A Study on the Utilization of Landmarks in Honey Bees

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Abstract-Using a digital quartz stopwatch and a transceiver system, we measured flight times of honey bees by getting 4 patterns in and out to a straight route of 80m set up between a hive and a feeding table.

When there were some changes in pattern arrangement, bees' behaviours were markedly disturbed, and they responded to it with lengthening or shortening their flight time than in control, i.e., normal arrangement of the patterns. From the degree of their disturbance, it was inferred that patterns at the foot of their hive and feeding table were both the most important cue for bees, and sometimes they neglect patterns placed between the two patterns just referred to. In normal arrangement of patterns, bees always took a longer time for outward flight rather than homeward one. This principle also, except by way of few exceptions, held for the cases in which pattern arrangement was modified.

When one pattern was removed, bees had much more time for outward flight than homeward one to examine the difference from normal arrangement of patterns.

Reversely, in mutual exchanges of 2 patterns, bees made much of homeward flight. Furthermore, when pattern arrangement was modified between outward and homeward paths, most of bees instantly reponded to the change. From this it was concluded that bees, taking a flight, constantly check whether the current path is appropriate or not, based on the memories of landmarks which were gotten during their flight made just before.

Honey bees use a celestial compass, the sun, and various landmarks like forests, bushes, houses, iron fences and so forth, as guideposts to indicate the route to their hive and food sources (Otto, 1959). For them, not only large, well-ordered structures but a trifling wooden paling that we pay no attention to, has eventually a decisive importance (Frisch, 1967). Thus honey bees choose adequate cues out of various objects in their environments and make the best use of it. But little has been known about the mode of utilization of guideposts. The purpose of this study, by getting definite patterns in and out to their route, is to investigate the biological meaning of the patterns, namely the perception structure for the flight route in honey bees.

Experimental place

We chose a concrete rooftop of our four-story school buiding as the experimental place, because, as seen in Fig. 1, granting that some structures on the rooftop became landmarks for bees, that seemed very few. Here conspicuous structures are exhausts (1.3m high, 1.3m wide, 1.2m high), a shed (3m long, 5m wide, 3m high) and a lift room (8m long, 8.8m wide, 4.5m high). The circumference of the rooftop is surrounded with a concrete outer wall (1.2m high), and here we could set up a straight route of about 80m, which has a wide field of vision from the observation hive to the feeding table.

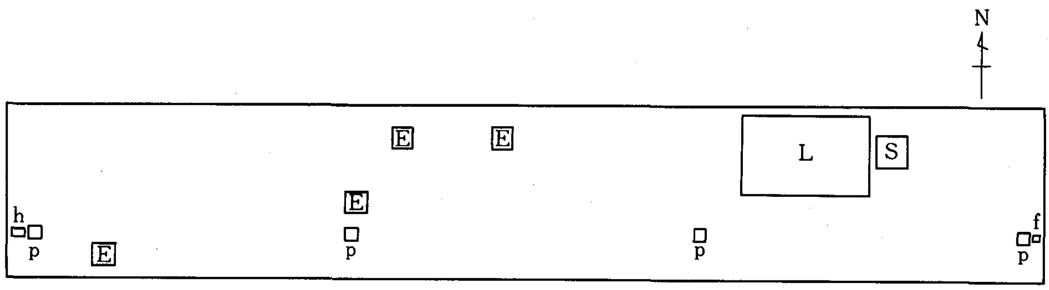

Fig. 1　A sketch of the experimental place.
L, lift room; S, shed; E, exhaust; h, observation hive;
f, feeding table; p, pattern.

Material and methods

In this experiment, we used a small observation hive (56.7cm long, 35.6cm high, 17.3cm thick), which can accomodate a single honeybee-comb of a standard size (34.5cm long, 23.5cm high). We introduced a colony consisting of a queen and about 1500 workers of the Italian honey bee, *Apis mellifera ligustica* Spinola, which has been maintained in our laboratory since 1978, into the above hive together with a single comb.

The hive, 5 days before starting experiments, was placed on a table (60cm long, 30cm wide, 75cm high) at the fixed point close to the west end of the rooftop (Fig. 1), and it was kept in darkness by applying wooden covers to glass windows on both the sides when not under observation. A corrugated cardboard box with outer covering of vinyl was further served, by cloaking the whole of the hive except an entrance, to protect it from rain and cold temperature at night. A round table (diam. 100cm, 75cm high) for feeding bees was placed near the east end of the rooftop, and bees were given a 60% sugar solution at the center of the table, which is in a straight line 80m distant from the hive entrance.

Four big patterns (90×90cm) were used as landmarks for bees (Fig. 2). b-Pattern consists of a checker of black and white quardrates (15×15cm). At the center of the checker, a yellow star (diam. 26cm) and a blue one were each placed in a-pattern and in d-pattern. c-Pattern has a yellow quardrate (55×55cm) fringed with 4 stripes (3-6cm wide) of blue, yellow and green colours at the center of the black and white checker.

