

Honeybees can learn the relationship between the solar ephemeris and a newly-experienced landscape

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Accepted 6 October 2008

SUMMARY

Many species learn the sun's daily pattern of azimuthal movement (the solar ephemeris function) for use in sun-compass orientation. In honeybees, this learning is accomplished with much innate guidance and yields stubborn, imprinting-like retention of certain aspects of the stored information. One such case involves the failure of transplanted bees to update their memories of the relationship between the solar ephemeris and a new landscape, even after many days' experience at the new site. In the present study, I ask whether the bees in previous transplantation experiments failed to update their memories of the relationship between the sun and landscape because the source and recipient landscapes were (rotated) panoramic twins of each other, each dominated by a conspicuous treeline. To test this hypothesis, I transplanted bees from their natal site at the bottom of a valley to a panoramically different, treelined site and later tested the bees' knowledge of the sun's course in relation to the treeline. The test involved observing the bees' communicative dances under overcast skies at a second treeline that was a mirror image of the first. The cloudy-day dances show that the bees had indeed learned the relationship between sun's pattern of movement and the (panoramically novel) treelined site, indicating that the bees' memory of the relationship between the ephemeris function and the landscape is not incapable of revision as the earlier results had suggested. I discuss these results in the context of a brief summary of our current understanding of solar ephemeris learning in bees.

Key words: honeybee, sun compass, landscape, learning, orientation.

INTRODUCTION

In order to use the sun and sun-linked patterns of skylight (Wehner and Rosset, 1985) as a compass, animals must know the time course of the sun's daily pattern of azimuthal movement (the solar ephemeris function). While some animals, for example sandhoppers, know the solar ephemeris function innately (reviewed by Scapini, 2006), most animals must learn it, as the sun's movements are different at different geographical locations and times of year. The process of learning the sun's course is best understood in desert ants (*Cataglyphis*), honeybees, and homing pigeons. In the latter, the fixed reference against which the sun's movements are learned appears to be earth's magnetic field (Wiltschko et al., 1983) (reviewed by Wiltschko and Wiltschko, 2003). In ants and bees, the fixed reference seems likely to be the landscape or skyline panorama around the nest (Dyer and Gould, 1981; Wehner and Lanfranconi, 1981; Dyer, 1987; Wehner, 1996; Towne and Moscrip, 2008), although other possible references have not been entirely ruled out (see Towne and Moscrip, 2008). All three animals can approximate parts of the sun's course that they have never seen [pigeons (Budzynski et al., 2000); ants (Wehner and Müller, 1993); honeybees (Dyer and Dickinson, 1994; Dyer and Dickinson, 1996)], indicating that the ephemeris is learned with much innate guidance. Thus, the learning mechanisms appear to be adaptively specialized and problem-specific (Gallistel, 2000; Gallistel, 2003).

Adaptively specialized, purpose-built learning mechanisms often entail sensitive periods – developmental windows of time during which the learning occurs best. Furthermore, the resultant memories are sometimes highly resistant to revision with further experience; in such cases, the sensitive periods are called critical periods (reviewed by Knudsen, 2004). Pigeons seem to have a sensitive

period for sun-compass learning: the relationship between the solar ephemeris function and geographic direction is learned best at a certain developmental age but the resultant memory can be revised with experience (Wiltschko et al., 1976; Wiltschko et al., 1984) (reviewed by Wiltschko and Wiltschko, 1998), although perhaps with a time lag (Schmidt-Koenig et al., 1991) (reviewed by Dyer, 1998). The possibility of a sensitive period in the sun-compass learning of ants and bees has not been studied in detail but in bees, at least, the solar ephemeris function seems to be acquired within several days of beginning flight (Lindauer, 1959) (reviewed on pp. 121–126 in Lindauer, 1971) and the ephemeris, once learned, appears to resist change. Lindauer (Lindauer, 1957), for example, transplanted bees from a tropical latitude where the sun, at the time, traveled counter-clockwise to a northern latitude where the sun travels clockwise, and his bees seemed unable to use the sun compass properly until weeks later, probably after the transplanted foragers had been replaced by younger bees. Based on these observations, Lindauer speculated that bees might 'become imprinted...with the direction of movement of the sun and its angular velocity across the sky' (p. 116 in Lindauer, 1971).

