Two spatial memories for honeybee navigation

Randolf Menzel[*], **Robert Brandt, Andreas Gumbert, Bernhard Komischke**
and Jan Kunze

Institut für Neurobiologie, Freie Universität Berlin, Königin-Luise-Strasse 28–30, 14195 Berlin, Germany

Insect navigation is thought to be based on an egocentric reference system which relates vector informa-
tion derived from path integration to views of landmarks experienced en route and at the goal. Here we
show that honeybees also possess an allocentric form of spatial memory which allows localization of
multiple places relative to the intended goal, the hive. The egocentric route memory, which is called the
specialized route memory (SRM) here, initially dominates navigation when an animal is first trained to a
feeding site and then released at an unexpected site and this is why it is the only reference system detected
so far in experiments with bees. However, the SRM can be replaced by an allocentric spatial memory
called the general landscape memory (GLM). The GLM is directly accessible to the honeybee (and to
the experimenter) if no SRM exists, for example, if bees were not trained along a route before testing.
Under these conditions bees return to the hive from all directions around the hive at a speed comparable
to that of an equally long flight along a trained route. The flexible use of the GLM indicates that bees
may store relational information on places, connections between landmarks and the hive and/or views of
landmarks from different directions and, thus, the GLM may have a graph structure, at least with
respect to one goal, i.e. the hive.

Keywords: navigation; spatial memory; honeybee; landmark orientation

1. INTRODUCTION

Foraging bees embark on their feeding flights and return
to the hive using sun compass information (Von Frisch
1965; Wehner & Menzel 1990), and visual distance esti-
mation (Esch & Burns 1996; Srinivasan *et al.* 1996;
Menzel *et al.* 1996). These sources of information are
tightly connected: compass directions are derived from
extended landmarks (e.g. when bees fly along the edge of
a forest) (Von Frisch 1965) and home vectors are asso-
ciated with local landmarks (Menzel *et al.* 1998), estab-
lishing a memory for the flight route between the hive
and feeding site. It thus appears that spatial navigation in
bees, as in other animals and humans, is not a unitary
process, but involves multiple navigational systems
arranged in a hierarchical order (O'Keefe & Nadel 1978;
Gallistel 1990; Collett 1996; Gillner & Mallot 1998;
Giurfa & Capaldi 1999). However, insects are thought to
refer to simpler reference systems, such as path integra-
tion ('dead reckoning') and sequential landmark learning
at the goal and along routes (Collett & Zeil 1998) and
these reference systems are considered independent of
each other. Although insects may use this information in
a flexible way, it was concluded that they store spatial
information solely in an egocentric (observer-centred)
way, lacking the capacity to combine multiple views and
movements into an allocentric (world-centred) represen-
tation (Wehner & Menzel 1990; Wehner 1992; Collett &
Zeil 1998). This conclusion is based on the fact that most
data have produced no evidence for novel short cutting, a
behaviour which, since Tolman (1948), is believed to indi-
cate an allocentric, topographic representation of space in
memory (O'Keefe & Nadel 1978).

There are some hints that this generalization may not
apply to all honeybee navigational performances.

(i) Bees trained simultaneously to two release sites, one
in the morning and one in the afternoon, develop
site-specific memories for the flight route towards the
hive, which they can also use when released unex-
pectedly at either site. When these bees are released
at a novel site halfway between the two feeding sites,
half of the bees fly directly back to the hive, choosing
a novel direction, whereas the other half fly in the
compass direction which they would have taken if
they had not been displaced (Menzel *et al.* 1998).

(ii) Bees displaced and released after orientation flights
but without training to a feeding site returned to the
hive (Becker 1958) and did so more reliably when
the release sites were in an open area surrounding
the hive but less reliably when the sites were located
behind an extended landscape barrier (Capaldi &
Dyer 1999). These observations indicated that bees
learn about the landscape surrounding the hive, but
this form of learning may lead to snapshot memories
of the location of the hive rather than to an allo-
centric representation of space. However, such a
seemingly parsimonious explanation does not rule
out the possibility that bees might have established
an allocentric representation for those areas
surrounding the hive which they had covered during
their orientation flights and they might not have
reached areas behind a landscape barrier during the
orientation flights; thus, they might lack a relational
representation of those locations to the hive.

(iii) Gould (1986) reported data which appeared to
support the conclusion that bees fly a short cut to a
feeding site if they are released at an unexpected
place which they might have known from former
experience. However, these observations could not
be confirmed in multiple studies, including those
which assured that bees had experienced the release
site during previous training (Menzel *et al.* 1990;