Among these 4 patterns, a- and d-pattern were each placed at the foot of the observation hive and of the feeding table. The rest, b- and c-pattern were alphabetically arranged with interval of 26m between the above two patterns.

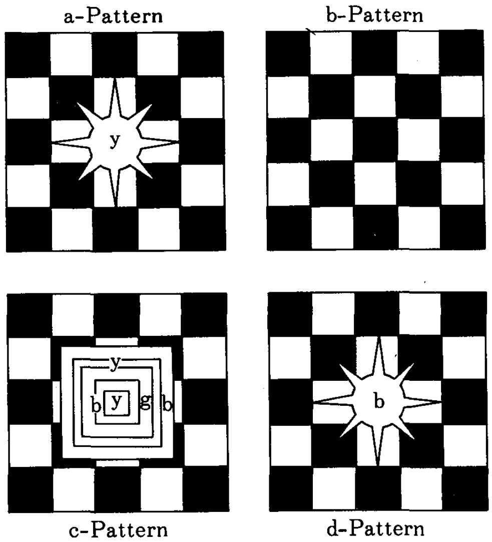

Fig. 2 Patterns used in the experiment.
y in a-pattern and b in d-pattern indicate yellow star and blue one respectively. b,g,y and b in c-pattern show blue, green, yellow and blue stripes in order from a central yellow quardrate to the outside.

General procedure

Firstly, we trained bees to come from the observation hive to the feeding table with the procedure described in detail in the previous paper (Suzuki et al., 1984), and numbered with coloured lacqueres on the thorax of bees taking food.

At least, three of us were needed for conducting the experiments: one, at the side of the hive, for recording bees'behaviours and keeping in wireless contact with the goal side; the other one, at the goal, for observing bees' behaviours and the last one, midway to the goal, for getting patterns in and out to the straight route by wireless contact from both the sides. Using a digital quartz stopwatch with scale division of 0.01 sec. (SEIKO, SO23), we measured the time spent by bees on outward flight to the goal and homeward flight from there. At the moment when a numbered bee took wing from the hive entrance, the observer on the hive side started the stopwatch, and told the bee's number to the observer on the goal side through a transceiver system (National, RJ-330). The arrival of the bee at a watch glass on the center of the feeding table was informed with the transceiver by return from the goal side; at the same time, the observer on the hive side read in the stopwatch a time taken for the flight to the goal, recording it. The same procedure was applied to the measurement of homeward flight time, too.

Prior to experiments, four patterns were alphabetically arranged in a straight line from the hive to the goal (normal arrangements), and flight times of individual bees which flied over the path were measured. When the variance in her flight times became very small by flying for a while, a bee was used for experiments, and her outward and homeward flight times were each measured 5-6 times (control experiments). Then we changed the arrangement of the patterns, and measured flight times of the bee responding to this change, 5-6 times on outward and homeward paths respectively.

Getting patterns in and out to the straight route is as follows: for instance, in the experiment that a pattern was removed from outward path and it was replaced to homeward one (Exp. 12), the observer on the intermedial zone, while the bee concerned was in the hive, removed a given pattern by wireless contact from the hive side, and after the bee arrived at the feeding table, while not taking wing from there, he put the pattern back by wireless connection from the table side.

In experiments of one group, 5 bees were used, and the result was expressed as a mean of their flight times. However, comparison of these flight times was made every individual bees: for instance, a difference between mean outward flight times of experimental and control cases was calculated in one and the same bee. Similarly, a difference in mean homeward flight times was also calculated in this bee. Then we tested with t-test the differences of outward flight time which were in this way gotten from 5 bees. The differences of homeward flight time was similarly dealt, too.

Before and after experiments, we recorded air temperature, relative humidity, direction of wind and its speed for 10 minutes on the hive side. Particularly, speed of wind has a great influence on bees' behaviours, so experiments were not carried out on the day that the mean speed was over 2m/sec on. Experiments were conducted from 26th October to 30th November, 1984.