Lindauer's experiment suggests that bees may never update their memories of the shape of the solar ephemeris function. Other experiments show that bees sometimes also fail to update their memories of the relationship between the solar ephemeris function and the landscape: when bees are transplanted from their natal landscape to a panoramically similar one, the bees do not learn the new relationship between the sun and landscape – they retain only their memory from their natal site (Towne and Kirchner, 1998; Towne et al., 2005). Dyer and Gould first showed that bees learn the relationship between the solar ephemeris and the landscape by

transplanting bees from their natal site alongside a conspicuous treeline to a differently oriented treeline (Dyer and Gould, 1981; Dyer, 1987). Under overcast skies, these bees oriented their communicative dances as if they were still at their natal treeline; the bees were using a memory of the sun's compass bearing in relation to their natal treeline at that time of day. Furthermore, this memory appears to encompass the entire landscape panorama, not only the bees' familiar flight route along the treeline (Towne and Moscrip, 2008). Towne and colleagues (Towne and Kirchner, 1998; Towne et al., 2005) used a minor modification of Dyer's technique by allowing the transplanted bees to live and fly at the recipient treeline for days or weeks. Under sunny skies, these long-term transplantees saw the sun and danced normally, as did Dyer's bees. But under subsequent overcast skies, most of the transplanted bees oriented their dances as if they were still at their natal treeline, even after considerable experience at the new site. The bees had failed to learn the relationship between the solar ephemeris function and the new treeline. This was true even when the bees were put through a swarming process as they were transplanted, mimicking a natural process wherein bees transplant themselves (Towne et al., 2005).

The failure of transplanted bees to re-learn the relationship between the solar ephemeris function and the landscape is surprising, as bees initially learn this relationship quickly and well, and they attend carefully to both the sun and landscape routinely as they fly. This failure could represent a form of blocking in which a previously learned association prevents a new association from forming (Kamin, 1969; Cheng and Spetch, 2001). In the experiments by Towne et al. (Towne et al., 2005), the recipient landscape closely resembled the bees' natal landscape, and several features of the food source at the recipient site – the design of the feeder, the scent of the food, the landmarks *en route* to the feeder, the feeder's distance from the hive, the local landmarks at the feeder and the times of day at which food was available – were all familiar. Indeed, the only conspicuous difference between the two sites, at least in the vicinity of the hives, was the sun's position in relation to the treelines. Thus, the previously learned relationship between the flight route or food source and the landscape may have blocked the formation of a new association between the sun and the landscape. Alternatively, the bees may have failed to update their memories of the sun–landscape relationship at the new site because they imprint on the relationship and cannot revise the resultant memory.

Therefore, in the present study, I ask whether bees can ever update their memories of the relationship between the sun and landscape. Specifically, I transplanted bees from their natal landscape to a panoramically dissimilar site, allowed the bees to forage at an unfamiliar food source at this site and asked whether these bees would learn the relationship between the sun and the novel landscape. The bees' natal hive was at the bottom of a thinly wooded valley, and the hive that received the transplanted bees was located alongside a sloping treeline in an entirely different landscape. After foraging at the treelined site for several days, the bees were moved to a second, mirror-image treeline on overcast mornings. The dances of these twice-transplanted bees were expected to indicate whether the bees had learned the sun's pattern of movement in relation to the treeline to which they were first moved: if the bees had learned the relationship, then their dances in the mirror-image test landscape (under overcast skies) would be based on their memory of the solar ephemeris function in relation to the first treeline. But if the bees had not learned the relationship between the solar ephemeris function and the first treeline, their dances at the test treeline (again under overcast skies) should be disoriented, as the bees would have no information as to the sun's compass bearing.

MATERIALS AND METHODS

Bees, hives and feeders

The bees (*Apis mellifera ligustica* L.), hives, feeders and all other basic methods were as in Towne et al. (Towne et al., 2005) and Towne and Moscrip (Towne and Moscrip, 2008). Feeders were generally set up for one feeding period every day, typically about 08:00–10:00 h local solar time (LST). All experimental bees were individually marked at the feeders with numbered tags, and the identities of all marked bees were recorded at the feeders daily. Hives were put in place at least four weeks before the experiments began in order to ensure that all forager bees were indeed native to their respective sites.

The natal site and transplantation to the training treeline

The natal hive of the experimental bees was at the bottom of a thinly wooded valley (Fig. 1A), and the bees visited a feeder placed approximately 2 m from the hive entrance. Meanwhile, bees from a second hive located along a sloping treeline 2.2 km away from the first hive visited a feeder of their own placed along the treeline 190 m uphill to the south-southeast (Fig. 1B) (hereafter the 'training treeline'). The training treeline was panoramically unlike the valley site, and the feeders at the two sites were different in color, scent and local landmarks.

For transplantation, groups of approximately 20–50 bees that had been marked at the feeder at the valley site at least three days earlier were captured at the feeder and placed into one or two small wire cages (2.5×2.5×13 cm). The cages were then carried to the hive at the training treeline and placed inside on top of the upper frame. The cages remained in the hive until the following morning when they were opened to release the transplantees into the hive. This technique prevented most of the transplantees from being rejected by their new nest mates, and many of the transplantees became regular visitors to the feeder at the training treeline.

Transplantation to the test treeline

To determine whether or not the transplantees from the valley could learn the relationship between the sun's course and the training treeline, I allowed the valley natives to forage under sunny skies at the training treeline for at least three days. I then transplanted the entire hive to an oppositely oriented treeline (the 'test treeline') (Fig. 1C) on an overcast morning. The valley natives (now twice-transplanted) and several control bees native to the training treeline visited a feeder placed in its usual location relative to the treeline, although now in the opposite compass direction (Fig. 1C). The dances of the transplantees revealed whether or not the bees knew the sun's pattern of movement in relation to the training treeline (from which they had just been transplanted).