961

© 2000 The Royal Society
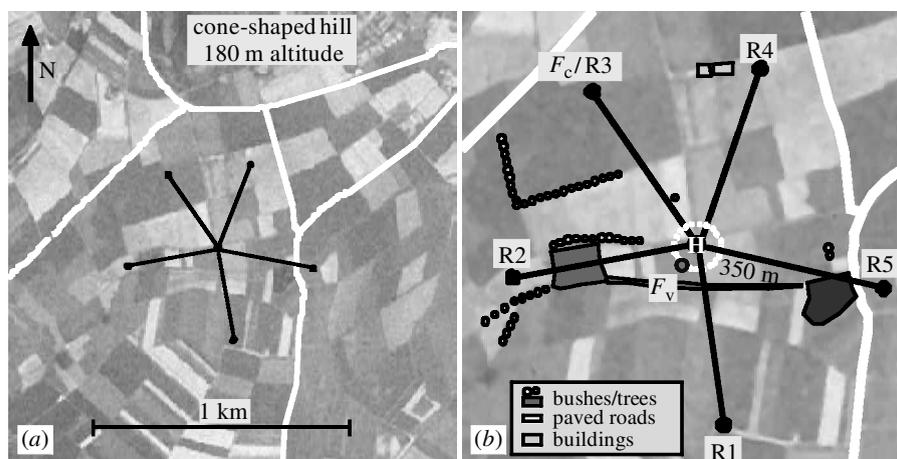
sequence A: R1 R1 R1 R3 R3 R3 R2 R2 R2 R4 R4 R4 R5 R1 R1 R1 R3 R3 R3
sequence B: R3 R3 R3 R5 R5 R5 R1 R1 R1 R4 R4 R4 R2 R3 R3 R3 R5 R5 R5
sequence C: R4 R4 R4 R1 R1 R1 R3 R3 R3 R5 R5 R5 R2 R4 R4 R4 R1 R1 R1

Figure 1. Layout of the countryside where the experiments were performed. R1–R5, release sites; H, hive; F_c, constant feeder (at R3); F_v, variable feeder. (*a*) Overview (satellite view) of the area in which the bees were expected to navigate. (*b*) Close-up of the experimental area. Two groups of bees were trained: C bees travelled over a distance of 350 m between the constant feeder at R3 and the hive and V bees visited a nearby feeder (10 m from the hive) which was moved around the hive (variable feeder). The release schedule is shown below the figures. Three sequences (A, B and C) were used. Each sequence was composed of sets of triple releases at the same site. At release number 13 one control release was performed at either R2 or R5 (see §2).

Wehner *et al.* 1990; Dyer 1998), a prerequisite which was not met in Gould's (1986) study.

On the basis of the controversial results on bee navigation, we hypothesized that the frequent failure to demonstrate richer forms of spatial memory as compared to egocentric route memories might result from the fact that the vector component of such route memories may override more flexible memories based on relational information which were established during orientation flights. We therefore developed a procedure which allowed the testing of bees' navigational capacities without training them along a fixed route to a feeding station and compared their orientation behaviour to bees trained along a fixed route as was done in most of the studies cited above.

2. METHODS

The experiments were performed in Amöneburg, Germany during three autumn sessions of two weeks each (1996–1998) when local food sources were almost non-existent. A beehive (from a spot 30 km north-east) was set up and bees were allowed to fly freely for two days. During this time, foragers which were new to the location and which had navigation experience at another location performed reorientation flights. Training began on the third day after the move. The bees were trained in one of two ways. One group (the variable or V bees) foraged at a feeder which was stepped around the hive in a circle with a 5–10 m radius (1 revolution 3 h^{-1}). A second group (the constant or C bees) were trained to a stationary feeder at R3, 350 m north-west of the hive (figure 1*a*,*b*). The V bees lacked experience of flying regularly from the hive and feeder along a constant route, whereas the C bees established this experience. The V bees were used to test the existence of a general landscape memory (GLM) and the C bees a specific route memory (SRM).

Two measures of navigational performance were made: vanishing bearings at the release site and flight time from the release site to the hive. In the first case a bee's spiralling flight was tracked by sight, keeping the bee in view from below against the sky and determining the compass direction at which the bee disappeared from sight. This usually happened at a distance of 25–35 m. The flight time was determined by recording the time of release at the release site and the time of arrival at the hive.

Trained bees were marked with numbered plastic tags and small metal rings weighing 1.1 mg which did not affect their flight behaviour. The bees were allowed to visit the feeding site several times in a row before they were captured after drinking *ad libitum* at the feeder and transported in glass vials in a pocket to one of the five release sites, all of them located 350 m from the hive (figure 1*a*,*b*). This distance was chosen to ensure a higher return rate since preliminary experiments had shown that bees released in this area returned to the hive with a probability of > 95% if the distance between the hive and release site was less than 500 m. During the release procedure the exact release time and the vanishing bearing were recorded. The arrival time of the returning bee at the hive entrance tube was registered by an observer and/or a computer-controlled video camera. A marked bee triggered a metal detector in the entrance tube with its metal ring and a video picture was taken of the tag number on the thorax, together with the exact time. Later these pictures were analysed, compared with the data taken at the release point and those of the entrance observer and the flight time was calculated. In total, 1997 flight times were recorded from 2687 releases. Each bee visited the feeder and returned to the hive at least once before being recaptured for the release procedure.

