RESEARCH ARTICLE

Coordinating compass-based and nest-based flight directions during bumblebee learning and return flights

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SUMMARY

Bumblebees tend to face their nest over a limited range of compass directions when learning the nest's location on departure and finding it on their approach after foraging. They thus obtain similar views of the nest and its surroundings on their learning and return flights. How do bees coordinate their flights relative to nest-based and compass-based reference frames to get such similar views? We show, first, that learning and return flights contain straight segments that are directed along particular compass bearings, which are independent of the orientation of a bee's body. Bees are thus free within limits to adjust their viewing direction relative to the nest, without disturbing flight direction. Second, we examine the coordination of nest-based and compass-based control during likely information gathering segments of these flights: loops during learning flights and zigzags on return flights. We find that bees tend to start a loop or zigzag when flying within a restricted range of compass directions and to fly towards the nest and face it after a fixed change in compass direction, without continuous interactions between their nest-based and compass-based directions of flight. A preferred trajectory of compass-based flight over the course of a motif, combined with the tendency of the bees to keep their body oriented towards the nest automatically narrows the range of compass directions over which bees view the nest. Additionally, the absence of interactions between the two reference frames allows loops and zigzags to have a stereotyped form that can generate informative visual feedback.

Key words: compass-based flight, nest-based flight, coordinating reference frame, insect navigation, learning flight.

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INTRODUCTION

Bumblebees perform learning flights to acquire visual information about the arrangement of landmarks around the nest that can help guide their later return flights. They control flight direction and body orientation in relation to both nest-based coordinates (Philippides et al., 2013) and compass bearings (Hempel de Ibarra et al., 2009). Bees thus obtain similar views when facing in directions close to the nest in particular segments of the stereotyped loop and zigzag motifs that characterize their learning and return flights (Philippides et al., 2013).

This dual control of flight can be seen in plots of the frequency distributions of body orientation and flight direction during these motifs. Body orientation has a more prominent and narrower peak than flight direction in both nest- and compass-based coordinates (Fig. 1). When plotted relative to the nest, the mode of the distribution is in the direction of the nest (Fig. 1A). Flight direction is less focused. There is a peak in the direction of the nest during zigzags and peaks either side of the nest during loops (Fig. 1B). The mode of body orientation plotted in compass coordinates is just west of north (Fig. 1C), whereas flight directions are broadly distributed in loops and zigzags (Fig. 1D). To face towards the nest while flying over a wider range of flight directions, bees adjust the angle between flight direction and body orientation (Philippides et al., 2013). The results presented here allow us to explain the similar concentration of viewing directions relative to compass bearings.

The bee's direction of travel in particular surroundings may in principle be controlled by the surrounding panorama (von Frisch

and Lindauer, 1954; von Frisch, 1967; Towne and Moscrip, 2008; Graham and Cheng, 2009), or by celestial compass information (Wehner and Rossel, 1985; Riley et al., 2005), or by both reference frames (Dyer, 1987; Towne and Moscrip, 2008). In familiar surroundings, the distant panorama and compass information usually provide concordant guidance cues. If the two are put in conflict, cues from the panorama can overwhelm compass information and control the insect's direction of movement (von Frisch, 1967; Graham and Cheng, 2009). In unfamiliar surroundings, or when flying insects are tethered, guidance can be by compass cues alone (Mouritsen and Frost, 2002).

Bumblebee learning flights provide an interesting case. Because body orientation is tied more closely to the position of the nest than is flight direction (Fig. 1A,B), the relation between body orientation and flight direction varies. Were body orientation to be fixed relative to flight direction, it would be straightforward to maintain a set flight direction by keeping features of the surrounding panorama in fixed retinal positions. It is more complicated if, as here, body orientation varies relative to flight direction. The image of the panorama on the retina is not then an easy cue to use for controlling flight direction. How do bees control their flight direction under these circumstances?

We approach this question by analysing how straight segments of flight are maintained and find that the direction of straight segments is probably set by compass cues. We then show that bees have preferred compass directions of flight associated with different phases of their nest-based loops and zigzags, and examine how nest-
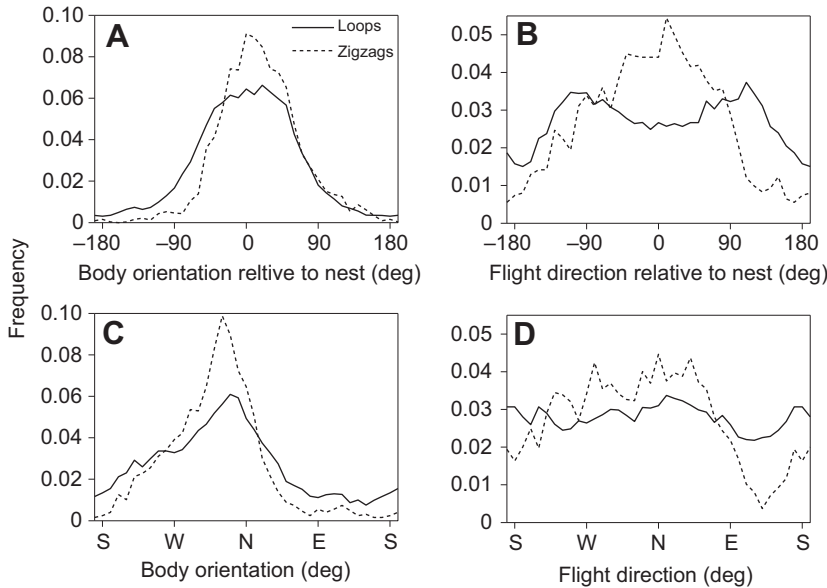
Fig. 1. Flight direction and body orientation during loops and zigzags of *Bombus terrestris*. (A,B) Distributions of body orientation (A) and flight direction (B) are plotted relative to the nest. (C,D) Distributions are replotted in compass coordinates: (C) body orientation, (D) flight direction. Continuous and dashed lines indicate loops (25,700 data points) and zigzags (3248 data points), respectively. Data pool: 375 loops and 130 zigzags from flights with two cylinders west of the nest and 401 loops and 149 zigzags from flights with two cylinders east of the nest.

based and compass-based flight directions combine to generate the bees' preferred viewing directions when facing the nest.

