

Naive Honey Bee Recruits to Foraging May Be Magnetotactic

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ABSTRACT

Evidence is presented that naive honey bees (*Apis mellifera*) on the threshold of becoming foragers, in a colony with active foraging and foraging cues, are magnetotactic when exposed to light.

Introduction

Honey bees (*Apis mellifera*) were first shown to be sensitive to the earth's magnetic field when Martin and Lindauer (1968)² demonstrated that "misdirections" (errors) in the accuracy of their in-hive dance language for communicating outside food source direction, described by Von Frisch (1967)³, are cancelled in a null magnetic field or one parallel to the direction of the food source.

Other evidence of field sensitivity has been found: Honey bees in a swarm tend to build new comb in the same compass orientation as that of the combs in their hive of origin⁴, and in the absence of all other cues are capable of setting diurnal rhythms according to daily fluctuations in the earth's magnetic field⁵. Also, magnetic field anomalies have been shown to elicit shock avoidance behavior⁶.

A direct role for the earth's magnetic field in honey bee navigation, either inside or outside of the hive, has not been demonstrated. Von Frisch⁷ in 1950 showed that honey bees in hives relocated to sites lacking useable land marks on cloudy days, when navigation by sun compass was improbable, were still able to locate feeding stations in the same compass direction to which they had been trained to fly in the original location. Dyer and Gould (1983)⁸ have speculated that honey bees in Von Frisch's experiment could have used the earth's magnetic field as a backup for navigation.

The general subject of magnetic sensitivity in honey bees has been reviewed by Gould (1980)⁹.

The present investigation of the factors by which honey bees navigate *inside the hive* was stimulated by some observations in previous studies on double-queening by the Consolidated Brood Nest plan^{10,11} which indicated the possibility of magnetic field navigation to exit the hive. When a queenright hive was moved and united in the top position over a queen excluder on a second queenright colony in the same apiary, the queen in the lower chamber was usually destroyed by the bees. Numerous beekeepers have reported that such a union, without an excluder and a new young queen in the top chamber for the purpose of requeening without dequeening, usually results in the elimination of the older queen below, as desired. The

popular explanation has been that the young queen survives combat with the older queen. But another explanation is required to account for loss of the lower queen in the double-queening attempts since it is protected by a queen excluder.

It was reasoned that the bees in the top chamber, alarmed by the intervention and finding no exit in the usual location to which they had previously become accustomed, hastily admixed with bees below and, in a defensive posture, killed the "strange" queen there. Support for this rationale came, in a sense, from subsequent reports on the use of the double queen Consolidated Brood Nest plan by others¹² in which the top queenright hive was transported from an apiary at a different location; then both queens survive. Such bees, disturbed by the rough handling, had predictably filled their honey sacs with honey which, in turn, cancelled aggressive behavior.

Hoping to avoid lower queen loss, the relocated queenright hives placed on top were given an exit (upper rear) in the same structural position on the hive body and in the same compass orientation as that at the previous location in-apiary, in keeping with this hypothesis. Then both queens survived.

To obtain some insight on whether retention of the former compass orientation was a contributing factor, the following experiment was conducted at that time, but not reported: The bottom board of a strong full sized (10 frame) Langstroth hive which had been on its stand with the entrance facing east for some time was exchanged for a bottom board with opposing entrances—the same east facing entrance and a similar west facing entrance. The bees continued to use the east facing entrance; only an occasional bee wandered out of the west facing exit, suggesting that light in itself was not sufficient to cause a change in entrance use. But when the hive body was switched 180° on this double entrance bottom board the bees exited full throttle in both directions returning only to the original east entrance. This behavior strongly suggested that a portion of these foraging bees were navigating to the hive exit by magnetic compass. The present investigation was initiated to study this finding further.

Materials and Methods

A glass observation hive with the capacity to hold two standard Langstroth brood frames, one over the other (Fig. 1), was mounted on a 360° rotating pedestal. Two entrances were provided at each end, one at the top and one at the bottom. Removable opaque side covers were provided to allow obser-

vation of movement inside the hive at any time or, as it turned out, to expose the bees to light as desired. The rotary observation hive was designed to accommodate double-queening studies along with those on the effects of the earth's magnetic field on in-hive navigation, sometimes simultaneously. Only the latter experiments are discussed here.