Recording and analysis of dances

The directions of the bees' dances under overcast skies at the test site were recorded on a small voice recorder by an observer at the hive, as in Towne and Moscrip (Towne and Moscrip, 2008). Each measurement was based on the visual average of at least five wagging runs, and each bee was scored only once for each round trip to the feeder. Dance directions were analyzed for clustering around predicted directions using the V-test (Batschelet, 1981). Because repeated dances by a single bee are not independent of each other, I used the overall mean direction for each bee as a single observation for the statistical analyses, regardless of how many dances each bee performed. Furthermore, the statistical analyses included only well oriented dances that occurred before the sun or blue sky first appeared; bimodal and disoriented dances (see

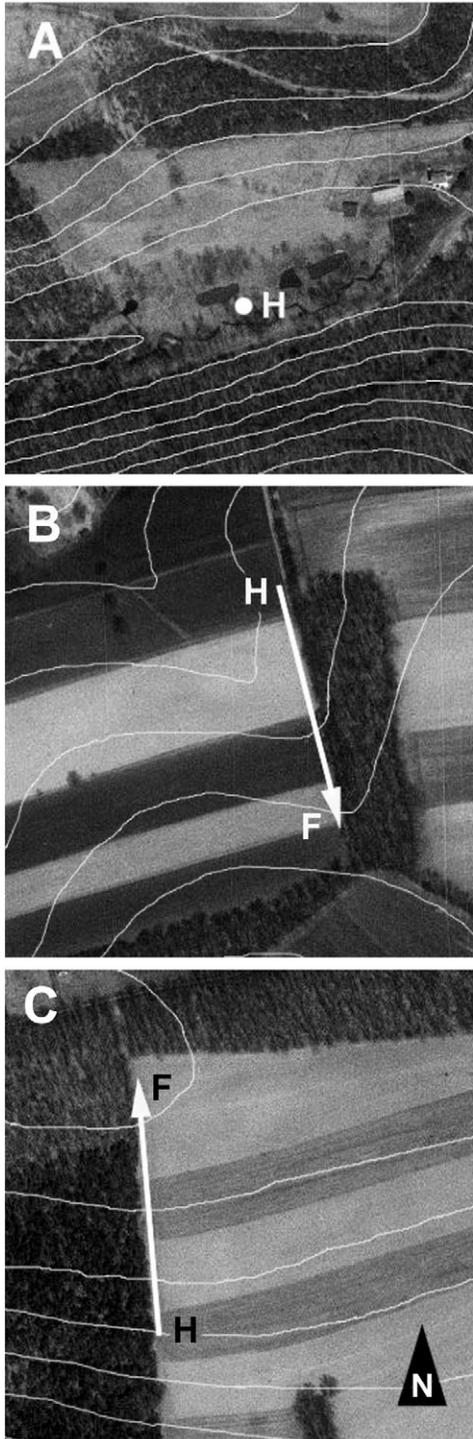


Fig. 1. Aerial views of the field sites indicating locations of hives (H) and feeders (F). The feeder at the valley site (A) was only 2 m from the hive entrance and is not shown. The white arrows in B and C are 190 m long and indicate the bees' outward flights to the feeder. North is indicated by the black arrowhead in C. Adjacent contour lines in all three figures are separated by 6.1 m of elevation. The hive at the valley site (A) was at the bottom of a thinly wooded valley. The hives at the treelined sites B and C were placed along sloping treelines adjacent to agricultural fields, and the bees flew uphill to the feeder in each case. The valley site A is at 75 deg.47'43.4"W, 40 deg.36'41.4"N; the training treeline B is at 75 deg.46'10.5"W, 40 deg.36'27.9"N; and the test treeline C is at 75 deg.47'10.2"W, 40 deg.37'12.9"N. Photos by the United States Geological Survey, courtesy of the USGS and TerraServer-USA.

Results) are reported below but are excluded from the statistical analyses as these dances gave no single direction. Finally, sky conditions during recordings were monitored continuously by an observer at the feeder.

RESULTS

In order to determine whether experienced bees can learn the sun's pattern of movement in relation to a novel landscape, I transplanted bees from their natal site at the bottom of a thinly wooded valley (Fig. 1A) to a panoramically different site dominated by a sloping treeline (the 'training treeline') (Fig. 1B). Every few days starting on 29 July 2005, groups of bees with at least three days' flight experience at the valley site were transplanted into the hive at the training treeline. The transplantees were then recruited to visit a feeder with novel color, scent and landmarks placed 190 m from the hive along the treeline to the south-southeast (Fig. 1B). The transplantees, along with several marked bees native to the training treeline, were thereafter fed and monitored daily at the feeder. The treeline natives, which of course knew the relationship between the solar ephemeris function and the treeline, served as controls for comparison with the valley natives.