MATERIALS AND METHODS

We have worked with the same set of recorded flights that we studied previously (Hempel de Ibarra et al., 2009; Philippides et al., 2013). Bees (*Bombus terrestris* Linnaeus) were video-recorded from above as they emerged from or returned to a small nest-hole in a table placed in the centre of a large lawn or on a roof. The two different panoramas around the table are illustrated elsewhere (Hempel de Ibarra et al., 2009).

In addition to the loops and zigzags of the bees' learning and return flights, we also examine straight segments of flight that occur commonly in both types of flight (for selected examples see Fig. 2A). We extracted these segments manually. Short stretches of flight separated from each other by changes in direction are only included in the analysis if they lasted at least 80 ms (4 half-frames) with no detectable change of direction within the segment (e.g. Fig. 3B). The median root mean square error of the distance of points from the line is 0.3 mm (90th percentile=1.0 mm). The modal duration of a straight segment is 100 ms (5 half-frames).
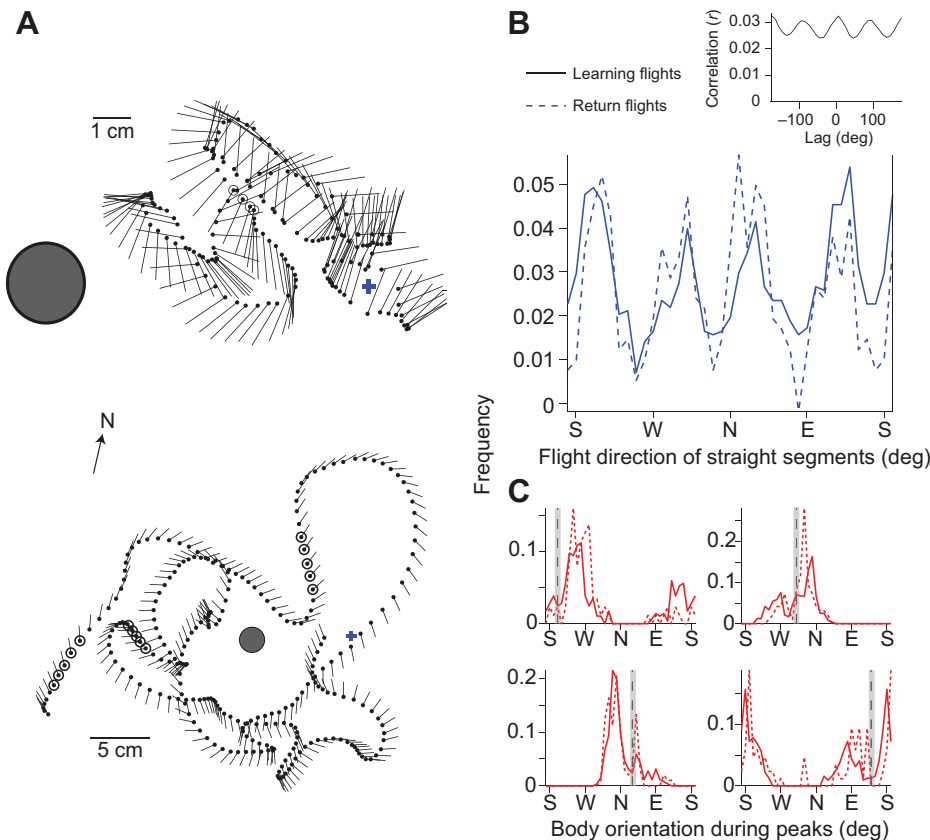

Fig. 2. Preferred compass directions during straight segments of flight in learning and return flights. (A) Two extracts from learning flights to illustrate brief straight segments. Some straight segments (but for clarity not all) are marked by halos around the bee's head. Grey discs mark the positions of cylinders and blue crosses the nest. (B) Frequency distributions of compass directions of straight segments during learning flights (continuous line, *N*=1278 segments) and return flights (dashed line, *N*=427 segments). Inset: cross-correlation between straight segments of learning and return flights. (C) Distributions of body orientation for flight segments that occur within 10 deg ranges of the four peak directions in B. Range of flight direction in each panel is marked by a 10 deg grey vertical bar superimposed on the distributions.
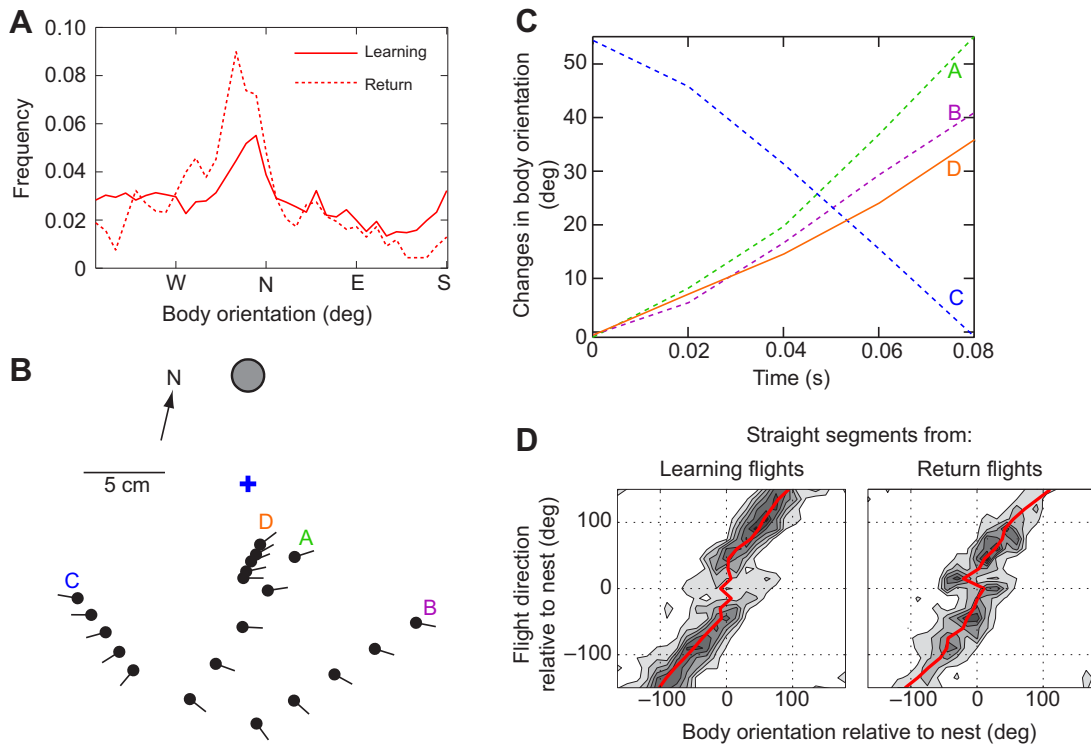
Fig. 3. Flight directions during straight segments are not linked to the orientation of the bee's body. (A) Distribution of compass orientations of body pooled over all frames of the distributions of straight segments of Fig. 2B. (B,C) Flight directions are straight despite large changes in the orientation of the body. (B) Example trajectories of straight flight direction but rotating body orientation. Letters mark the start of each sample. A–C are from return flights and D is from a learning flight. (C) Plots of body orientation during these trajectories with orientation normalized to 0 deg at the start of the sample. (D) Contour plots of flight direction relative to the nest against body orientation relative to the nest during the straight segments of learning and return flights. Learning flights: 5775 data points, contours step in tens from 0 to 70. Return flights: 1859 data points, contours step in fives from 0 to 30. Bin widths are 15 deg. The red line shows median flight direction.

