized in this paper.

Before going further we must express our warm thanks to Mr. Yoshiteru Nishida and also to Mr. Mosuke Tsuji for their kind assistances in the painful experiments.

1. The distance-limit of the orientation of the honey bee

The hives used in the experiments were placed in the courtyard of the Faculty of Science, Hokkaido University. The homing experiments were in most cases executed in the direction toward west or north, because close on the western and northern sides of the institute are situated farms and meadows, which are luxuriant with nectariferous plants. Thence, for the bees belonging to the experimental hives any point in the environs to the hives surely forms a "bekannter Weg". Prior to creeping into the entrance of the hives, the homing bees carrying honey and pollen were seized with a fine forceps by their thorax and marked on the back of their thorax with a paint dissolved in 50% alcohol, and were kept in a small box of wire-gauze (2.5cm × 3cm × 5cm) separately or 10–20 bees in a group in larger tin box (18cm × 1cm × 5cm) lined with wire-gauze on the upper surface. 30 bees thus prepared were carried by one of the investigators on foot or on bicycle to the position in due distance, while another investigator engaged in counting the return of marked bees before the entrance of the hive. The two investigators, one carrying the boxes containing bees and another observing marked bees at the hive, had each their stopwatch adjusted previously, and the carrier opens the boxes at a certain spot. The observer at the hive counted the marked individuals which had returned in the limited period of minutes and recorded the time of arrival of each marked individual. In this way we could obtain the time record of the homing of the bees from different distances and compared them. In each experiment the marked individuals so far returned were recaptured and destroyed in order to avoid confusion of marks in the later experiments. The colour of the marks on the bees and position of the colour-marks were changed so far possible in each experiment. Every experiment was executed in the wind of average velocity lower than 5m and at the temperature between 28°C-31°C; in the range of temperature the honey-bee is most active.

The results obtained in these experiments are shown in the table 1. We

Table 1

Date	Time	Weather	Direction & velocity of the wind	Direction & distance carried over	No. of carried individuals	No. of returned individuals	% of returned individuals	Time interval of observation	Time of the 1st arrival
VI. 20. 1943	12 : 25	cloudy	0	W 500m	30	9	30%	15′	2′30″
VI. 21. 1943	11 : 45	clear	—	,,	,,	13	40%	,,	2′40″
VI. 22. 1943	12 : 00	,,	0	,,	,,	14	47%	,,	1′50″
VI. 24. 1943	14 : 25	,,	—	,,	40	17	43%	30′	1′10″
VI. 25. 1943	10 : 10	,,	SW 2m	,,	30	29	97%	,,	1′20″
VI. 26. 1943	10 : 20	,,	E 4-5m	,,	,,	13	43%	,,	2′30″
VI. 28. 1943	11 : 05	cloudy	W 2m	,,	,,	21	70%	15′	1′50″
VI. 28. 1943	16 : 40	,,	,,	,,	,,	24	80%	30′	—
VII. 10. 1943	10 : 30	—	—	,,	,,	18	58%	,,	3′25″
VII. 13. 1943	10 : 50	cloudy	S 2m	N 1000m	30	24	80%	30′	2′55″
VIII. 21. 1945	14 : 00	clear	0	,,	34	21	62%	,,	5′25″
VIII. 23. 1945	10 : 00	,,	SE 0.7m	,,	,,	27	79%	,,	4′20″
VIII. 24. 1945	11 : 00	,,	SE 1.1m	,,	30	22	73%	,,	3′00″
VII. 19. 1943	11 : 00	clear	NE 2m	N 2000m	40	21	52%	60	6′30″
VII. 20. 1943	—	—	NE 1m	,,	,,	18	45%	,,	5′30″
VII. 24. 1943	10 : 40	cloudy	SE 4m	,,	,,	12	30%	,,	10′08″
IX. 10. 1943	—	—	—	,,	30	15	50%	30	3′00″
VIII. 5. 1943	—	cloudy	0	W 3000m	50	3	6%	60	12′35″
VIII. 21. 1945	—	clear	0	N 4000m	88	3	3%	60	44′10″
control (1000m)				N 1000m	34	21	62%	30	5′25″
VIII. 23. 1945	—	clear	SE 0.7m	N 5000m	85	3	4%	90	53′00″
control (1000m)				N 1000m	34	27	79%	30	4′20″
VIII. 24. 1945	11 : 00	clear	SE 1.1m	N 6000m	90	7	8%	150	38′05″
,,	,,	,,	,,	N 7000m	,,	4	4%	,,	44′35″
,,	,,	,,	,,	N 8000m	,,	0	0%	,,	
control for last 3 experiments (1000m)				N 1000m	30	22	73%	30	3′00″

