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On the Encoding of Panoramic Visual Scenes in Navigating Wood Ants

Highlights

- Ants navigating within a panorama composed of two shapes identify each shape

- Shapes are identified through their intrinsic visual features

- Shapes are also identified through the relative positions of their centers of mass

- Ants learn a direction of travel relative to each shape and merge the directions

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In Brief

Buehlmann et al. infer how navigating ants encode a two-shape panorama. Imagine a ring of beads fixed on top of an ant's head, of which two are colored. Each colored bead denotes the horizontal position of the center of mass of one shape learned when approaching the goal. The ant then aims at the goal by turning to align both beads with the shapes.

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Report

On the Encoding of Panoramic Visual Scenes in Navigating Wood Ants

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http://dx.doi.org/10.1016/j.cub.2016.06.005

SUMMARY

A natural visual panorama is a complex stimulus formed of many component shapes. It gives an animal a sense of place and supplies guiding signals for controlling the animal's direction of travel [1]. Insects with their economical neural processing [2] are good subjects for analyzing the encoding and memory of such scenes [3–5]. Honeybees [6] and ants [7, 8] foraging from their nest can follow habitual routes guided only by visual cues within a natural panorama. Here, we analyze the headings that ants adopt when a familiar panorama composed of two or three shapes is manipulated by removing a shape or by replacing training shapes with unfamiliar ones. We show that (1) ants recognize a component shape not only through its particular visual features, but also by its spatial relation to other shapes in the scene, and that (2) each segmented shape [9] contributes its own directional signal to generating the ant's chosen heading. We found earlier that ants trained to a feeder placed to one side of a single shape [10] and tested with shapes of different widths learn the retinal position of the training shape's center of mass (CoM) [11, 12] when heading toward the feeder. They then guide themselves by placing the shape's CoM in the remembered retinal position [10]. This use of CoM in a one-shape panorama combined with the results here suggests that the ants' memory of a multi-shape panorama comprises the retinal positions of the horizontal CoMs of each major component shape within the scene, bolstered by local descriptors of that shape.

RESULTS AND DISCUSSION

To investigate how wood ants (*Formica rufa* L.) encode multi-shape scenes, we trained wood ants to go from the center of a circular platform to collect sugar water at the periphery (Figure 1A). The feeder was positioned relative to a 360° panorama consisting of a low black border on which two or three shapes (triangles and rectangles) were placed. This panorama was fixed to the white inner wall of a rotatable cylinder (diameter 3 m; height 1.8 m). Such sparse scenes are experimentally tractable,

and, because ants maintain the same heading when a natural panorama is reduced to a crude black replica of the skyline [8], these artificial scenes are likely to engage visual mechanisms that guide ants in a natural panorama. To ensure that the panorama alone guided the ants' behavior, the cylinder and feeder were rotated relative to the room after each trial. Ants were trained in groups for the first 30 or so trials and then trained singly with tests introduced every three or four training trials. A new batch of ants was trained for each experiment.

We ask first whether ants can recognize a single shape from a two-shape panorama solely by its intrinsic features, such as the orientation of its bounding edges [9, 12, 13] and its width [14]. Ants were trained to find food between a rectangle and an isosceles triangle. In one experiment (Figure 1C1) the food was closer to the triangle and in others closer to the rectangle (Figures 1B1 and S1). The individual shapes were bilaterally symmetric so that the shape's intrinsic properties did not bias the ants' heading direction to one side. We analyzed the ants' heading direction over the initial 30 cm of their path both during training and in one-shape tests in which the panorama comprised just the rectangle or the triangle (Figures 1B and 1C). By limiting analysis to a short initial segment, we hoped to avoid problems that are caused by changes to the scene imaged on the ant's retina during the ant's approach to the feeder.

The ants' headings in one-shape tests were significantly closer to the shape than they would be had ants kept the shape's center of mass (CoM) in the retinal position appropriate for reaching the feeder (the CoM-defined direction, C). Headings in tests with the rectangle tended to be to the correct side of the shape (Figures 1B2, 1C2, and S1), but it was unclear whether ants headed directly at the triangle or just to one side of it (Figures 1B3, 1C3, and S1). In two (Figures 1B and 1C) out of the three experiments, the angle between the shape's CoM and the ants' median headings differed significantly between the rectangle and triangle. Thus, ants can discriminate the rectangle from the triangle, but they fail to head in the CoM-defined direction.