In Figs 2–4, the data come from a set of 299 learning and 242 return flights recorded in 2007 (Philippides et al., 2013). For the analysis of the relations between nest-based and compass-based directions during loops and zigzags shown in Figs 5–8, we examined motifs from flights with two arrangements of cylinders. In one arrangement two cylinders were placed 20 cm to the east of the nest, and in the other they were placed to the west of the nest. We excluded arrangements in which cylinders were close to the nest, because in these cases loops can be focused on the cylinder rather than the nest (Philippides et al., 2013).

Loops were extracted semi-automatically as described in the companion paper (Philippides et al., 2013). The beginning and end of each loop was defined as the point where the flight path into and out of the loop crossed. We extracted obvious zigzags by hand. To obtain start and end points for these zigzags, we took half a zigzag, centred about a turn, as equivalent to a single loop. We estimated the direction of the major axis of the zigzag from the mean flight direction over at least one zigzag cycle. The start and end of a zig or zag are taken to be points on the rungs of the zigzag where the absolute angle between the direction of flight and the axis is at a maximum.

RESULTS
The directional control of straight segments of flight direction
Examination of learning and return flights reveals numerous short segments of straight flight that seem to be directed along particular compass directions (Fig. 2A). Frequency distributions of the compass directions of these straight segments exhibit four major peaks (Fig. 2B). The pattern of peaks is similar across learning and return flights and it is largely invariant to the arrangement of cylinders close to the nest (data not shown). The cross-correlation between the two distributions has four equally spaced peaks and troughs with a peak at zero lag that is marginally larger than the others (inset to Fig. 2B). The modulation depth is shallow, reflecting the noisy distributions. Learning and return flights thus appear to share a common directional framework based on compass direction.

How are these preferred flight directions controlled? To see what role might be played by the surrounding panorama, we examined the range of compass orientations of the bee's longitudinal axis associated with the preferred directions of the straight segments. The range of body orientations associated with each of the peak flight directions (±10 deg) extends over more than 50 deg (Fig. 2C). Body orientation usually varies little within each straight segment – by less than 10 deg in 40% of cases. However, sometimes orientation changes smoothly by as much as 50 deg without affecting the straightness of the segment (Fig. 3B,C). Further signs of a disjunction between body orientation and flight direction is that the distribution of the compass orientation of the body pooled over all straight segments has a single peak just west of north (Fig. 3A) that is quite different from the multi-peaked distribution of flight directions (Fig. 2B). In this case, it seems unlikely that compass directions of flight are set by keeping features of the surrounding panorama in fixed retinal positions. It is more plausible that the control of flight direction involves celestial and/or magnetic compass cues.

This independence between the bee's body orientation and its direction of flight in compass coordinates (cf. Fig. 2B and Fig. 3A) allows the bee to adjust its body orientation relative to the nest during straight segments. A plot of flight direction against body orientation, with both parameters measured relative to the nest, shows that during the straight segments bees keep their body oriented closer to the nest than their flight direction (Fig. 3D), as they do generally in learning and return flights (Philippides at al., 2013).

Compass-based and nest-based flight directions during loops and zigzags

Roughly 50% of the extracted straight segments of Fig. 2 occurred during loops and 25% during zigzags. The percentage during zigzags is probably an underestimate, as we were conservative in only extracting obvious motifs (Philippides et al., 2013). Both subsets of straight segments have a multiply peaked distribution of flight directions (Fig. 4A), which resembles closely the distribution of all the straight segments of Fig. 2B. As might be expected from the tear-like shapes of loops and the straight 'rungs' of zigzags (Fig. 4C), straight segments occur mostly at the entrances and exits of loops and during the rungs of zigzags (Fig. 4B) and are less frequent in the middle when bees fly towards and face the nest (Philippides et al., 2013).

These data lead us to ask whether bees fly in preferred compass directions at the start and end of loops and zigzags. This possibility is examined in Fig. 5 using data from flights with two cylinders east of the nest separated into clockwise (CW) and counter-clockwise (CCW) loops and zigs and zags. Plots show compass directions of flight when bees fly towards and face the nest plotted against flight directions at the start (left-hand column) or end (right-hand column) of the motif. There are correlated clusters of flight directions between the start of a loop or zigzag and the point at which bees fly towards the nest. Similar correlated clusters of directions occur between flying towards the nest and the end of the motifs. Bees flying CW loops tend to start in a flight direction that was just W of S. Their

flight direction when facing the nest rotated to N or ENE. They exited from the loop flying E. Bees performing CCW loops started from the E or close to S. They faced the nest flying N or WNW and left heading SW. Zigzags are similar but with tighter clustering.