Frames with sealed brood and bees of all ages were used to stock the rotary observation hive and, after extant foragers had returned to the parent stand, given a queen or a mature queen cell. As the field force re-developed the bees were allowed to choose from the multiple exits. The rotary hive was maintained in a fixed north/south alignment (Fig. 1, configuration 1).

Once a pattern of exit and return was established, a series of calculated rotations were conducted, with and without exposure to light preceding the hive rotations, and the effects on exiting behavior were observed. The status of foraging and foraging cues was visually monitored.

Results

New foragers in the rotary observation hive immediately chose to use the upper north entrance exclusively over the other options, and continued to do so over time. Even the virgin queen was observed to exit from the upper north entrance for orientation and mating flights¹³. The north(A)/south(B) alignment was maintained throughout the entire experimental procedure (Fig. 2a) except for those brief periods when rotation studies were being conducted.

When the observation hive with side covers in place was rotated 180° at anytime after a flow of foragers had developed at the upper north entrance a portion of bees exited unhesitatingly from the upper south entrance, confirming the early observation in a full size Langstroth hive. All bees returned to the upper north entrance. This split of exiting bees between the north and south entrance following a switch of hive ends could be observed repeatedly during foraging hours over several weeks. Limited use of the upper south entrance developed when the hive is maintained in the N/S reference position for some time:

On one occasion when the side covers had been removed to see how travel patterns inside the hive before and after

rotation correspond with the switch in exit use, an unexpected phenomenon was observed. The bees began to mill around excitedly at the upper north end and to fly out, hovering at this location in a manner reminiscent of orientation flight by young bees. Then when the hive was again rotated 180° with the side covers still off, the bees which had been milling around the north entrance (I in Fig. 1 and A, Fig. 2a) at once promptly marched back in a stream next to the top of the upper frame to the true north location (II in Fig. 1 and B, Fig. 2b), and resumed the pattern of excited behavior there. Repeated 180° rotations in succession at this time elicited the same result irrespective of which end of the hive faced north (Fig. 2b). The procedure was repeated at different times on the next day (10:00 am, 1:00 pm and 5:00 pm) to determine whether the position of the sun was a factor. The streaming effect was the same at any time of day.

Attempts to elicit this remarkable streaming phenomenon again in the course of double-queening experiments failed for some time.

Retrospectively, it was postulated that in the earlier experiment the marching bees were those bees which had just reached the threshold of foraging activity; and that all of the cues which normally stimulate foraging and recruitment of foragers were present on that first occasion and not in follow-up experiments. Exposure to strong light, it was reasoned, was the precipitating cue to trigger attempts by these naive bees to exit from the hive. Overwhelmed by so much light, low level entrance light was cancelled as a navigational guide revealing that these naive bees were navigating by other means. Could they be magnetotactic?

In mid-June of 1990 the rotary observation hive was again stocked with frames of brood and bees as before and given a mature queen cell. Now the hive would be maintained well into a state of mature population dynamics; exposure to light and rotation would be conducted from time to time expecting that streaming might again be seen at a time when active foraging and foraging cues coincide with the appearance of a new population of young bees of foraging age.

After two weeks, June 29, when the new queen was first seen to be laying eggs and most of the original sealed brood