Results

The results were shown in Table 1. When a-pattern was removed, bees took much more time for outward flight than in control (Exp. 1, $p < 0.05$), but no significant difference was found in return time between them ($P < 0.2$). Likewise, when b- and c-pattern were each removed, significant difference was found only in outward flight time between experimental bees and their controls (Exp. 2 & 3). d-Pattern being removed, however, a particularly notewothy result was obtained; it is that bees needed much more time for coming back from the feeding site than going there (Exp. 4). Throughout the present study, in all normal arrangement of patterns, outward flight was always needed a longer time than homeward flight. Therefore, the above result was very few exceptions together with the results of Experiments 5 and 6. Next, it is given that outward flight time of bees tended to be a little shortened than that of control, though there was no significant difference between them. And, on their way home, too, the bees spent a considerably longer time than

Table 1

Exp. No.	Arrangement of patterns	Flight	Repl.	Mean of exptl. group (sec.)	Mean of contr. group (sec.)	Diff.	t	P
1	H ⓐ b c d F	Outward	25	19.92	17.49	2.43	2.44	<0.05
		homeward	25	16.58	15.78	0.8	1.63	<0.2
2	H a ⓑ c d F	Outward	25	49.08	18.07	31.01	2.96	<0.02
		Homeward	25	20.42	17.08	3.33	1.23	<0.3
3	H a b ⓒ d F	Outward	29	28.57	21.72	6.85	3.29	<0.05
		Homeward	29	18.62	15.92	2.7	1.47	<0.1
4	H a b c ⓓ F	Outward	25	21.77	22.27	-0.49	0.14	<0.5
		Homeward	25	27.67	20.09	7.58	1.31	<0.3
5	H $\widehat{a\ b}$ c d F	Outward	25	19.12	19.63	-0.51	0.36	<0.5
		Homeward	24	19.39	16.45	2.94	2.39	<0.05
6	H a $\widehat{b\ c}$ d F	Outward	24	18.5	19.24	-0.74	1.42	<0.5
		Homeward	25	19.93	16.39	3.54	2.39	<0.05
7	H a b $\widehat{c\ d}$ F	Outward	24	21.97	19.65	2.32	1.37	<0.3
		Homeward	24	16.66	16.28	0.38	0.36	<0.5
8	H ⓐⓑⓒⓓ F	Outward	30	25.01	19.89	5.13	2.41	<0.05
		Homeward	30	19.69	17.43	2.25	4.17	<0.01
9	H ⓐⓑ c d F	Outward	25	18.46	19.06	-0.59	1.2	<0.3
		Homeward	25	14.25	12.97	1.28	1.41	<0.3
10	H a ⓑⓒ d F	Outward	24	17.65	16.27	1.38	1.39	<0.3
		Homeward	25	15.96	13.89	2.07	1.11	<0.4
11	H a b ⓒⓓ F	Outward	25	22.28	16.88	5.4	12.27	<0.005
		Homeward	25	11.57	14.07	-2.5	6.41	<0.005
12	H ⓐ b c d F	Outward	25	17.44	15.21	2.23	3.48	<0.05
	H a b c d F	Homeward	25	15.14	14.38	0.77	1.26	<0.3
13	H a b c d F	Outward	25	15.59	15.2	0.39	0.81	<0.5
	H ⓐ b c d F	Homeward	25	15.55	14.38	1.17	3.0	<0.05
14	H a ⓑⓒ d F	Outward	30	19.49	18.87	0.62	0.74	<0.5
	H a b c d F	Homeward	30	15.6	14.69	0.91	0.71	<0.5
15	H a b c d F	Outward	25	18.46	18.84	-0.38	0.18	<0.5
	H a ⓑⓒ d F	Homeward	25	18.26	14.42	3.84	2.64	<0.05
16	H a b c ⓓ F	Outward	25	23.21	15.34	7.87	3.67	<0.05
	H a b c d F	Homeward	25	16.71	13.7	3.01	1.52	<0.2
17	H a b c d F	Outward	25	15.31	15.46	-0.15	1.36	<0.3
	H a b c ⓓ F	Homeward	25	12.86	13.56	-0.71	1.73	<0.2

The pattern in a circle, and arrowed patterns indicate the pattern removed from the route in course of experiment, and exchange of arrangement order between these two patterns respectively. H and F each show the observation hive and the feeding table, namely the goal.

in control, but no significant difference was found between the time and its control(Exp. 4). This means that differences between individual bees were so big that statistical variance increased markedly.

When a- and b-pattern were mutually exchanged in arrangement order, homeward flight time was fairly lengthened than that of control, but in outward flight time, no significant difference was founed (Exp. 5). A similar result was gotten in the mutual exchange of b- and c-pattern (Exp. 6). However, when c- and d-pattern were exchanged each other, both outward and homeward flight times were not different from the respective controls (Exp. 7).

Two patterns like b- and c-pattern were removed together, flight times were not significantly different from those of control (Exp. 10). It was also the case with the removal a- and b-pattern (Exp. 9). But in this case, there was seen a tendency of bees to arrive at the feeding table faster than in control. Unexpected result was gotten in the simultaneous removal of two patterns, c- and d-pattern (Exp. 11). Bees arrived at the goal much later than in control ($P < 0.005$), and returned to their hive earlier than in control ($P < 0.005$). Thus in behaviours of the bees, there was seen as a big confusion as when all patterns were removed from their path.