Our definitions of start and end points of loops and zigzags may not match the bees' decisions. But we and the bees can agree on the direction in which bees fly towards the nest (ordinates of Fig. 5). The uncertainty of our definitions of start and end points is emphasized by the asymmetry of the data clusters in zigzags. The clusters are consistently wider at the assumed start and end of the motif (along the abscissa) than when bees face the nest (along the ordinate).

More detail of the compass directions of flight in loops and zigzags when bees both fly towards and face the nest is given in Fig. 6. Flight directions during zigzags have a single prominent peak (Fig. 6A). The distribution of compass directions is broader during loops and the peaks lie slightly to the west of the corresponding peaks of zigzags (Fig. 6A). Because bees tend to leave towards the south during learning flights and to arrive from the south on their return flights (see example in Fig. 4C), CCW peaks are to the west of CW peaks. These similarities in compass bearings across loops and zigzags are reflected in the similar views of the more northerly of the two cylinders that the bees obtain when facing the nest (Fig. 6B). As body orientation is more focused on the nest and is distributed over a tighter range of compass directions than flight direction (Fig. 1C,D), the distributions of retinal positions are correspondingly narrower (cf. Philippides et al., 2013).

How are nest-based and compass-based flight directions coordinated?

The data in Figs 1, 5 and 6 confirm that flight directions in loops and zigzags are controlled relative to both nest-based and compass-based reference frames, and raise the question of how these two reference frames are coordinated. The orderly change in compass-
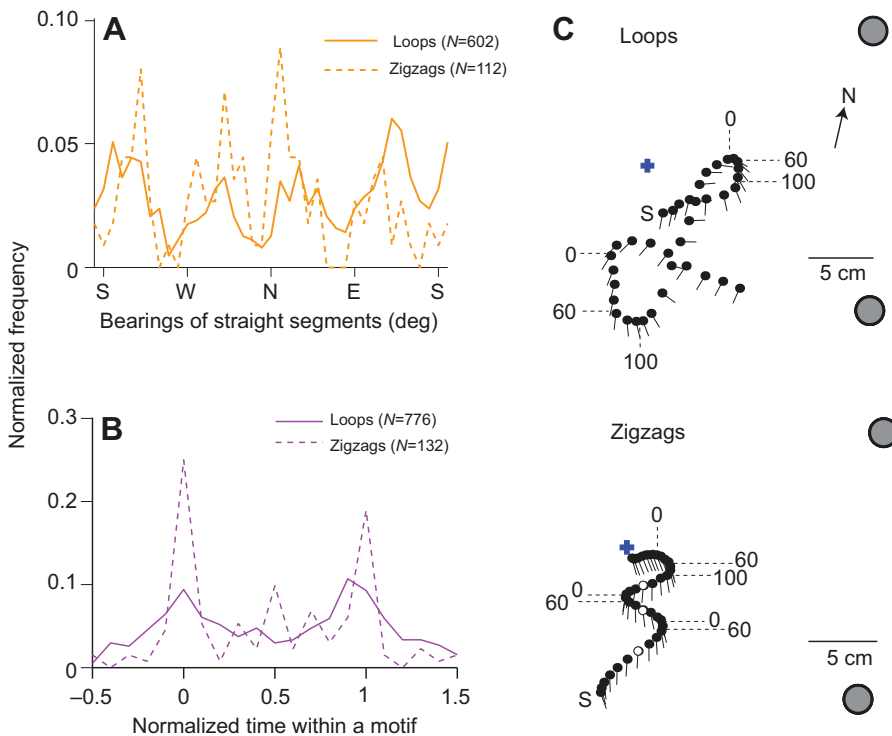