On the morning of 7 August 2005, the sky was overcast, and the hive from the training treeline was transplanted as a whole to a second, mirror-image treeline (the 'test treeline'). The feeder was set out in its usual location relative to the hive and treeline, although now in the opposite compass direction (Fig. 1C). The bees began to visit the feeder and dance at 08:00 h (LST) under a light rain, and the dances of the marked bees were recorded at the hive for the next 1.5 h. Before the sun first appeared at 08:38 h (Fig. 2A,B, vertical lines), two different control bees performed a single dance each and both oriented as if they were still at their natal treeline (Fig. 2A) ('training treeline' prediction; $\Theta=151$ deg.; $N=2$ dances by 2 bees; $r=0.97$; $P<0.03$, V-test with a predicted direction of 165 deg.). This was more-or-less opposite the correct direction for the current site, indicating that the control bees had mistaken the test treeline for the training treeline (their natal site) and were dancing according to their memories of the sun's course in relation to the latter. This is what Dyer observed in his treeline-to-treeline transplantation experiments (Dyer, 1987).

Meanwhile, seven different bees native to the valley site (each indicated with a unique symbol in Fig. 2B) performed a total of 20 dances before the sun first appeared, and all, like the control bees, oriented according to a memory of the sun's course in relation to the training treeline (Fig. 2B, left) ('training treeline' prediction; $\Theta=156$ deg.; $N=7$ bees that had performed 1–5 dances each; $r=0.99$; $P<0.001$, V-test with a predicted direction of 165 deg.). In addition, within the next 15 min, but after the sun first appeared to us as a dim disk, six additional valley natives performed a total of eight more similarly oriented dances (Fig. 2B) (open squares near the 'training treeline' prediction between 08:40 h and 08:55 h). Thus, a total of 13 different valley natives first danced on this morning according to a memory of the sun's course in relation to the training treeline. These bees must have learned this relationship during the several days (mean: 7 days; range: 3–9 days) that they had spent at the training treeline, and they were now using that memory to locate the sun (erroneously) at the test site.

The sun became continuously visible at approximately 08:50 h, and the dances of all bees soon shifted to the correct direction for the test site (Fig. 2A,B, right). The remainder of the day was partly cloudy, and the next day (8 August 2005) promised to be overcast so I left the hive at the test treeline overnight and returned at 06:00 h the next morning to perform another trial of the experiment, or

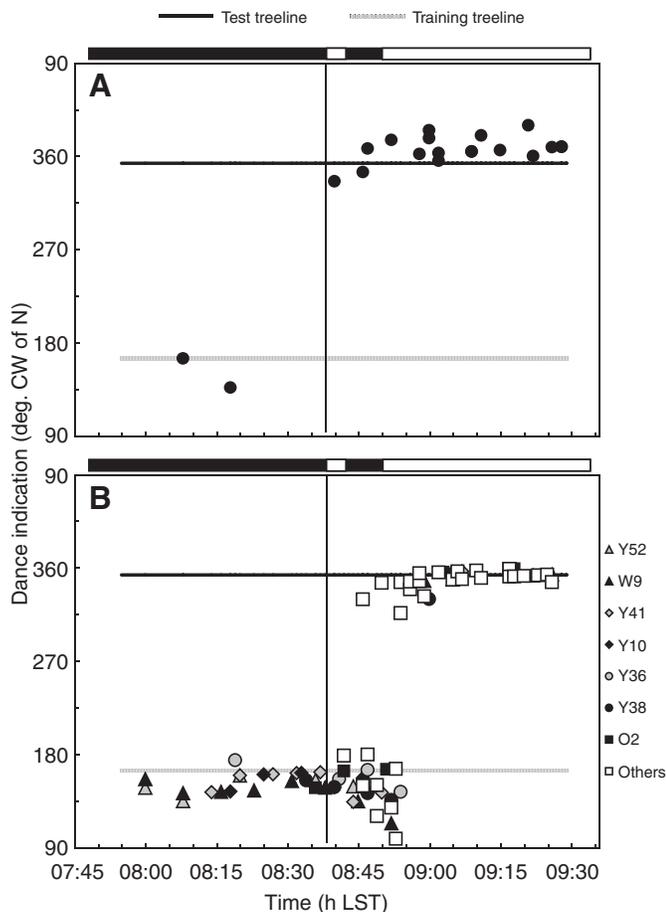


Fig. 2. Dance indications of control bees native to the training treeline (A) and experimental bees native to the valley site (B) under overcast skies at the test site on 7 August 2005. Times are given in local solar time (LST). The valley natives had recently acquired several days' experience at the training treeline. Each symbol represents the visual average of at least five wagging runs during a single bout of dancing; each bee was scored only once after a single trip to the feeder. The hive was at the test treeline (Fig. 1C), where the direction to the feeder, and thus the correct dance indication, was 353.5 deg. (horizontal black line in each panel). The predicted direction for dances oriented by memory of the sun's course at the training treeline was 165 deg. (horizontal gray line in each panel). The dances of seven different valley natives that started dancing before the sun first appeared (vertical line at 08:38 h) are shown with unique symbols in B (the bees' identities and symbols are given in the legend), and the dances of six additional bees that started dancing after the sun appeared are all shown with open squares ('others' in the legend). The sky bar above each panel indicates sky conditions: black indicates complete overcast; white indicates that the sun was visible. There were no periods of blue sky without sun. Statistical analyses include only those dances that occurred before the sun first appeared (thin vertical line at 08:38 h). CW; clockwise.