In the experiments, longer than 4000 m, the control experiment of 1000 m was simultaneously carried on with individuals belonging to the experimental hive. The results of the control experiments are not different from the normal data of 1000 m.

can see in the table 1 that the percentage of the returned individuals to the whole number of the individuals used in the experiment falls discontinuously at the distance of 3000m, and the length of the time elapsed in the homing increases abruptly at the same distance. From this point the decrease of individuals and prolongation of time show rather gradual change up to 7000m but at the distance of 8000m the percentage of the returned bees drops finally to zero.

From these results, however, it cannot be easily concluded that the distance-limit by the orientation sense of the honey bees is 7000m and does not exceed over 8000m. In fact, the discontinuous decrease of percentage of the returned bees and the abrupt delayed returning from the spot at the distance of 3000m seem to be due to the fact that the honey bees can fly over only the distance of 3000m by a flight without a rest, and they must rest several times in order to fly over the distance of 7000m. Indeed it was observed in the case of 8000m experiment that the bees after liberation from the confinement flied away directly following the direction towards the hive and they never returned to the box as in the "Schachtel Experiment" by A. Bethe and E. Wolf. It is surmised that the bees maintained to orientate towards the hive, when liberated at the distance of 8000m, but they could not reach the goal probably on account of deficiency of the glucose in the body or some other accidents. Judging from the facts just considered, it seems rather proper to conclude that the honey bees maintain their orientating flies at least as far as their wings can carry the body.

2. The homing to displaced hives

It is well known that, when the hive, after having been placed at a certain spot for the due length of time, is displaced to a short distance, the homing bees come back to the very original spot where the hive was situated and usually make a swarm there. Under the similar circumstances, however, when the hive is displaced to a much longer distance, for instance over 3km, the bees do not come back to the original spot of the hive. In this case the bees which crept out the hive do not fly far away but fly about in a peculiar way ; they fly over the hive, drawing the pendulating lines as if they examine the new environmental conditions of the hive for 30-60 minutes and then creep into the hive again. The peculiar flight is the so-called "orientation flight" and by this flight the bees presumably acquire the orientation to the new situation of their hive rather in short time. It cannot be determined, however, whether the bees can acquire the perfect orientation to the new situation by only an orientation flight or they become to be furnished gradually by accumulated experiences of flight over surrounding vicinities for some time. At any rate, the bees which have finished the orientation flight can return to their hive even though they may be liberated from the spot where they have never been acquainted with before.

In this experiment a hive had been remained to place in a spot for the due long time and then it was displaced to a new spot more than 3km apart from the previous one. Prior to the displacement, the entrance of the hive was closed in the evening after all the working bees returned. In the morning the entrance of the hive thus brought to the new spot was opened. The bees flied out of their hive and displayed the typical orientation flight above the hive. After the flight they once entered to the hive and having took up a small quantity of the preserved honey, then started for the first flight for ingathering. Immediately after the first coming back of an individual bearing the pollen ball on its hind limbs, 60 homing bees were obtained at the entrance of the hive. The honey bees belonging to the series (a) of the following experiment were caught, when they just returned after the completion of the orientation flight. Thence, they had no experience of ingathering. These bees were always divided into 3 groups, each composed of 20 individuals, separately in 3 closed boxes, A, B and C. The boxes A, B and C were then carried to the spots at the distances of 2000m, 1000m and 500 m respectively and were opened simultaneously at each spot, whereas an observer remained at the hive counted the number of the homing bees from the 3 different distances. The similar experiments were repeated over again with various interval of time, until the flying out of the bees was ceased in the evening. On the next morning the similar experiments were again commenced at 10 o'clock and carried out in the same manner until the evening. The results obtained in these experiments are given in tables 2(a–c).