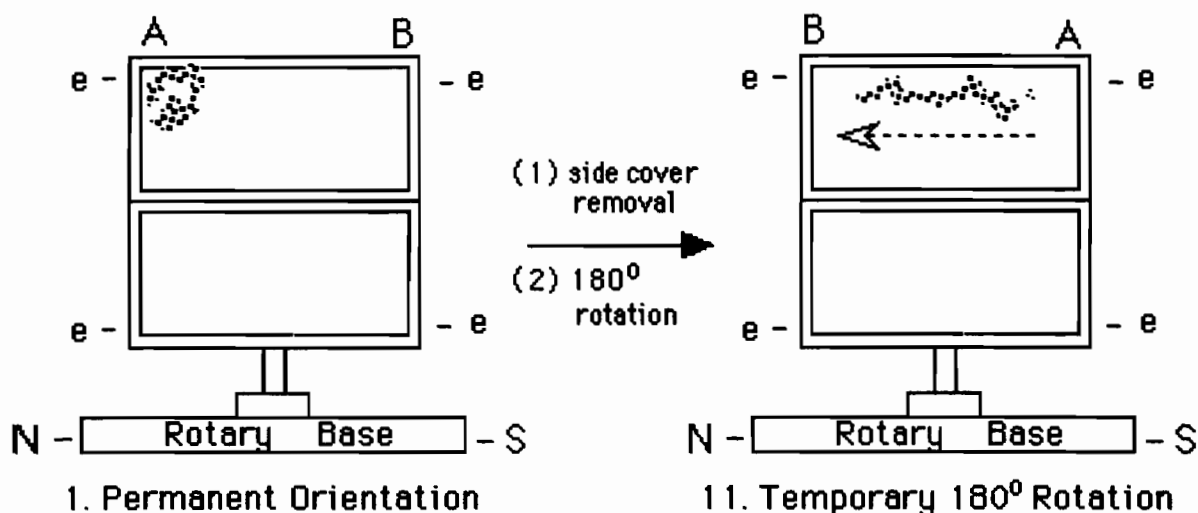


Fig. 1: Profile of rotary observation hive showing basic rotation scheme. Entrances are marked e.

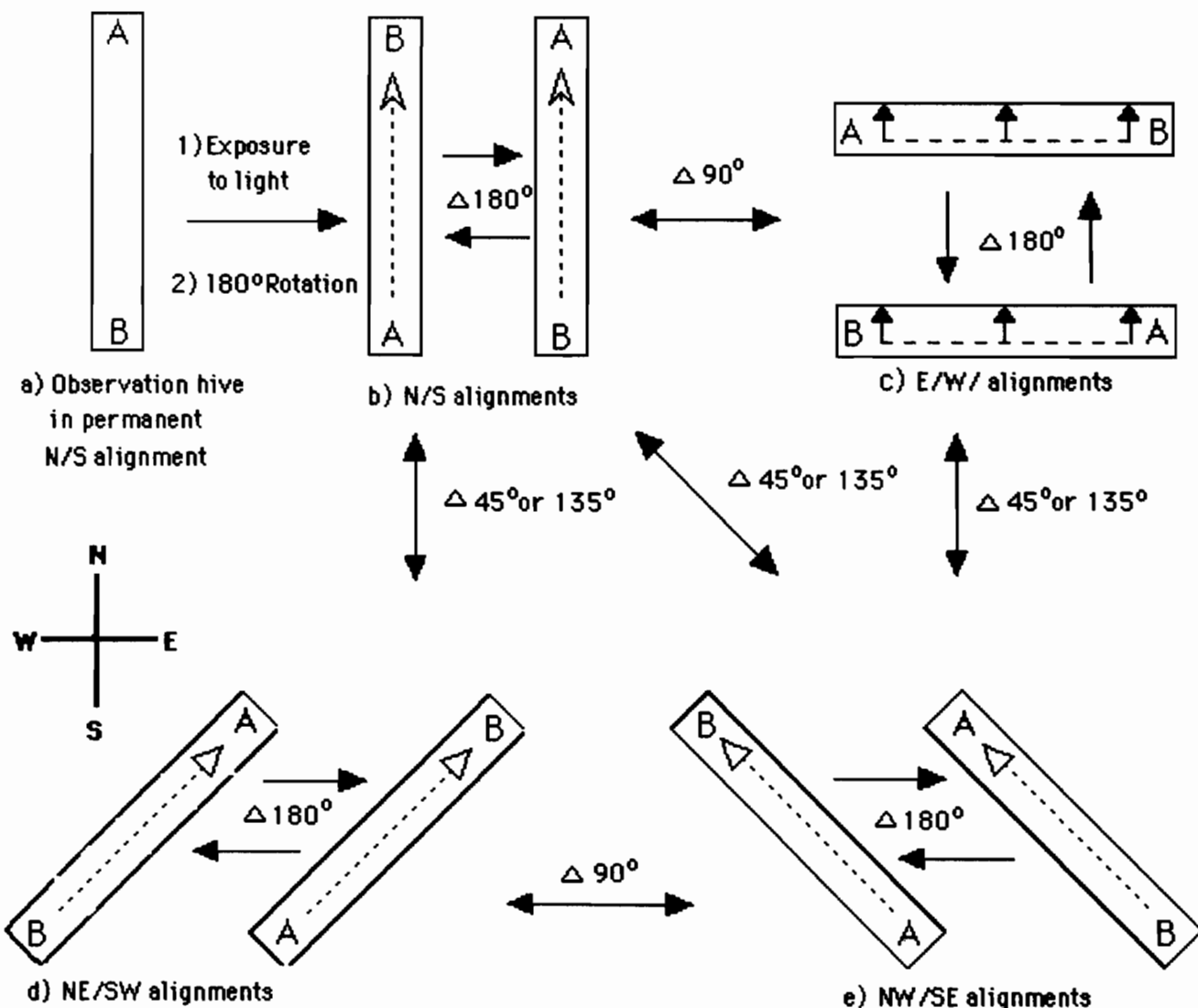
had hatched, the north bound streaming effect could not yet be elicited, although some bees were now foraging and using the upper north entrance exclusively. After 3 1/2 weeks (July 10) the brood frames were nearly solid with sealed brood from the new queen.