to close the hive and move it back to the training treeline if the clouds failed. At 06:00 h, the sun was visible as a dim disk so I closed the hive and waited to see if the clouds would thicken. Meanwhile, several marked bees had escaped and they were excluded from the experiment. The clouds did indeed thicken such that the sun was no longer visible by 07:00h, at which time I opened the hive and put out the feeder.

Nine different control bees native to the training treeline danced before the sun again appeared at 08:22h, and their dances are shown in Fig. 3A. In this figure, the two bees that danced the most are

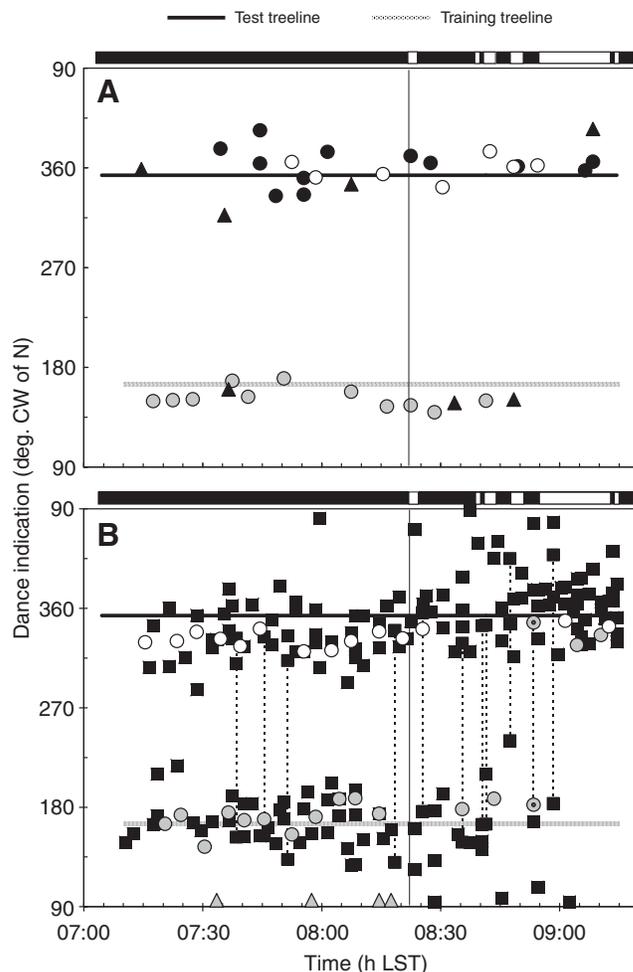


Fig. 3. Dance indications of control bees native to the training treeline (A) and experimental bees native to the valley site (B) under overcast skies at the test site on 8 August 2005. In A, the dances of three different control bees are distinguished with unique symbols: these are the two control bees that danced the most (open and shaded circles) and a third bee (triangles) that showed an unusual dancing pattern. The other six bees are all shown with black circles. In B, the two valley natives that danced the most are shown with unique symbols (open and shaded circles); all other bees (26) are shown with black squares. In B, bimodal dances, in which the bee indicated two different directions on alternate wagging runs, are indicated with broken vertical lines connecting the two dance directions. One of the bees that danced the most (shaded circles) performed one bimodal dance; the two directions are indicated by shaded circles with dots in the center connected by a broken vertical line (further explanation in the text). Disoriented dances are indicated with shaded triangles on the bottom axis. The control bees A performed no bimodal or disoriented dances. Other symbols and conventions as in Fig. 2.

distinguished with open and shaded circles and a third bee that danced toward both predicted directions at different times is shown with black triangles. The remaining six bees are all shown with black circles. Overall the dances are significantly clustered around the 'test treeline' prediction (Fig. 3A) ($\theta=2$ deg.; $N=9$ bees that had performed 1–8 dances each; $r=0.73$; $P<0.001$, V-test with a predicted direction of 353.5 deg.). Seven of these bees (open and black circles) danced only according to the sun's actual location (the 'test treeline' prediction), another (shaded circles) danced only according to a memory of the sun's course in relation to the bees' natal site (the

‘training treeline’ prediction), and one other bee (black triangles) danced in both directions at different times.

The control bees that oriented correctly (Fig. 3A) (‘test treeline’ prediction) are unlikely to have learned the sun’s course in relation to the test treeline (Towne et al., 2005), so they were probably detecting the sun’s azimuth using weak skylight polarization or spectral cues (Wehner and Rossel, 1985; Wehner, 1994; Labhart, 1999; Hegedüs et al., 2007) that we ourselves could not detect. The dances of the control bees, therefore, indicate that there were probably weak celestial cues available to some of the bees on this morning.