Each bee was released 19 times in six sets of three consecutive releases at the same site plus a single release site after the fourth set (13th release) at a site different from all the other release sites (figure 1). Following the additional single release, the first
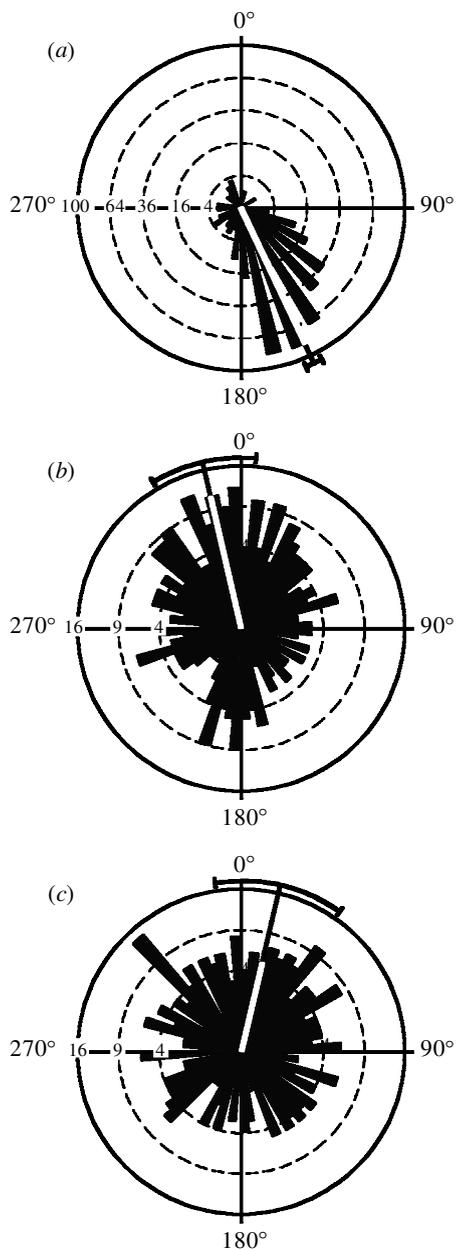
Figure 2. Distributions of the vanishing bearings, mean vector direction μ and statistical values. (*a*) Vanishing bearings of C bees at all five release sites ($\mu = 155°$, $r = 0.87$, $p < 0.001$ and $n = 420$). The frequencies within $10°$ class ranges are shown as the areas of the dark wedges. The dark spoke and segment indicate the mean vector μ and 95% confidence interval, respectively. (*b,c*) Relative vanishing bearings of V bees. (*b*) The vanishing bearings are expressed as the angular differences to the direction from the particular release site to the hive. Thus, the relative direction to the hive is $0°$ ($\mu = 347°$, $r = 0.25$, $p < 0.001$ and $n = 298$). (*c*) The vanishing bearings of V bees expressed as the angular differences between the vanishing angle at any of the five release sites and the angle between the feeding spot and the hive at the time of the test. Thus, $0°$ coincides with the direction from the variable food site to the hive ($\mu = 13°$, $r = 0.22$, $p < 0.01$ and $n = 278$). For both evaluations there are significant though weak tendencies to depart either in the direction bees would have taken from the variable feeding site to the hive or directly to the hive.

two sets in the whole sequence were repeated. Three different sequences of triple sets were performed. The three sequences were run in parallel for either V or C bees and performed with both V and C bees.

Two groups of control bees were tested for each of the experimental conditions (V or C bees). One control group was also released 19 times, as were the experimental bees, but always at the same site (R1 or R4, except for the single thirteenth release at a different site which was R2 or R5). Another group of bees was released once only at each release site.

(a) *Statistics*

The Mann–Whitney *U*-test was used to compare the flight times. The results are given as the median flight time t_f, standard normal deviate z, probability p, number of observations n and number of animals N. Vanishing bearings were analysed according to Batschelet (1981) circular statistics using the Rayleigh test of uniformity with mean vector μ, vector length r, probability of uniformity p and number of observations n.

(b) *Model calculation of the flight time in V bees*

If V bees were to perform a spiralling search flight at any release site, one can estimate their flight distances and flight durations from their known flight speeds. A common formula of a spiral is given by

$$\rho(\phi) = a\phi \quad \text{Archimedes}, \tag{1}$$

where ρ is the radius, ϕ the angle and a the rate of radius gain per angular unit. Thus, the increase in the radius per revolution $\Delta\rho$ is equal to $a2\pi$. The average flight speed of the bees was estimated from the median of all the flight times of foraging bees at R3 and was $2.9\,\text{m s}^{-1}$. The median flight time of all V bees was 4.33 min, which means that, on average, they travelled a distance of *ca.* 750 m. It is clear that the distance between consecutive spiral arms cannot exceed twice the detection range, because otherwise they would have a high probability of missing the hive. The detection range d is estimated from the angular resolution of the bee eye for achromatic targets ($5°$) (Giurfa *et al.* 1996) and the size of the tent in which the hive was set up (*ca.* $2\,\text{m} \times 2\,\text{m}$) which was 22.9 m. The length of a spiral (l) is given by

$$l = a/2(\phi\sqrt{(1 + \phi^2)} + \operatorname{arcsinh}(\phi)). \tag{2}$$

From the detection range we estimated the maximal value of a to be equal to $7.3\,\text{m rad}^{-1}$ and $\phi = (350\,\text{m}/2d)2\pi = 48$. Insertion into equation (2) yielded a length of the hypothetical trajectory of *ca.* 8.4 km, meaning that a return flight would take *ca.* 48 min.