When a-pattern close to the hive was removed from outward path and it was restored to homeward path, outward flight time was lengthened much more than in control (Exp. 12, $P < 0.05$), but return time was not significantly different from that of control ($P < 0.5$). Bees in this case quickly responded to the change of pattern arrangement. A similar result was obtained when pattern arrangement on outward path was in normal state and a-pattern was taken off from homeward path (Exp. 13). When d-pattern near the feeding table was removed from outward path, only flight over the path spent a longer time than in control (Exp. 16, $P < 0.05$). Result was somewhat different from the above result when the d-pattern was left intact on outward path and removed from homeward path; flight times of each path were shortened than in respectve controls, but the differences were not statistically significant (Exp. 17). Also in the case of removal of both b- and c-pattern from outward path and replacement of them to homeward path, flight times were not significantly different from those in normal arrangement of 4 patterns (Exp. 14). When these two patterns were removed from homeward path, however, bees coming home were strikingly disturbed, so that their flight time was considerably later than that of control (Exp. 15).

Discussion

When four patterns were all together removed, bees' behaviours were highly disturbed, and their outward and homeward flight times were each much later than those under the normal condition in which the bees had flied over an alphabetical arrangement of the patterns (Exp. 8). The result shows that the bees memorized the existence of 4 patterns in the control experiment performed just before, and checked the propriety of the current path with the memory. In this way, bees making a flight must constantly examine the way to food sources, baced upon their memories about landmarks of the path. According to

Cartwright and Collett (1982), such memories in bees are likely to be momentarily stored as a snapshot. Seeing from the results of the present study, it may be possible to support the snapshot theory. To cite an example, when two patterns like b- and c-pattern which existed on outward path, were removed from homeward path, bees were aware of the change on their return, and searched the path for the lost two patterns for a long time (Exp. 15). As a similar example, the result of Experiment 13 is given.

There have been much disputes in relation to the problem which of outward and homeward path bees attach great importance to (Frisch, 1967; Heran and Wanke, 1952; Shaposhnikova, 1958; Otto, 1959; Bräuninger, 1964). We got decisive experimental results suggesting that outward flight has great weight with bees; that is to say, in the normal arrangement of 4 patterns, bees, without an exception, took a lot of time for outward flight rather than homeward one. Furthermore, the tendency toward putting emphasis on the outward flight continued also in experiments that one pattern like a-, b-, and c-pattern was separately was absent on the path to the feeding table in (Exps. 1, 2, and 3).

When d-pattern near the goal was taken off, however, bees reponded with unexpected behaviours (Exp. 4); they spent much more time for homeward flight than for outward one ($P < 0.05$). As stated before, in the normal arrangement of 4 patterns, their homeward flight time never got later than outward flight. It will be, therefore, sure that most of bees found unusual indication on their return path with the disappearance of a cue for the feeding table.

When the order of neighbouring two patterns was exchanged like from a-b to b-a, bees took much time on their way home (Exps. 5 and 6). In this case, the bees tended to arrive at the goal earlier than in the normal arrangement of patterns. Perhaps this indicates that during outward flight, the bees noticed about a change on pattern arrangement to some extent, and they examined the change throughly for a considerably long time on their return. c-Pattern being exchanged with d-pattern, both outward and homeward times were not significantly different from respective control times (Exp. 7). This seems to suggest that owing to equivalence of c- and d-pattern in degree of stimulation, bees in flight were fairly difficult to discrminate them.

When two patterns were removed together, there was found in bees' behaviours as a big variation as when 4 patterns were taken off all together; for instance, in removal of both c- and d-pattern (Exp. 11), bees came to the goal later than in the normal arrangement of patterns, and they returned much earlier to the hive. Thus in addition to the equivalent c-pattern, removal of d-pattern from the foot of the feeding table had a great influence on bees' behaviours. But when both a- and b- pattern were removed together, the influence on bees was not so big as in the simultaneous removal of c- and d-pattern (Exp. 9); outward flight time inclined to be a little shortened than in control. Judging from the result of separate removal of a- and b-pattern (Exps. 1 and 2), this seems strange because removal of only a-pattern had much bigger influence upon bees' behaviours than in the simultaneous removal of a- and b-pattern. The latter may be a turning point for bees to find out a new route, but that was not confirmed in the present study.

When b- and c-pattern were taken off together from the intermediate zone of a- and d-pattern, bees' behaviours were not different from those in control experiments (Exp. 10). This trend in bees was also seen when both the same b- and c-pattern were removed together from outward path and they were replaced again to homeward path (Exp. 14). The above two results show that bees sometimes neglect the patterns lying between a- and d-pattern. On the contrary, a- and d-pattern each placed at the foot of the hive and the goal, seem to have much more important meaning than b- and c-pattern as landmarks; removal of a-pattern from outward path brought the behaviour of bees going to the goal a great disturbance (Exp. 12). Also in removal of d-pattern from outward path, a similar result was gotten (Exp. 16).

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