Numerous valley natives with experience at the training treeline (mean: 8 days; range: 3–9 days) also danced before the sun first appeared on this day, and their combined dances (Fig. 3B) are not significantly clustered around either predicted direction ($\theta=242$ deg.; $N=28$ bees that had performed 1–11 dances each; $r=0.04$; $P>0.4$, V -tests for both predicted directions), although the dances clearly cluster around the two predicted directions. Furthermore, each valley native danced consistently toward just one of the two predicted directions; typical are the dances of the two individual valley natives that danced the most this morning (distinguished by open and shaded circles in Fig. 3B). Altogether, 14 different bees danced (only) toward the ‘test treeline’ prediction, and 14 danced (only) toward the ‘training treeline’ prediction (ignoring bimodal and disoriented dances, which are discussed below).

These observations show that at least half of the valley natives had learned the sun’s course in relation to the training treeline and that the bees were flying under a sky that allowed some of the bees to determine the sun’s actual location at the test site using fresh celestial cues. When the sun eventually emerged, all of the bees shifted their dances toward the ‘test treeline’ prediction (Fig. 3B, far right).

A few of the dances of the valley natives on 8 August 2005 were bimodal, that is, the bees consistently indicated the two different predicted directions on alternate wagging runs within a single bout of dancing. Such dances occur when bees have two conflicting sources of information as to the sun’s position, in this case, a memory of the sun’s course in relation to the training treeline and weak, fresh celestial cues (Dyer, 1984; Dyer, 1987; Towne et al., 2005; Towne and Moscrip, 2008). Moreover, these bimodal dances occur especially when bees have been dancing by memory of their natal site and have detected conflicting celestial cues on the preceding flight, that is, the bees were simultaneously expressing old and newly acquired memories – from their natal site and acquired on the preceding flight – in a single dance. Dyer discusses these dances further (Dyer, 1984; Dyer, 1987). A typical pattern can be seen in Fig. 3B, where the individual bee whose dances are shown with shaded circles danced first toward the ‘training treeline’ prediction, then bimodally after a flight under clearing skies (two shaded circles with dots in the center connected by a broken vertical line), and finally toward the ‘test treeline’ prediction. Altogether on this day, six different bees performed a total of nine bimodal dances (Fig. 3, broken vertical lines connecting two dance directions), and all but one of these bees had danced first according to a memory of the sun’s course at the training treeline; the other bee danced bimodally on her first dance. Overall, the bimodal dances are consistent with the results of the well oriented (unimodal) dances discussed above: there were weak celestial cues available throughout the morning but some of the bees nonetheless initially danced according to their memories of the sun’s course in relation to the training treeline, indicating that they had learned that relationship.

On this same morning, two different bees performed a total of four disoriented dances, which had distinct but inconsistently

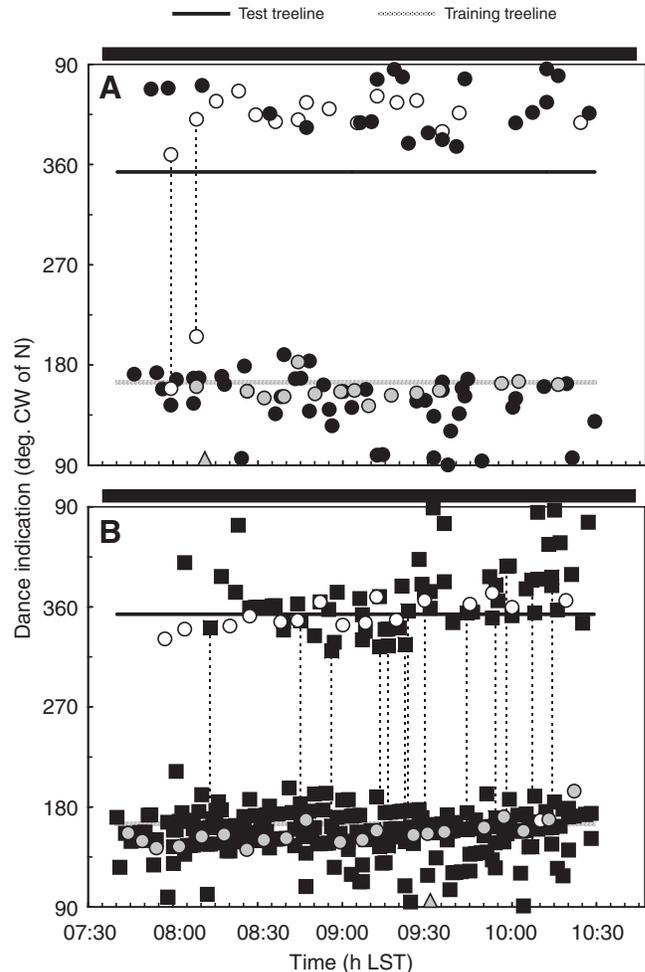


Fig. 4. Dance indications of control bees native to the training treeline (A) and experimental bees native to the valley site (B) under overcast skies at the test site on 16 August 2005. The two bees that danced the most are indicated by open and shaded circles in each panel; these two bees happened to dance in different directions in each case. All other symbols and conventions as in Fig. 3.

oriented wagging segments (Fig. 3B, shaded triangles on the bottom axis). All of these dances occurred just before or after the same bee danced bimodally, suggesting that disoriented dances can result when bees are forced to orient by conflicting or ambiguous cues. Towne et al. (Towne et al., 2005) and Towne and Moscrip (Towne and Moscrip, 2008) have observed disoriented dances under similar conditions.