3. RESULTS

We expected that both the V and C bees would need considerable time to find their way back to the hive when released for the first time in an unfamiliar spot several hundred metres away from the hive. On the basis of previous results (Wehner & Menzel 1990; Wehner 1992; Capaldi & Dyer, 1999), we also expected the C bees to fly along their compass direction when released at the new sites. Therefore, we released each test bee three consecutive times at the same site, because multiple consecutive releases at an unfamiliar site lead to a gradual improvement in orientation towards the hive and a shortening of the flight time, indicating spatial learning via path integration and
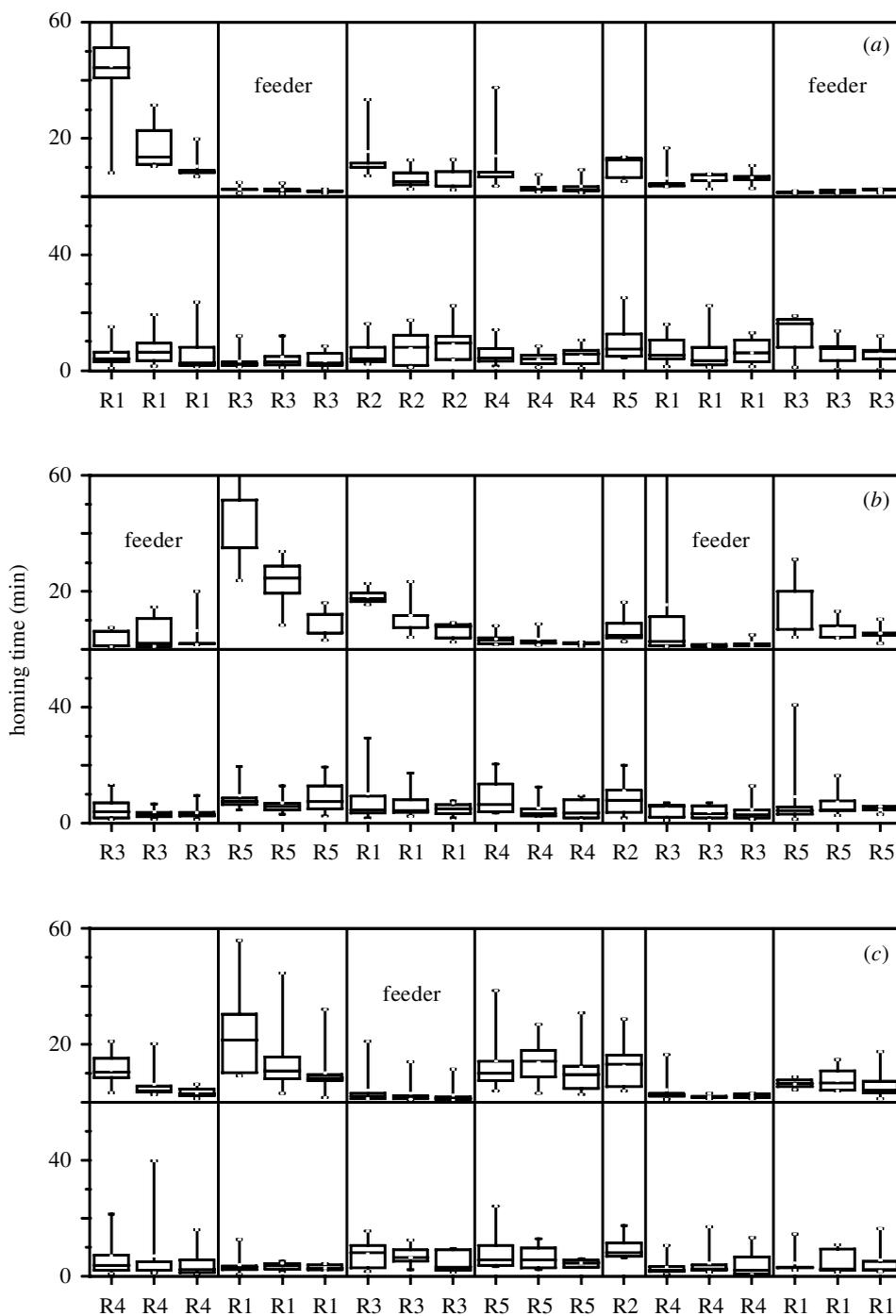
Figure 3. Box plots of the medians, interquartiles and standard deviations of the flight times of C bees and V bees tested in three different sequences ((*a–c*) sequences A–C, respectively). The ordinate gives the flight time from the release site (given at the abscissa) to the hive. N is the number of bees tested and *n* the number of measured flight times. The notation feeder marks release site R3 for C bees, the location of their training site. (*a*) C bees, $N = 5$ and $n = 87$, and V bees, $N = 13$ and $n = 176$; (*b*) C bees, $N = 5$ and $n = 87$, and V bees, $N = 17$ and $n = 244$; (*c*) C bees, $N = 9$ and $n = 159$, and V bees, $N = 12$ and $n = 192$.