Fig. 4. (A) Distribution of the compass directions of those straight segments of flight in which some part of the segment occurs within loops and zigzags. Bin width is 10 deg. '*N*' shows the number of segments. Data extracted from 299 learning and 242 return flights. The preferred compass directions of this subset of straight segments match those from whole flights (see Fig. 3B). (B) Distribution of straight segments over the course of a loop and a half-zigzag. Motifs are normalized to 0 at the start, and 1 at the end. Bin width is 0.1. Data contain all lines occurring between 0.5 normalized units before and 0.5 units after the motif. (C) Examples of a pair of loops from a learning flight and a zigzag sequence from a return flight. The labels (100, 60, 0) indicate flight directions relative to the nest in degrees. Positions (•) and orientations (/) of bees are shown every 40 ms during loops and every 20 ms during zigzags. 'S' indicates start of excerpt and the schematic bees with empty heads indicate the assumed start or end of a zigzag. The grey discs denote the cylinders.
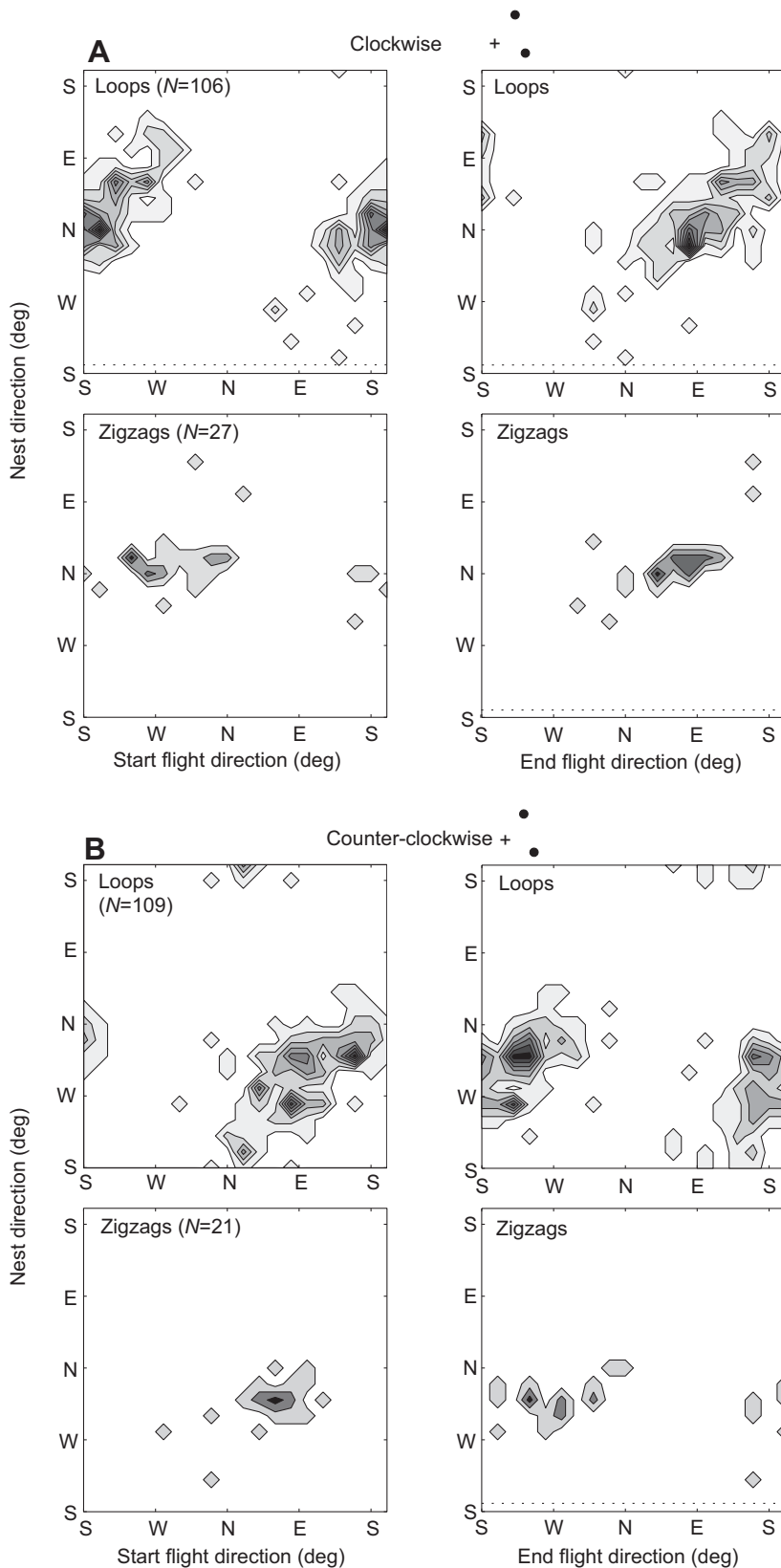
Fig. 5. Correlations between the compass directions of flight at different stages of loops and zigzags. For each loop and zigzag with a coincidence between flying towards and facing the nest, the compass direction of flight at the start (left-hand column) or end of the motif (right-hand column) is plotted on the abscissa and the bee's flight direction when heading towards the nest is shown on the ordinate: (A) CW loops and zigzags. (B) CCW loops and zigzags. Contour lines are in integer steps between 1 and a maximum value that differs with conditions (CW loops, maximum=10; CW zigzags, maximum=4; CCW loops, maximum=8; CCW zigzags, maximum=3).

based and nest-based directions during loops and zigzags (Fig. 5) may reflect a process in which bees begin a loop or zigzag in a preferred compass direction and then progress through a stereotyped nest-based manoeuvre. Alternatively, there may be continuous interactions between the two coordinate frames in which a bee adjusts its flight direction throughout the motif to ensure that it faces the nest in a preferred compass orientation. This adjustment could, for instance, account for the tighter clustering in flight directions seen when bees fly towards the nest than at the assumed start of the motifs (Fig. 5).
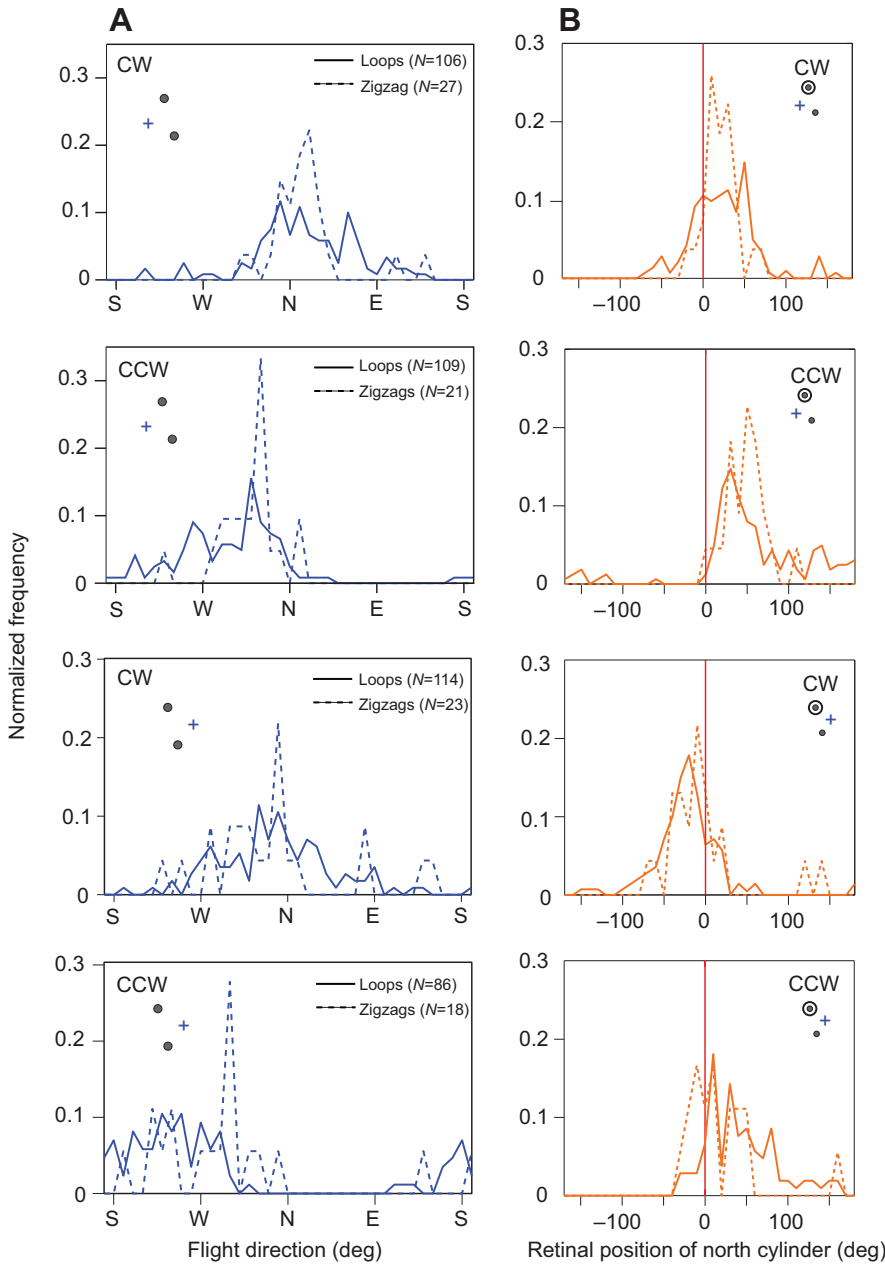
Fig. 6. (A) Distribution of compass directions during moments within loops and zigzags in which facing the nest (±10 deg) coincides with flying towards it (±10 deg). Inset shows whether cylinders (•) are to the west or east of the nest (+). Data from CW (rows 1 and 3) and CCW (rows 2 and 4) motifs are plotted separately. For both cylinder arrangements, the median compass directions towards the nest during CW loops and zigzags differ significantly from those of CCW loops and zigzags ($P<10^{-6}$, test for equal medians). (B) Data from same frames are replotted as retinal position of more northerly cylinder (shown by encircled •). Negative and positive angles are to the left and right of the bee's midline (red vertical line), respectively.