At the end of the day on 8 August 2005, the hive was returned to the training treeline, and the following morning another group of approximately 50 marked bees from the valley site was released into it. The next overcast morning occurred on 16 August 2005, and the entire hive was once again transplanted to the test treeline for a third trial. By this time, the valley natives had 7–18 days (mean: 10 days) of experience at the training treeline. The results of the third trial were similar to those of the second: there were evidently weak celestial cues available, as some of the bees (control bees and valley natives) danced toward the ‘test treeline’ prediction (Fig. 4A,B), although most danced according to a memory of the sun’s course in relation to the training treeline. Overall, the dances of the control bees (Fig. 4A) and those of the valley natives

(Fig. 4B) are clustered around the 'training treeline' prediction (control bees: $\Theta=117$ deg., $N=13$ bees that had performed 1–16 dances each, $r=0.72$, $P<0.01$; valley natives: $\Theta=143$ deg., $N=25$ bees that had performed 1–21 dances each, $r=0.60$, $P<0.001$; V-tests with a predicted direction of 165 deg.). As in the second trial, individual bees tended to dance in only one direction throughout the morning, although one control bee (Fig. 4A, open circles) danced bimodally before switching exclusively to the test site prediction. The results again show that the valley natives had learned the solar ephemeris function at the training treeline and used that memory to orient their dances on a day when weak celestial cues allowed a few bees to determine the sun's actual location at the test site.

DISCUSSION

Honeybees learn the daily pattern of rotation of the sun and skylight, probably using the landscape or skyline panorama around their nests as a fixed reference (Dyer, 1987), although it is possible that the sun's ephemeris is learned first with respect to another reference and only later connected to the landscape (see Towne and Moscrip, 2008). Thereafter, experienced bees retain the spatial connection between the solar ephemeris and the landscape and can recall the sun's compass bearing at any time of day using the landscape alone (Dyer, 1987). Moreover, the relevant landscape memory seems to encompass the entire landscape panorama, not only familiar flight routes (Towne and Moscrip, 2008). Once acquired, the bees' memory of the spatial relationship between the solar ephemeris and the landscape sometimes strongly resists revision: when bees trained to visit a feeder placed alongside a treeline at their natal site are transplanted to a differently oriented treeline, most or all of the bees fail to update their memories of the relationship between the sun's ephemeris and the new treeline, at least when they forage at a familiar feeder in a (seemingly) familiar location along the new treeline. This is true even for bees that are put through a swarming process as they are transplanted and even if the bees have ample experience at the new site (Towne et al., 2005). One possible explanation for these observations is that the learned relationship between the sun and landscape is imprinted and unchangeable.

I show here, however, that experienced bees can learn the relationship between the solar ephemeris function and an entirely novel landscape, that is, a landscape panoramically unlike the bees' natal one. Specifically, bees transplanted from their natal site at the bottom of a thinly wooded valley to a second site dominated by a sloping treeline were able to learn the relationship between the solar ephemeris and the treeline. This result contrasts starkly with those of previous treeline-to-treeline transplantation experiments (Towne et al., 2005). It remains possible that bees imprint on the relationship between the sun's ephemeris and their natal landscape but can replace the memory – or add a new one – only when the visual scenery around the nest must be learned anew. But it is also possible that bees do not imprint on the sun–landscape relationship and that the similarities of the flight routes and feeders at the source and recipient sites blocked the bees' re-learning in previous treeline-to-treeline transplantation experiments. In this context, it would be useful to know whether bees would update their memories of the sun–landscape relationship if they were transplanted between panoramically similar sites and forced to forage at entirely novel food sources at the recipient site. The latter experiment has yet to be done.

If the bees' memory of the relationship between the sun's pattern of movement and the landscape is updated only when the visual scenery around the nest must be learned anew, would this mean

that the stored ephemeris function is inextricably tied to the landscape in which it was learned? In one sense, certainly not, as the mature ephemeris function has been shown to function in any landscape, familiar or not. If, for example, a hive is transplanted into unfamiliar terrain, the bees can use their skylight compass to find a feeder in a familiar compass direction (pp. 333–338 in von Frisch, 1967), (pp. 112–118 in Lindauer, 1971). And bees and ants both routinely use their skylight compass in path integration, the process by which they integrate the various legs of a meandering journey to a food source in order to return home (and in bees, in order to dance), even if the trip takes the insects into unfamiliar territory [bees (reviewed by Collett and Collett, 2000; Menzel et al., 2006); ants (Wehner et al., 1996; Wehner, 2003; Wehner and Srinivasan, 2003)]. Bees also use their sun compass as a directional reference in learning landmarks at a feeder (Dickinson, 1994), as do ants in learning landmarks around their nests (Åkesson and Wehner, 2002).