reference to landmarks (Menzel 1989). Furthermore, we reasoned that repetition of multiple releases at different sites around the hive may allow the bee to integrate the home flights and, thus, make it familiar with the layout of landmarks guiding navigation back to the hive. Therefore, the test procedure allowed for learning during the return flights from the release sites and for integration of the

memories established during multiple return flights from the multiple release sites (figure 1). The 19 releases were arranged in six sets of three consecutive releases at the same place plus a single release after the fourth set at a site different from all other release sites. The results of this additional single release were then compared with the results obtained in each of the three different release
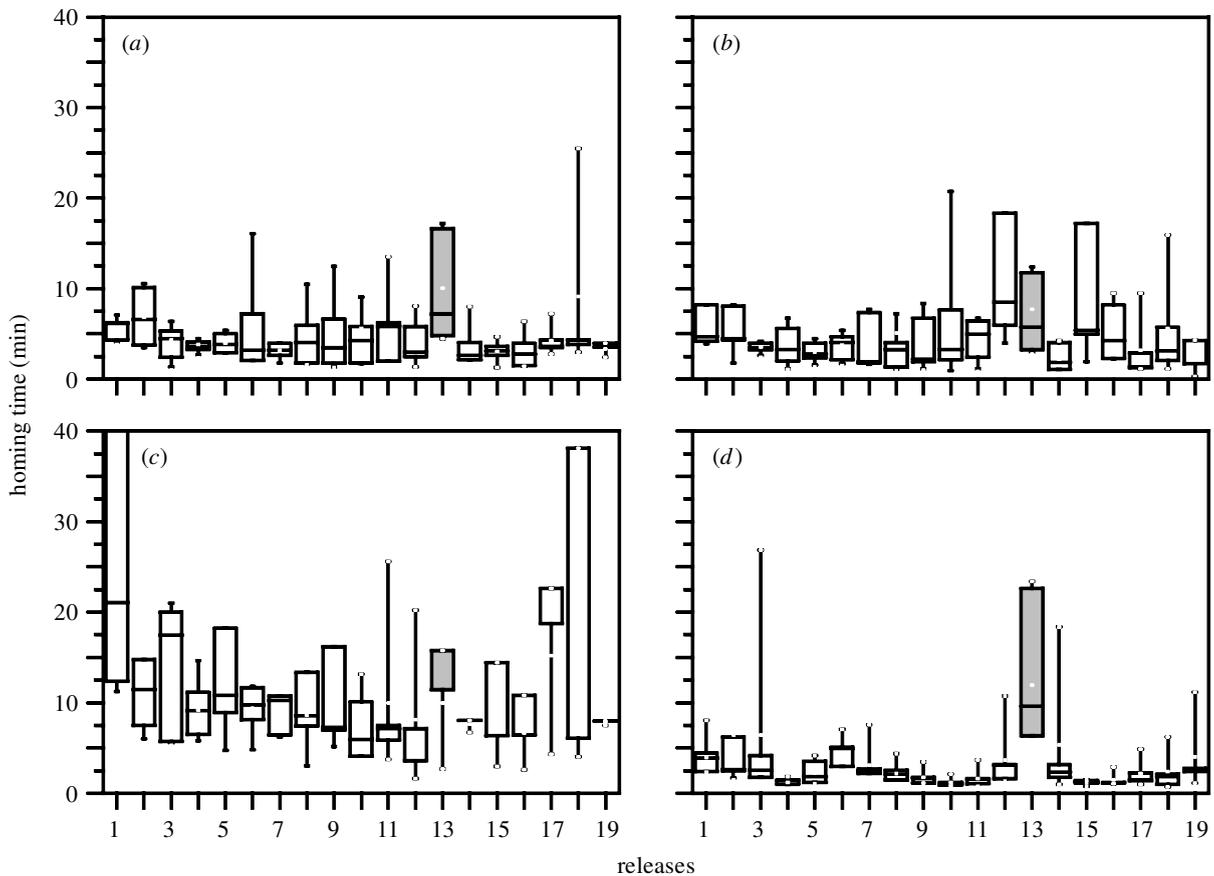
Figure 4. Box plots of the flight times of the control bees ((*a*, *b*) V bees and (*c*, *d*) C bees) released only at R1 or at R4. The 13th release was at R2 (grey boxes). (*a*) R1, $\mathcal{N} = 10$ and $n = 140$; (*b*) R4, $\mathcal{N} = 11$ and $n = 155$; (*c*) R1, $\mathcal{N} = 9$ and $n = 104$; and (*d*) R4, $\mathcal{N} = 7$ and $n = 109$.

sequences. The three different sequences (figure 3*a–c*) allowed us to test whether the bees' behaviour depends on particular features of the landscape, because each sequence started with a different release site and the triple releases followed a different pattern.

The vanishing bearings at the five release sites indicated compass-guided flights in the C bees as expected (figure 2*a*) ($\mu = 155°$, $r = 0.87$, $p < 0.001$ and $n = 420$), and weakly-directed flights towards the hive in the V bees (figure 2*b*) ($\mu = 347°$, $r = 0.25$, $p < 0.001$ and $n = 298$). A statistical analysis of the vanishing bearings of the V bees at their first release at any of the five release sites indicated that they had a significant but low directionality towards the hive at R1–R3, but not at R4 and R5 (R1, $r = 0.49$, $p < 0.004$ and $n = 23$; R2, $\mu = 58°$, $r = 0.53$, $p = 0.010$ and $n = 16$; R3, $\mu = 149°$, $r = 0.62$, $p < 0.001$ and $n = 20$; R4, $\mu = 337°$, $r = 0.60$, $p = 0.94$ and $n = 18$; and R5, $\mu = 134°$, $r = 0.19$, $p = 0.62$ and $n = 13$). When released at any of the five release sites, the V bees also showed a significant but low tendency to fly towards the direction which they would have taken if they had departed from the variable food site at the time of the test (figure 2*c*) ($\mu = 13°$, $r = 0.22$, $p < 0.01$ and $n = 278$). Since bees can be observed only within a radius of up to *ca.* 30 m, their flight times tell us how they perform when out of sight.