Judging from the table 2, we can see that the orientation of the honey bee to the new situation of the hive has been established soon after the accomplishment of the orientation flight, without accumulated experiences of flying over the environments of the hive. As is shown in the experiment (a) the bees which had been captured immediately after the orientation flight were capable of homing from the point of 2000m apart, where surely they have never flown over. But it must be noted in this case, that in the experiment (a) the homing is generally delayed and the percentage of returned individuals is exceedingly lower than in the normal case as is illustrated in the table. According to the table 2 the delay of the homing and the lowering of the percentage of homing individuals become in general gradually improved with the lapse of time by the repetition of ingathering and finally nearly

Table 2 (a) (60 minutes after the exposure of the entrance of the hive.)

Date	Time	Weather	Temperature	Direction & velocity of the wind	Direction & distance carried over	No. of carried individuals	No. of returned individuals	% of returned individuals	Time of the 1st arrival
VII. 28. 1944	11 : 05	clear	29°C	SE 3m	S 500m	20	5	20%	4′18″
,,	,,	,,	,,	,,	S 1000m	,,	3	15%	9′50″
,,	,,	,,	,,	,,	S 2000m	,,	3	15%	6′40″

Table 2 (b) (3 hours after the exposure of the entrance of the hive.)

Date	Time	Weather	Temperature	Direction & velocity of the wind	Direction & distance carried over	No. of carried individuals	No. of returned individuals	% of returned individuals	Time of the 1st arrival
VII. 28. 1944	13 : 05	clear	29°C	SE 3m	S 500m	20	8	40%	6′35″
,,	,,	,,	,,	,,	S 1000m	,,	5	25%	10′20″
,,	,,	,,	,,	,,	S 2000m	,,	1	5%	14′55″

Table 2 (c) (5 hours after the exposure of the entrance of the hive.)

Date	Time	Weather	Temperature	Direction & velocity of the wind	Direction & distance carried over	No. of carried individuals	No. of returned individuals	% of returned individvals	Time of the 1st arrival
VII. 28. 1944	14 : 55	clear	29°C	SE 3m	S 500m	20	10	50%	2′30″
,,	,,	,,	,,	,,	S 1000m	,,	3	15%	11′20″
,,	,,	,,	,,	,,	S 2000m	,,	4	20%	6′20″

Table 2 (d) (24 hours after the exposure of the entrance of the hive).

Date	Time	Weather	Temperature	Direction & velocity of the wind	Direction & distance carried over	No. of carried individuals	No. of returned individuals	% of returned individuals	Time of the 1st orrival
VII. 29. 1944	10 : 30	clear	29°C	0	S 500m	20	19	95%	4′55″
,,	,,	,,	,,	,,	S 1000m	,,	12	60%	8′40″
,,	,,	,,	,,	,,	S 2000m	,,	4	20%	14′37″

Table 2 (e) (28 hours after the exposure of the entrance of the hive.)

Date	Time	Weather	Temperature	Direction & velocity of the wind	Direction & distance carried over	No. of carried individuals	No. of returned individuals	% of returned individuals	Time of the 1st arrival
VII. 29. 1944	14 : 18	clear	29°C	0	S 500m	20	17	85%	2′30″
,,	,,	,,	,,	,,	S 1000m	,,	15	75%	2′50″
,,	,,	,,	,,	,,	S 2000m	,,	7	35%	2′30″

time interval of observation =30′

arrived at the control (normal) data as in the experiment (e) which was performed 28 hours after the opening of the hive.

Inferring from the results above given, it is ascertained that the orientation of the honey bees to the new situation has been established soon after the accomplishment of the orientation flight, and the facilities of the homing increase thereafter gradually along with the accumulation of the experience of flying out, probably due to the increase of the sensory cues.