Given the usefulness of a portable sun compass, one wonders why bees retain the relationship between their natal landscape and the sun's ephemeris so strongly. If bees use the landscape as the fixed reference against which the solar ephemeris is first learned, which is likely but uncertain (Towne and Moscrip, 2008), then bees must learn the spatial relationship between the sun and landscape in order to learn the shape of ephemeris at all. This would be true, in fact, for any animal that relies on the landscape as the reference for solar ephemeris learning (Dyer, 1984; Dyer, 1987). It would then be a very small step for the bees to retain this relationship after the learning is done, which would allow the bees to use the dance communication on overcast days (Dyer and Gould, 1981; Towne and Moscrip, 2008). This is the only obvious benefit of retaining the relationship, but perhaps this is benefit enough, as the only cost would be the production of navigational errors when the bees happen to move into a new landscape that resembles their natal one, and even then only under overcast skies. In this context, it would be interesting to know whether ants – which have no communication system that requires all individuals to know the sun's compass bearing around the nest at all times – permanently retain a strong connection between the solar ephemeris function and the landscape in which it is learned.

When ants and bees learn the solar ephemeris function for the first time, they begin with an innate expectation that the sun's azimuth in the morning is 180 deg. from its azimuth in the afternoon [ants (Wehner and Müller, 1993); bees (Dyer and Dickinson, 1994)]. The insects then fill in the details of the local ephemeris function with experience (Lindauer, 1959) (reviewed by Dyer, 1996), interpolating between observed positions of the sun to estimate unobserved positions or positions that cannot be resolved, as when the sun is near the zenith [bees (New and New, 1962; Dyer, 1987); ants (Wehner and Lanfranconi, 1981)]. It may be that the bees in the current experiments re-learned the solar ephemeris function in the novel landscape (the training treeline) as if they were learning it anew, that is, beginning (again) with their innate 180 deg. step-function ephemeris. A long-distance transplantation experiment by Lindauer (Lindauer, 1957) suggests, however, that the bees simply brought their mature ephemerides into the correct relationship with the new landscape: Lindauer transplanted a colony of bees from a tropical location to a northern one where the sun and skylight patterns rotated in the opposite direction, and the displaced bees seemed unable to use, or learn to use, the skylight compass at the northern site (although Lindauer did not mark individual bees, so one cannot be certain). If true, this implies that the shape of the solar ephemeris function – that is, the sun's direction of movement and its varying

speed throughout the day – is learned during a critical period after which the function is permanently fixed in the bees' memory. This hypothesis could now be tested using the re-learning reported in the present study.

Our current working hypotheses regarding how bees learn the solar ephemeris function can be summarized as follows. First, the shape of the solar ephemeris function is learned as each bee begins to fly, starting with an innate expectation that the sun's compass bearing in the morning is opposite to its bearing in the afternoon (Dyer and Dickinson, 1994). Second, this learning occurs during a critical period, in that the shape of the function, once acquired, becomes permanently fixed in the bees' memory. While this second hypothesis is consistent with the available evidence, as discussed above, it has yet to be rigorously tested. Third, the spatial relationship between the ephemeris function and the natal landscape may also be learned during the same critical period, as the landscape is probably the frame of reference against which the shape of the ephemeris is first learned (Dyer, 1987; Towne and Moscrip, 2008), and at some point the ephemeris becomes permanently linked to the bees' memory of the landscape or skyline panorama around the nest (Towne et al., 2005; Towne and Moscrip, 2008). Finally, however, the stored ephemeris can be used for sun-compass orientation independently of the landscape, and the relationship between the sun and landscape can be updated in novel landscapes or, possibly, if bees are forced to visit novel food sources in familiar landscapes.

Many important details remain unknown but it is clear that the behavioral mechanisms underlying the bees' learning of the solar ephemeris function – and re-learning, to the extent that it happens – are highly specialized. Furthermore, although these mechanisms can yield nonsensical behavior when presented with unnatural situations, as when bees fail to update their memories of the relationship between their solar ephemeris and a new landscape that happens to be a panoramic twin of their natal one, the mechanisms accomplish their task quickly and well under natural conditions.

I thank Paul Bauscher, Greta Campbell, Walter and Doris Fink, and Ernest and Ida Roth for allowing us to work on their properties; Kevin Frey, Ann Priester, Lisa Shinn, and Tom Summer for assisting in the field; Rudolf Jander, Thomas S. Collett, and an anonymous reviewer for many useful comments on the manuscript; and the USGS and TerraServer-USA for permission to use their aerial photographs. This work was supported by the National Science Foundation (USA) under grant IBN-9816691 (RUI program).

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