Unexpectedly, the V bees already performed very well at the first release and found their way back to the hive very quickly (figure 3*a–c* for V bees). Their performance

was maintained throughout the experiment and did not improve during the three releases within a set, nor with more than three releases at the same site (figure 4*a,b*), indicating that the bees already performed at their best at the first release. The flight times of the V bees starting at R2 and R3 during their first releases were longer than those of the C bees at their trained foraging site R3 (figure 5) (C bees at R3 and V bees at R2, $p < 0.01$, $z = -3.806$ and $n = 64$; and C bees at R3 and V bees at R3, $p = 0.012$, $z = -2.367$ and $n = 49$) (see figure 3, C bees) but are not significantly longer when starting from R1, R4 or R5 (V bees at R3 and V bees at R1, $p = 0.613$, $z = -1.871$ and $n = 39$; V bees at R3 and V bees at R4, $p = 0.195$, $z = -1.295$ and $n = 42$; and V bees at R3 and V bees at R5, $p = 0.115$, $z = -1.577$ and $n = 36$). Comparing the flight times of V bees from the five release sites indicated statistically significant differences only between release site R2 and all other sites (figure 5), indicating that the V bees found it somewhat difficult to return to the hive quickly from R2. In the case of the C bees, significant differences in the flight times were found between those from R3 and those at R1, R2, R4 and R5 (figure 5) (R1/R3, $z = 5.0$, $p < 0.001$ and $n = 36$; R2/R3, $z = 4.1$, $p < 0.001$ and $n = 29$; R4/R3, $z = 3.4$, $p < 0.001$ and $n = 33$; and R5/R3, $z = 4.5$, $p < 0.001$ and $n = 23$). The V bees were significantly faster than the C bees from R1, R4 and R5 but not at R2 (R1, $z = 4.0$, $p < 0.0001$

(a)

(b)
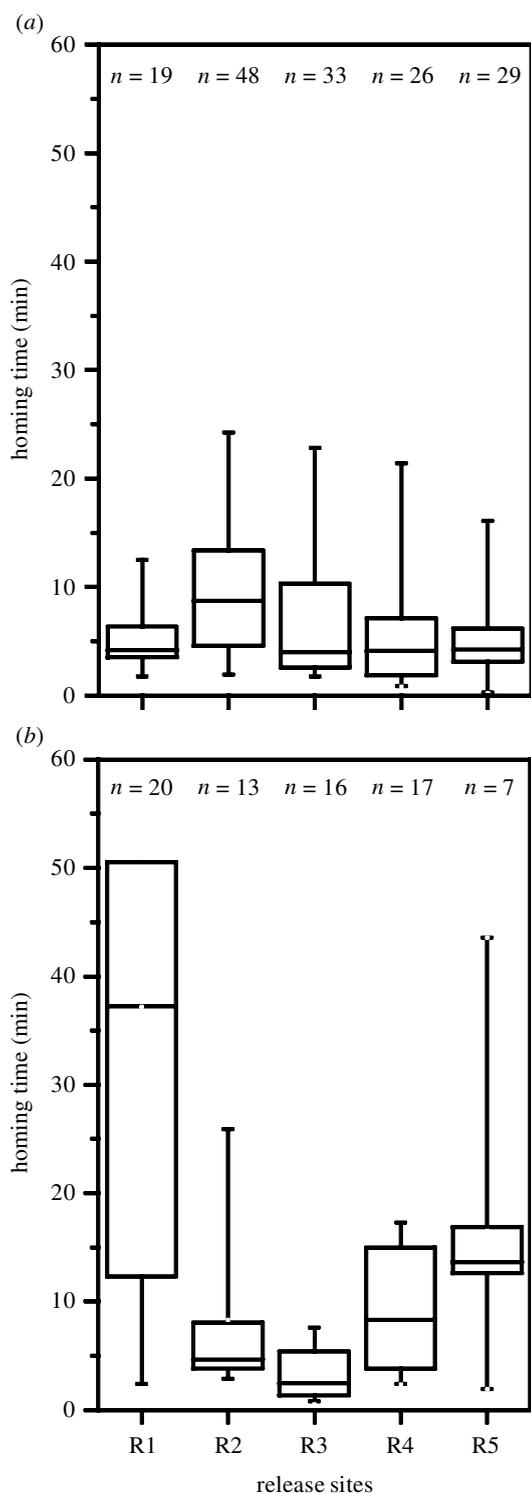
Figure 5. Box plots of the flight times of (*a*) V bees and (*b*) C bees on their first release at sites R1–R5.

and $n = 39$; R2, $z = 1.3$, $p = 0.199$ and $n = 61$; R3, $z = 2.4$, $p = 0.018$ and $n = 49$; R4, $z = 2.3$, $p = 0.024$ and $n = 43$; and R5, $z = 2.7$, $p = 0.007$ and $n = 36$).

The reason for the very long homing flights of the C bees at R1, R4 and R5 is that they headed in the compass direction that they would have taken when flying back from the feeder to the hive (figure 2*a*). This took them further away from the hive when released at R1 and R5, but to a smaller degree when released at R4 and not closer, but within a radius of *ca.* 300 m from the hive

when released at R2. Although the C bees flew further away from the hive, all of them returned to the hive.