In 4 1/2 weeks (July 16), when the emergence of new bees from the new queen resumed, the hive was reinforced by the bees from a full frame of bees minus its field bees; these bees were added to restore somewhat the gap in age-continuity due to the hiatus in egg laying in those first 10-12 days required to establish the new queen.

One week later (July 23), when the main honey flow in this region was in full force, the northbound marching phenomenon could again be triggered by 180° rotation of the hive following exposure to light (Fig. 1). This could be repeated at any time during foraging hours, and continued on any day until near mid-August when the nectar flow subsided. The intensity of excitement and the number of bees marching, estimated

visually, differed from time to time. Northbound streaming was sometimes dramatic. Repeated 180° back-to-back rotations of the N/S aligned pair (Fig. 2b) from one to the other caused the bees to march back and forth as shown.

Variations in the rotation scheme were conducted. When the hive, after the light cue, was rotated just 90° (Fig. 2c) either to the east or the west, or rotated the usual 180° until the start of streaming and then back to 90°, in each case perpendicular to the north/south axis, the marching bees distributed themselves back and forth along the north facing glass surface in attempts to move northward. A 45° turn in either direction or rotation of the hive 180° and then back to 135° after the start of streaming, so that the hive is aligned 45° off from the north/south axis, either northwest or northeast, the bees streamed in each case (Figs. 2d & 2e) in the most northerly direction (northwest or northeast) just as though the glass were a barrier to be circumvented in order to go north. In either pair of positions aligned 45° from the permanent reference position



Figs. 2a-2e: Rotation scheme for the rotary observation hive (horizontal cross sections). The dotted arrows indicate the direction of streaming.

(Fig. 2a), either clockwise or counter clockwise, (Figs. 2d and 2e) repeated rotations between pair members also cause the marching bees to reverse their direction to maintain the same compass direction.

Discussion

That the streaming effect could not be induced in the short term after stocking the rotary hive was, according to the working hypothesis, to be expected; all of the foraging bees had returned to their parent stand and foraging and forager recruitment activity, nil at the outset, were recovering gradually; queen status had been reduced to a mature queen cell, resulting in a brood rearing hiatus, thus imposing a considerable reduction in those foraging cues associated with the presence of a mature laying queen and her unsealed brood.