Current data favour the possibility that bees select a compass direction in which to start a motif and then continue the motif with no further interaction between nest-based and compass-based flight control. The evidence comes from tests that ask whether compass directions converge during the course of a loop or zigzag towards the bees' preferred compass direction when flying towards the nest. Because, the starting points of these manoeuvres are uncertain, we have worked backwards from the coincident point at which bees fly towards and face the nest.

Individual CW loops and half-zigzags were plotted as lines on a phase plane in which the ordinate is the bee's compass direction of flight and the abscissa is its flight direction relative to the nest (Fig. 7). The lines from individual loops and zigzags are parallel, indicating that, over this range of directions, the compass direction at the start of the loop or zigzag segment is a good predictor of the compass direction that is reached when the bee flies towards the nest. Flight directions do not converge towards a preferred compass direction during these segments.

The examples in Fig. 7 are corroborated by an analysis of all CW loops from flights with two cylinders to the east and west of the nest (Fig. 8). Because loops and zigzags are relatively similar over flight directions from about −80 to +80 deg relative to the nest, but then diverge (Philippides et al., 2013), we have restricted the range of flight directions that we examine. The analysis extends from 100 deg away from the nest until the bee flies towards the nest, as marked by '100' and '0' in Fig. 4C. For each CW loop and zigzag, we calculated the angular difference between the bee's compass direction of flight, when it flew at −100 or −60 deg relative to the nest, and its compass direction when flying towards the nest. These angular differences are plotted against the bee's compass direction when the flight direction relative to the nest was −100 or −60 deg (Fig. 8A,C). The distributions of the bees' initial compass directions are shown in Fig. 8B.

Convergence of flight directions towards a preferred compass bearing over the course of a loop or zigzag should show up in a dependence of angular difference on initial compass direction, but
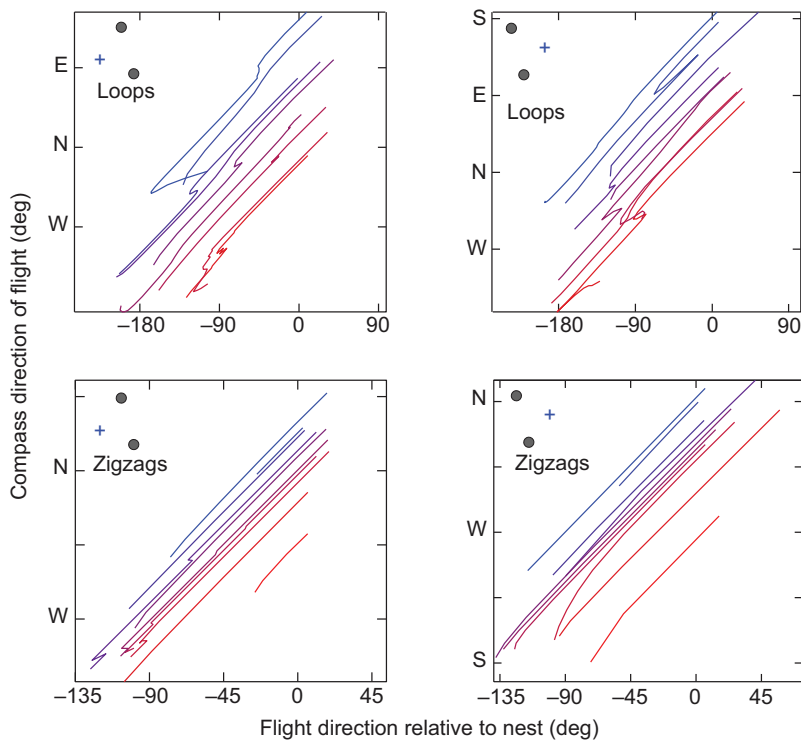
Fig. 7. Compass direction of flight *versus* flight direction relative to the nest during loops and zigzags. Individual CW loops and CW zigzags are shown as lines with compass direction of flight plotted against direction of flight relative to the nest.

in fact the angular differences for loops (Fig. 8A) and zigzags (Fig. 8C) are almost constant and are unrelated to the bee's starting compass direction. They give no evidence that bees adjust their flight direction during this segment of a loop or zigzag to converge on any particular compass direction.