These results indicate that the C bees might have switched to a different mode of navigation after terminating their compass-related vector flights. As a result, they could return to the hive more quickly when they were closer to it and more slowly when they were further away. In contrast to the V bees, the flight times improved for the C bees over repeated releases at the same site. This was highly significant ($p < 0.01$) for five out of eight sets of releases at R1 and R5. The three cases which did not show an improvement were late sets of triple releases in the sequence (see figure 3*a*, second set at R1 and figure 3*c*, R5 and R1). The flight times from R2 and R4 became significantly shorter in three out of five sets; again, the non-significant cases were late in the sequence (figure 3*b,c*, R4). The same effect was found in control bees released at the same site 18 times (figure 4) when the first four releases are considered. In the case of multiple R1 releases, the homing-time scatter increases for later releases (> 14) for unknown reasons.

The C and V bees which experienced the same number of releases (but always at the same site, R1 or R4) showed a constant performance, at least from the third release onwards in the case of the C bees (figure 4). For the C bees, this constant level was significantly higher for releases at R1 as compared to those at R4. This indicates that the strong route memory acquired during training to R3 could not be fully overcome even after 18 releases at the same site.

To test whether the V bees reached the hive if they performed a systematic search strategy without reference to landmarks, i.e. a strategy without prior knowledge about the homing direction from the area around the release site, we reasoned that they would continue their circling behaviour, thus increasing its radius, which we observed close to the release site. The result of such a model calculation (see § 2) allowed us to reject the possibility of a non-directed flight path: tracing a spiral, they would have had to fly *ca.* 8.4 km which would take them 48 min.

4. DISCUSSION

When a colony of bees is moved to a new site, experienced bees perform orientation flights similar to those they had performed when learning the site of the hive for the first time (Vollbehr 1975). In our particular experimental set-up such reorientation flights by forager bees did not lead to new foraging flights because no natural food sources were available at the time. Thus, what the bees had learned during their reorientation flights was acquired only during latent learning and not by reward-guided learning. The data for the V bees indicated that they had established a familiarity with the landmarks around the hive which allowed them to return to the hive efficiently. This information was most probably acquired during orientation flights prior to training to the variable feeder, because bees were observed flying directly between the feeder and hive. However, the possiblity that they made wider excursions between foraging flights or before or after the feeder was set up in the morning and late afternoon cannot be excluded. In any case, these

orientation flights would have provided them with the same information as those before training to the variable feeder. The experimental site provided ample landmarks, both nearby and distant, which structured the landscape surrounding the hive according to local and overall features. The hive was not marked by close landmarks and could not be seen from a distance of more than 20 m. The model calculation assuming a spiralling search flight showed that random or systematic search flights without reference to a memory about the spatial relationship between landmarks and the hive cannot explain the findings. Since the V bees could not use a beacon at the hive to orientate towards the hive over most of their return flight, they must have referred to some relational information about the landscape or its local features relative to the hive. This knowledge is general in the sense that bees can use any landmark constallations surrounding the hive for identification of the spatial relationship between release site and hive, since bees returned reliably from all directions (although they were slower when starting at R2; see below). We thus characterized the structure of this knowledge as the GLM and separated it from the specialized knowledge established during the route flight (SRM) the compass component of which is applied when bees depart from an unexpected release site. The GLM appears to have enable the bees to localize the release site relative to the hive. A localization performance based on the GLM might be rather imprecise and spatially extended, as can be inferred from the finding that the bees covered a rather large area during their initial circling flight. It seems likely that the bees selected the landmarks to be used during this circling flight.

The GLM was suppressed but not erased by the SRM, since if the SRM did not lead back to the hive, the bees appeared to be able to recruit their GLM from a remote store and use it for homing. The speed and effectiveness of recruiting the GLM in animals with an active SRM improves from multiple experiences with a misleading SRM. This indicates that additional processes of integration between consecutive return flights add to the improvement in navigation. Therefore, the spatial representation referred to by the C bees may not only have been learned during the orientation flights, but also during the return flights during repeated translocations in the course of the experiment.

The GLM was used less effectively for the area around R2. This cannot result from the fact that R2 lies behind a barrier of trees when seen from the hive, because R5 lies behind an equally large thicket with even higher trees. The area west of the hive was frequently mown pasture and might have been less attractive for orientations flights than the other areas surrounding the hive.

Our results do not confirm Gould's (1986) findings because he tested bees after route training, but they support the general notion of hierarchically organized navigational systems in bees, including some form of allocentric mapping of the landscape. The neural mechanism underlying the mapping process is unknown. One possibility is that bees link homeward-directed vector memories to local features of the landscape when they perform orientation or reorientation flights. In this case the allocentric representation would consist of multiple but isolated vector memories which point to the hive and, thus, define isolated spatial positions with respect to one specific spot (the hive) but not with respect to any other spot. Alternatively, bees might establish memories of multiple sequences of views of the landmarks experienced during orientation or reorientation flights. Such sequential memories were demonstrated in bees for a small number (three) of cues characterizing feeding spots (Collett *et al*. 1993) and in ants for a limited number of views of landmarks experienced en route to and from the feeding spot (Collett *et al*. 1998; Judd & Collett 1998). If such sequences of landmark views did indeed guide the bees' return from any direction around the hive, they would have to consist of quite a considerable number of associatively connected memory items. Another alternative would be a geometric representation in which the spatial relationships between many spots are defined and stored in spatial memory with a graph structure (Gillner & Mallot 1998). Our data do not require the latter assumption as an explanation and the former two may appear as more parsimonious explanations. However, what appears as parsimonious on logical grounds might, in a mechanistic sense, not be the simpler solution.