It follows that when active foraging was restored, it was the naive forager recruits coming on stream at the time of light exposure which were the likely marching bees. These bees, having no foraging experience and having no specific guidance from the non-specific flood of light (the precipitating cue) navigated by the only means left to them. Being sensitive to the earth's magnetic field, they responded to an innate attraction to the north. The intensity of this streaming effect varied from day-to-day. This can be explained by the differences in the number of young bees which reached foraging age each day.

The results seem to rule out the possibility that pheromones of any kind, or acquired in-hive geographical familiarity, or previous compass orientation are providing the cue to guide the northbound marching bees. Northbound marching at any time of the day during active foraging hours rules out navigation by the sun compass. Full exposure to an indiscriminate flood of outside light by removing the side cover(s) cancels the possibility that entrance light is the in-hive navigational cue to the exit, even though such light is probably the normal navigation cue for first time flight. The possibility that the marching bees had already, prior to rotation, selected and learned the north exit over the south exit on the basis of small differential entrance light levels is unlikely since their choice of the north exit is *exclusive*.

Further, the entrance to the hive from which the bees were taken to stock the rotary hive was east facing with east/west aligned frames, so previously north-oriented bees could not have been brought along to "seed" the use of the north exit. Also, most of such field bees had returned to the parent stand.

The renewed population of experienced foragers which developed in the first days after setting up the rotary hive are not likely a portion of the marching bees later on, since streaming could not be induced for some time after foragers were coming and going freely. Also, recall that experienced foragers exit unhesitatingly and, unlike the marching bees, do not hover at the entrance.

In the case of the cover-protected rotary hive, it is likely that it was the experienced foragers which continued to exit in the same compass direction as the original exit, while those that switched compass direction must have been younger bees navigating by other in-hive cues.

For the marching bees, the only feasible navigational cue seems to be the earth's magnetic field; the instant reversal of streaming direction, repeatedly and always to the north in a succession of back-to-back 180° rotations in each of the axis pairs of Fig. 2 is in itself convincing evidence that the north magnetic pole is the factor to which light-stimulated naive bees respond in order to exit the hive. They must be magnetotactic.

The *exclusive* use of the north exit at the outset while the

hive is in its fixed position, given essentially equal light at all entrance choices, also supports the conclusion of light-cued magnetotaxis.

The conclusion that the marching bees are cued by magnetic field should be verifiable by the classical method used for proof of other in-hive utilizations of the earth's field, noted in the introduction, namely artificial field manipulation. Use of this technique is obviously not possible to verify the speculation of Dyer and Gould (1983) noted earlier that Von Frisch's bees navigating in the outside environment may have used the magnetic field as a backup navigational cue. However, such unequivocal proof of in-hive navigation by compass in the present instance would increase the odds that they are correct.

Unequivocal proof that honey bees use the north magnetic pole as a *fixed reference* for navigation would provide a valuable new dimension which could possibly be the missing link in explaining other well known navigational skills.

Since one caste of bees seems to be magnetotactic in the special circumstances described here, it can be deduced that other castes of bees, e.g. virgin queens and drones, may possess the same characteristic in other circumstances. The fact that a virgin queen was observed to elect the upper north entrance of the rotary hive on several orientation and mating flights may be of importance. Since worker bees are known to prod virgins toward the exit and to guide virgins to the exit by Nasanov gland pheromones, the significance of this observation is muted for now.

The case for a role of the earth's magnetic field in drone orientation and navigation is also still unclear. Drones older than six days have been shown to possess magnetite formations by Loper¹⁴. Loper suggests that magnetic sensitivity may be used by drones to locate mating congregation areas, presumably by detecting localized magnetic or electrical anomalies.

If both the virgin queen (a naive bee with respect to the external environment) and the naive drone prove to be magnetotactic in navigating inside the hive as are the naive workers, continuation of this preference for northbound flight outside the hive would have to be considered a possibility. This could be an important factor, along with terrain characteristics¹⁵, in directing their flight to common mating areas.

It is anticipated that the rotary observation hive procedures will prove to be a valuable model for determining whether virgin queens and/or immature drones also exhibit a similar magnetotactic behavior *inside the hive* at the time they normally begin orientation flights in search of mating congregation areas.

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