A similar analysis shows that these angular differences are also independent of the size of a loop. We measured loop size (Fig. 8D) as the distance between the start of a loop as given by the crossing point of a bee's entrance and exit to the loop (Fig. 4C) and the point of the loop in which the bee faces and flies towards the nest (● in Fig. 8D). Two major features of this distribution are that loops are larger the further the bee is from the nest, and that CW loops are oriented in a roughly SE to NW direction. No systematic variation in angular differences with loop size is seen (Fig. 8E), indicating that the shape of a loop is invariant to size (cf. Philippides et al., 2013).

We conclude that the compass direction of flight, when bees fly towards the nest during loops and zigzags, is fixed by the compass direction chosen earlier in the motif and that over a large segment of the motifs there is no adjustment to enhance the coherence of the compass directions of flight when bees come to face the nest.

DISCUSSION
This and other work (Hempel de Ibarra et al., 2009; Philippides et al., 2013) shows that bumblebees use both compass-based and nest-based references to control their flight and facing directions during learning and return flights. The first conclusion of the present paper is that brief straight segments of flight are oriented preferentially in four compass directions that are the same across learning and return flights. The control of these directions seems to be independent of body orientation and is likely to come from compass cues rather than by keeping features of the surrounding panorama in fixed retinal positions.

Further evidence that straight segments of flight are in part controlled by compass cues comes from the comparison of learning flights recorded in two locations: on an open roof and on a lawn that is surrounded by trees, buildings and a hill (Hempel de Ibarra et al., 2009). The peak directions of the straight segments in the two locations exhibit close similarities, but also striking differences (Fig. 9). The peaks located roughly 'north' and 'south' are in the same direction in both surroundings, but the directions of the roughly orthogonal 'east' and 'west' peaks differ between the two locations (Fig. 9A). The same pattern is found for flights with the same cylinder arrangement (one cylinder to the north of the nest) on the lawn and on the roof (Fig. 9B). It seems that there is a roughly north–south directional axis, which is independent of local cues. The flexible orthogonal peaks suggest that bees also adopt preferred compass directions that are modulated by local variations, such as the prevailing direction of wind or light distribution (Hempel de Ibarra et al., 2009).

Setting flight direction through compass cues means that a bee can change its body orientation to keep the nest within its fronto-lateral visual field without disturbing control of flight direction. Additional mechanisms are needed to sustain a straight path should there be any external or internal perturbations. It is thought that honeybees (Heran and Lindauer, 1963; von Frisch, 1967) and bumblebees (Riley et al., 1999) exploit the separation between body orientation and direction of flight in order to maintain a fixed compass direction in varying crosswinds. The stronger the crosswind, the larger is the divergence between body orientation and flight direction (Heran and Lindauer, 1963; von Frisch, 1967). In principle, the bee can control its flight direction through the optic flow field generated by the ground beneath it. To do so, it adjusts its flight direction to keep the major axis of the flow field at a desired angle relative to the sun or sky polarization pattern, irrespective of the retinal position of the flow field (Collett et al., 1993; Riley et al., 1999).

The second conclusion of this paper is that the preferred compass directions that bees assume when facing the nest are accomplished without direct interactions between nest-based and compass-based
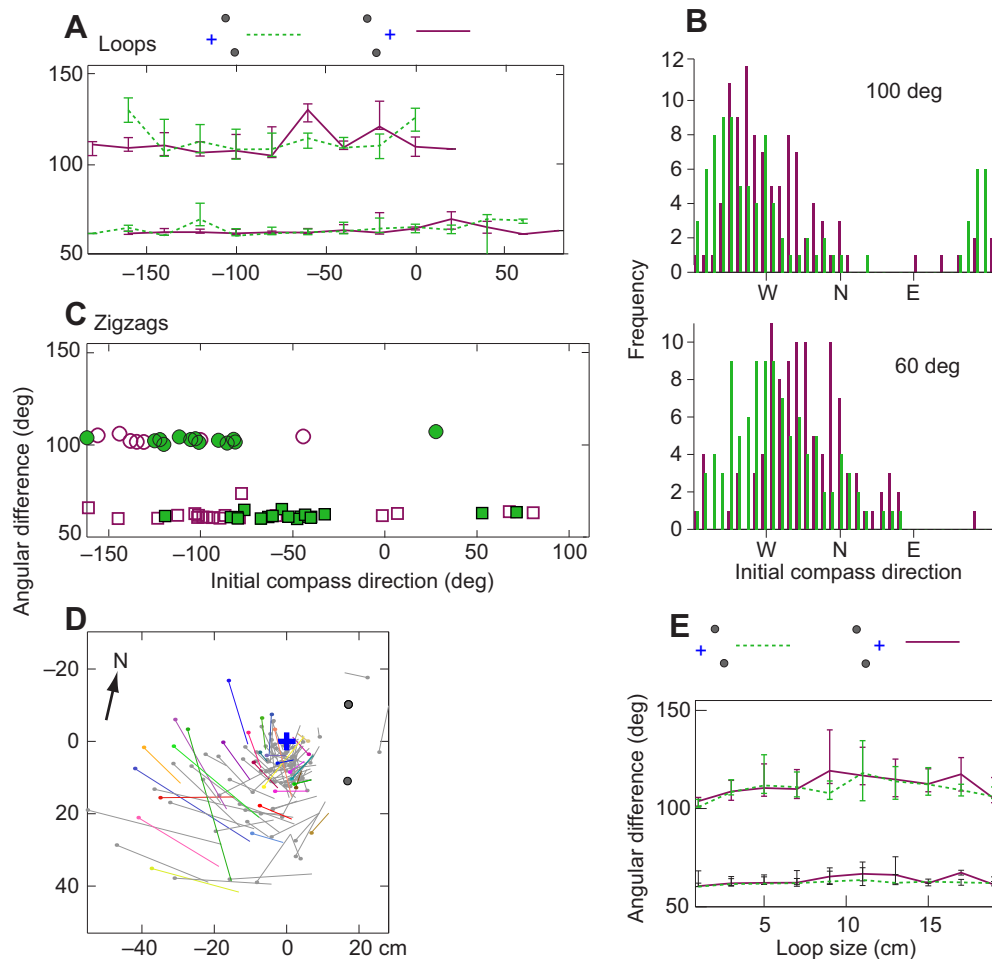
Fig. 8. Tests for direct interaction between a bee's compass direction of flight and its flight direction relative to the nest during segments of loops and zigzags. For each loop or zigzag, angular differences between the compass direction when the bee flew at −100 or −60 deg relative to the nest (Fig. 1) and the compass direction when the bee flew towards the nest are plotted against the bee's compass direction at these starting points. '0' on the abscissa indicates north; negative and positive values indicate west and east of north, respectively. (A) Angular differences of CW loops from flights with two cylinders to the east (dashed green lines) or the west (continuous purple lines) of the nest. In plots of compass direction *versus* direction relative to the nest, 207 out of 209 loops extend smoothly backwards from flying towards the nest to 60 deg away from the nest (cf. Fig. 8). One hundred and eighty-six of these loops extend further back to 100 deg. Data shown are median values of the angular differences for these loops within 20 deg bins. Error bars extend from the 25th to the 75th percentile. The median duration of the period between 100 and 0 deg relative to the nest is 41% of the period from the start of the loop to when the bee flies towards the nest. (B) Distributions of compass directions of these loops when the bee's flight direction is either 60 or 100 deg relative to the nest. Green bars: cylinders east of the nest. Purple bars: cylinders west of the nest. (C) Data for zigzags. Each data point plots a single CW half-zigzag. Filled green symbols are for cylinders east of the nest. Total number of half-zigzags is 27, of which 19 extend back to 60 deg and 13 to 100 deg. Open purple symbols are for cylinders west of nest. Twenty out of a total of 23 half-zigzags extend back to 60 deg, and nine to 100 deg. The median duration of the period between 100 and 0 deg relative to the nest is 45% of the period from the start of a half-zigzag to when the bee flies towards the nest. (D,E) Lack of correlation between loop size and angular difference. (D) Size of CW loop was estimated by the distance (line on plot) between the start of the loop and the point at which the bee faces and flies towards the nest (•). (E) Angular difference between bee's compass direction, when it flew at −100 or −60 deg relative to the nest and towards the nest, is plotted against the size of the loop. Data come from same CW loops analysed in A–C. Dashed green lines show data from flights with two cylinders east of nest. Continuous purple lines show data with cylinders west of nest.