REFERENCES

Batschelet, E. 1981 Circular statistics in biology. In *Mathematics in biology* (ed. R. Sibson & J. E. Cohen), pp. 1–372. London: Academic Press.

Becker, L. 1958 Untersuchungen über das Heimfindevermögen der Bienen. *Zeitsch. Vergleichende Physiol.* **41**, 1–25.

Capaldi, E. A. & Dyer, F. C. 1999 The role of orientation flights on homing performance in honeybees. *J. Exp. Biol.* **202**, 1655–1666.

Chittka, L. & Geiger, K. 1995 Can honeybees count landmarks? *Anim. Behav.* **49**, 159–164.

Chittka, L. & Kunze, J. 1996 The significance of landmarks for path integration in homing honeybee foragers. *Naturwissenschaften* **82**, 341–343.

Collett, M., Collett, T. S., Bisch, S. & Wehner, R. 1998 Local and global vectors in desert ant navigation. *Nature* **394**, 269–272.

Collett, T. S. 1996 Insect navigation *en route* to the goal: multiple strategies for the use of landmarks. *J. Exp. Biol.* **199**, 227–235.

Collett, T. S. & Zeil, J. 1998 Places and landmarks: an arthropod perspective. In *Spatial representation in animals* (ed. S. Healy), pp. 18–53. Oxford University Press.

Collett, T. S., Fry, S. N. & Wehner, R. 1993 Sequence learning by honeybees. *J. Comp. Physiol.* A **172**, 693–706.

Dyer, F. C. 1998 Spatial cognition: lessons from central-place foraging insects. In *Animal cognition in nature* (ed. R. Balda, I. Pepperburg & A. Kamil), pp. 119–154. London: Academic Press.

Esch, H. E. & Burns, J. E. 1996 Distance estimation by foraging honeybees. *J. Exp. Biol.* **199**, 155–162.

Gallistel, C. R. 1990 *The organization of learning*. London: MIT Press.

Gillner, S. & Mallot, H. A. 1998 Navigation and acquisition of spatial knowledge in a virtual maze. *J. Cognit. Neurosci.* **10**, 445–463.

Giurfa, M. & Capaldi, E. A. 1999 Vectors, routes and maps: new discoveries about navigation in insects. *Trends Neurosci.* **22**, 237–242.

Giurfa, M., Vorobyev, M., Kevan, P. G. & Menzel, R. 1996 Detection of coloured stimuli by honeybees: minimum visual angles and receptor specific contrasts. *J. Comp. Physiol.* A **178**, 699–709.

Gould, J. L. 1986 The locale map of honey bees: do insects have cognitive maps? *Science* **232**, 861–863.

Judd, S. P. D. & Collett, T. S. 1998 Multiple stored views and landmark guidance in ants. *Nature* **392**, 710–714.

Menzel, R. 1989 Bee-havior and the neural systems and behavior course. In *Perspectives in neural systems and behavior* (ed. T. J. Carew & D. Kelley), pp. 249–266. New York: A. R. Liss.

Menzel, R., Chittka, L., Eichmüller, S., Geiger, K., Peitsch, D. & Knoll, P. 1990 Dominance of celestial cues over landmarks disproves map-like orientation in honey bees. *Z. Naturforsch.* C **45**, 723–726.

Menzel, R., Geiger, K., Chittka, L., Joerges, J., Kunze, J. & Müller, U. 1996 The knowledge base of bee navigation. *J. Exp. Biol.* **199**, 141–146.

Menzel, R., Geiger, K., Müller, U., Joerges, J. & Chittka, L. 1998 Bees travel novel homeward routes by integrating separately acquired vector memories. *Anim. Behav.* **55**, 139–152.

O'Keefe, J. & Nadel, J. 1978 *The hippocampus as a cognitive map.* New York: Oxford University Press.

Srinivasan, M. V., Zhang, S. W., Lehrer, M. & Collett, T. S. 1996 Honeybee navigation *en route* to the goal: visual flight control and odometry. *J. Exp. Biol.* **199**, 237–244.

Tolman, E. C. 1948 Cognitive maps in rats and men. *Psychol. Rev.* **55**, 189–208.

Vollbehr, J. 1975 Zur Orientierung junger Honigbienen bei ihrem. 1. Orientierungsflug. *Zool. Jahrbücher Physiol.* **79**, 33–69.

Von Frisch, K. 1965 *Tanzsprache und Orientierung der Bienen.* Heidelberg, Germany: Springer.

Wehner, R. 1992 Arthropods. In *Animal homing* (ed. F. Papi), pp. 45–144. London: Chapman & Hall.

Wehner, R. & Menzel, R. 1990 Do insects have cognitive maps? *A. Rev. Neurosci.* **13**, 403–414.

Wehner, R., Bleuler, S., Nievergelt, C. & Shah, D. 1990 Bees navigate by using vectors and routes rather than maps. *Naturwissenschaften* **77**, 479–482.