Furthermore to ascertain the fact in this respect the following experiments were performed. Immediately after exposure of the entrance of the hive which was brought in a new district to the inhabitants, 60 individuals, which had just accomplished the orientation flight, were captured at the entrance of the hive, and were divided into two groups, each composed of 30 bees and differently marked respectively. The group R, one of the 2 was kept in a box and carried over 1 km at distance, whereas the group W also kept in another box was remained there intact. The carried box R alone was opened, and in the usual way the data were taken, but in this case the returned individuals of the group were all recaptured and were again locked in the box. The individuals thus recaptured of the group R were again carried over 1 km apart as before. Besides the group R the box of the group W was also carried to the same point. These two boxes, R and W, were opened simultaneously and the data obtained from two different groups, one once flied over the course and the other quite unfamiliar to the course, were compared. The results are given in the table 3 (a) and (b). The table 3(b) shows the fact that the individuals belonging to the group R are superior undoubtedly to those belonging to group W both in the homing percentage and in time of homing. The percentage of returned individuals and the time of the first arrival of the group R are 60%

Table 3 (a) (R group, immediately after being captured).

Date	Time	Weather	Temperature	Direction & velocity of the wind	Direction & distance carried over	No. of carried individvals	No. of returned individuals	% of returned individuals	Time of the 1st arrival
VIII. 27. 1944	10 : 17	clear	24°C	E 2.4m	N 1000m	60	10	17%	11′55″

Table 3 (b)

Order of arrival	Mark	Time	Order of arrival	Mark	Time	Order of arrival	Mark	Time
1	R	4′30″	6	W	18′55″	11	W	36′05″
2	R	8′00″	7	W	19′45″	12	R	39′05″
3	R	8′25″	8	R	24′25″	13	R	39′05″
4	R	15′40″	9	W	28′05″			
5	R	17′50″	10	R	34′00″			

and 4′30″ respectively, whereas those of the group W indicate 13% and 18′55″.

The result shown by the group W seems to correspond to that of the group R in the experiment (a) in the table 3. There is no room for doubt from these results that the homing capacity of the honey bee in a certain course increases in its steadiness along with repetition of flying through that course.

3. The influence of meteorological and topographical conditions on the homing of the honey bees

The homing of the honey bees is remarkably affected by temperature and wind, obviously as the result of impaired flying. For instance, it was observed that the honey bees failed the homing even from a point 300 m of distance at the temperature below 20°C, though successful from a point of 100 m. While at the temperature above 23°C the homing was always normal, regardless to the direction of wind, in case the averaged velocity of wind was not higher than 5 m. The geographical conditions must be also taken into consideration for the homing. For the experiment the environs of Sekigahara, Gifu Pref., was chosen, because the landscape is equipped with several topographical conditions. From the result of the experiment carried on in April and May, 1944, it can be concluded that the delay of time always occurs, when a hill rather high stands on the way of the course of the homing. The topographical influence is particularly remarkable

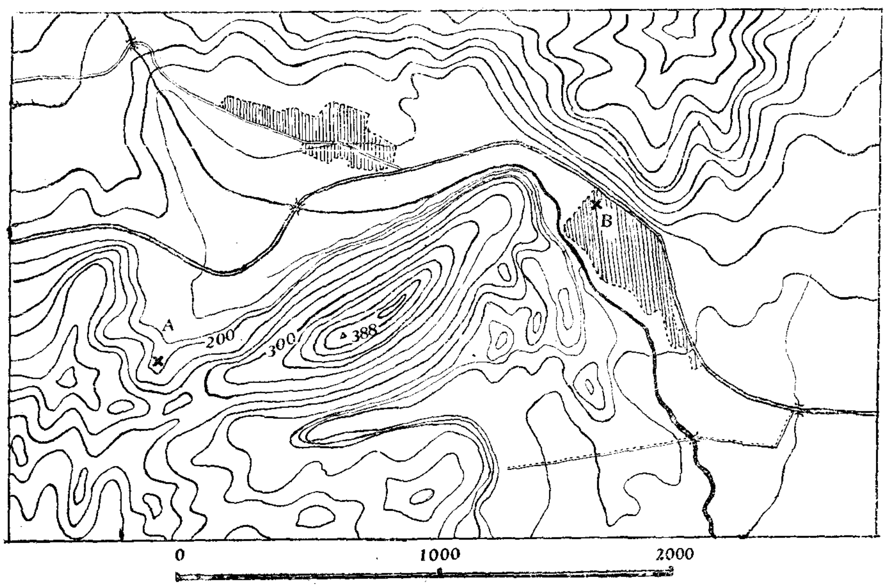

Fig. 1.