control of flight direction. Instead, loops are sufficiently stereotyped so that when a bee starts a loop or zigzag in a given compass direction, it will face the nest after a predictable change of compass direction. Such stereotypy of flight motifs should simplify the task of decoding the visual input generated during a motif's execution and help the bee acquire reliable visual information about the nest's surroundings.

The stereotypy of loops and zigzags implies that bees 'know' where to begin a motif. During the loops of learning flights bees can in principle know their direction relative to the nest through path integration and begin a loop when they are flying in an

appropriate nest-related direction. The start of a turn during a zig or zag can only be determined by reference to landmarks. As yet we do not understand how it is done, except that it probably depends upon interactions between learnt compass directions of flight (Hempel de Ibarra et al., 2009) and the retinal positions of landmarks.

Finally, the findings presented here and in the companion paper (Philippides et al., 2013) suggest why it is that the frequency distribution of body orientations has a narrower range of compass bearings than that of flight directions (Fig. 1C,D), even though it is flight direction, rather than body orientation, that seems to be under direct compass control. An explanation begins with Fig. 5 where it
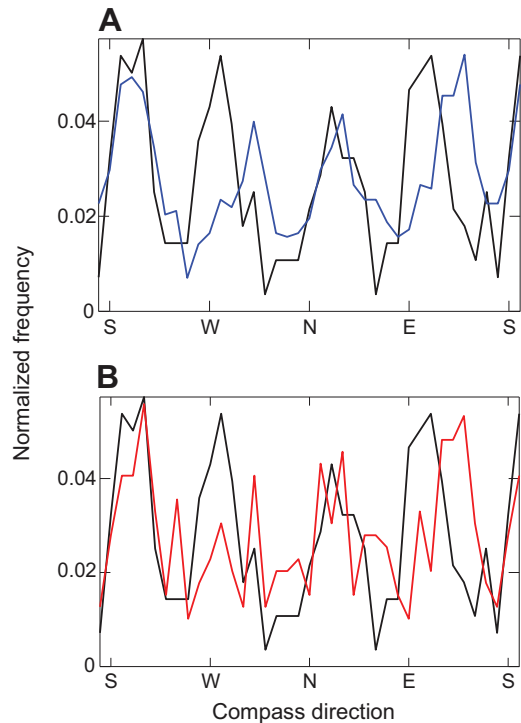
Fig. 9. Comparison of the peak compass directions of the straight segments of learning flights in two locations. (A) The black line shows distribution of compass direction of 279 straight segments from learning flights recorded on an open roof with one cylinder north of the nest. The blue line gives similar distribution of 1278 straight segments recorded on an enclosed lawn with data drawn from all cylinder arrangements. (B) The black line is as in A. The red line shows distribution of orientations of a subset of 394 of the 1278 straight segments recorded on the enclosed lawn. The subset contains straight segments from flights with a single cylinder north of the nest, to correspond to the arrangement on the roof.

that there is a phase lead of body orientation relative to flight direction before the bee flies towards and faces the nest and a phase lag after flying towards the nest. This combination means inevitably that body orientation has a relatively narrow range of compass directions. Thus by varying the angle between body orientation and flight direction, bees not only ensure that their viewing direction is concentrated around the nest, but also that they view the nest over a narrow range of compass bearings.

is shown that the compass bearing of flight direction rotates over the course of loops and zigzags from a consistent direction at the start, to another when flying towards the nest in the middle, and a third when ending the motif. During the same motifs, body orientation is more focused on the nest than is flight direction, so

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