when the hive is newly displaced to a new spot. For instance, the following result was obtained in an experiment executed on May 2, 1944, at Sekigahara. The hive was located at the base of a mountain, approximately 200 m high. Some of the honey bees in the hive were carried to the spot A in a dale. The lineal distance between A and the hive B is 2000 m, and on the way between two points there stands a mountain, 388 m high. The results of the experiment were shown in the table 4. The percentage of the returned bees in 30 minutes were 17%, and the time

Table 4

Date	Time	Weather	Temperature	Direction & velocity of the wind	Direction & distance carried over	No. of carried individuals	No. of returned individuals	% of returned individuals	Time of the 1st arrival
V. 2. 1944	13 : 00	clear	23°C	0	W 2000m	30	7	29%	16′30″

time interval of observation =60′

spent in the first arrival was 16′30″. This experiment was made 28 hours after the opening of the entrance of the hive newly situated. Therefore the data of the experiment correspond just to those in the experiment (e) of 2000 m distance in the table 2, in which the percentage of the returned bees was 35% and the time of the first arrival was 2′30″. Judging from the differences lying in these two corresponding data, it can be concluded that in the latter experiment the homing was apparently disturbed by the existence of the mountain. Such a disturbance of the homing behavior did not possibly occur in experiments in which the bees were started from a thick forest. In this case the bees flied at first directly upwards through the tangle of ramifications, presumably searching after light, until they reached the top of the forest, then they possibly flew, inferring from the time record of their homing, straight on to the hive. As is above described the topographical conditions sometimes disturb the homing of the honey bees.

4. The limit of the time interval, so far as the orientation to the original hive is retained

How long the orientation to the original hive shall be retained by the honey bees which have been kept out of the hive ? To answer this question some honey bees just returned from ingathering were captured and were kept in captivity each in a small box of wire-gauze separately. These boxes containing food of enough quantity for the honey bee were kept in a dark chamber of 30°C. The isolated rearings were continued for 48 hours in a case and for 96 hours in another one respectively, but the further rearing was not successful, because the isolated bee-individuals could not be alive longer than 4 days, in spite of the careful treatments to keep the environmental conditions of the isolated bees similar to those of the hives as far as possible. The results of the experiments are summarized in the table 5. The orientation of the honey bee is undoubtedly retained still for 96 hours

Table 5

Hours kept isolated	Distance carried over	% of returned individuals	Time of the first arrival
48hrs	1000m	25%	5′30″
96hrs	500m	25%	3′30″

time interval of observation =30′

after the isolation. The low percentage of the individuals which could return does not indicate the fail of the orientation in this case, for the lowering of the percentage of returned bees is, in most probabilities, due to the decline in the energy of flying, owing to the isolated captivity from the colony for a long time. When the boxes were opened, most of the individuals fell on the ground and were unable to fly away. It is confirmed from the results that the honey bees retain their orientation at least as long as they are alive, after the isolation from their colony.

5. Summary

To investigate the limit of the homing instinct of the honey bees, the experiments were made and the following results were obtained.

1) The longest distance of the orientating flight of the honey bees recorded in the experiments was 7000 m, but they maintain the orientation to their hive at least as far as the wings allow them to fly over possibly without a rest.

2) The orientation to the new situation of the hive is established soon after the "orientation flight", but it increases its steadiness with the laspe of time, by the accumulation of experiences of flying over the surrounding ground.

3) Topographical conditions hindering the lineal flight of the bees along the line of orientation, disturb more or less the homing behavior.

4) The bees isolated from the colony retain their orientation to the original hive as long as they are alive.

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