A testable explanation of this failure to take the CoM-defined direction is that recognition of a component shape within a panorama is incomplete when the shape is not set in the context of its neighbors. Since ants trained to guide their path with a single shape seem to do so by keeping the shape's CoM in a remembered retinal position [10], we suggest that directional guidance within a multi-shape panorama is similar. On this hypothesis, an ant's memory of a panoramic scene consists primarily of the retinal position of each component shape's CoM, forming a kind of "bar code" that is enhanced by linking each shape's visual features to its CoM position (Figure 1D). To clarify what

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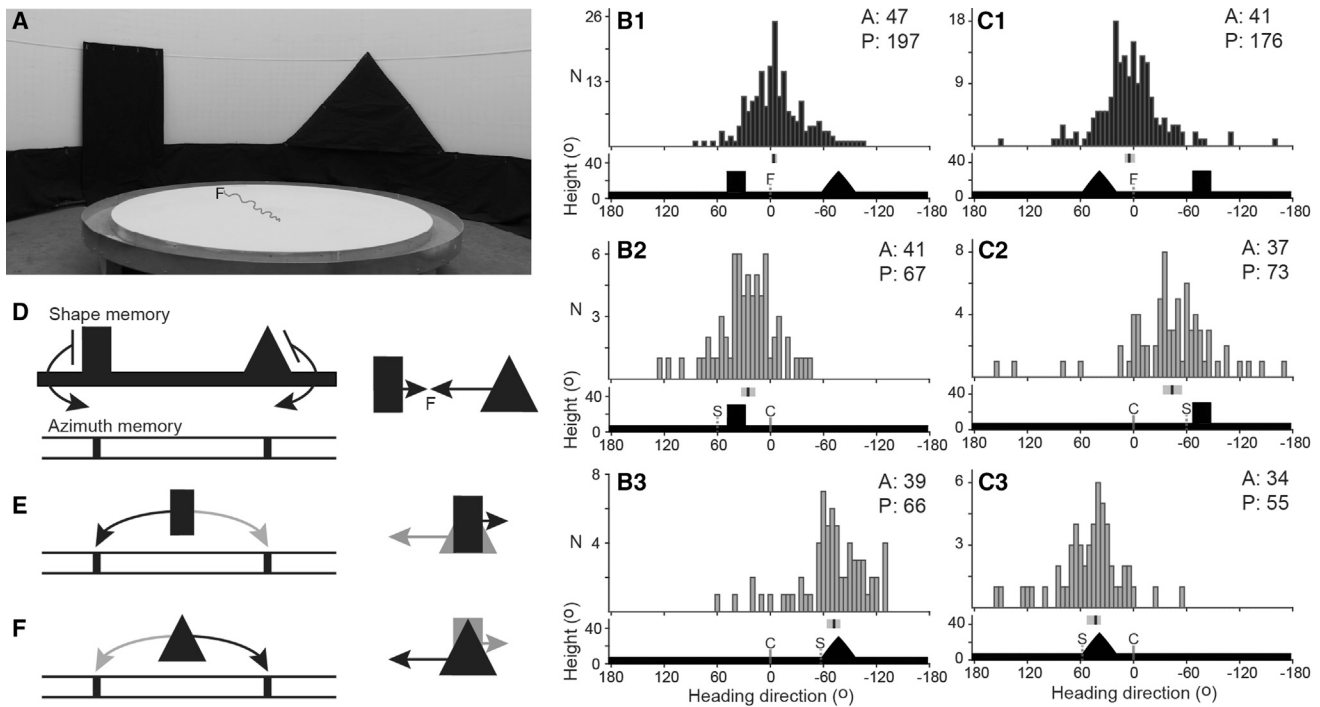
Figure 1. Headings of Ants Trained to a Feeder between a Rectangle and a Triangle

(A) Experimental setup with example ant path: "F" denotes feeder at the edge of the circular platform.

(B and C) Training and one-shape tests.

(B1 and C1) Training conditions. Here and elsewhere, the lower part of each panel shows the unwrapped panorama centered on the direction of the food (dotted line labeled "F"). Above is the distribution of individual heading directions (black) during training projected on to the panorama. The black vertical line and gray bar below each histogram show respectively the median heading and its 95% confidence interval. "A" indicates number of ants. "P" indicates number of paths.

(B2 and C2) Tests with rectangle (distributions in gray). Line labeled "C" gives the CoM-defined direction of the feeder and "S" the predicted direction of the feeder for a CoM computed across both shapes. 0° in tests indicates the predicted CoM-defined direction relative to the test shapes.

(B3 and C3) Tests with triangle. The headings in all four tests differed significantly from the CoM-defined direction (paired Wilcoxon signed rank test comparing CoM-defined directions between training and test distributions; B2: n = 41, Z = 4.98, p < 0.0001; C2: n = 37, Z = 4.67, p < 0.0001; B3: n = 39, Z = 4.95, p < 0001; C3: n = 34, Z = 4.68, p < 0001). In (B), the angular separation between the CoM of the rectangle and the ants median heading (12.2°) was significantly larger than the 4° difference between the ants' median heading and the CoM of the triangle (paired Wilcoxon signed rank test: n = 37, Z = −2.8, p < 0.01). In (C), the same two angular separations (rectangle: 38°; triangle: 5°) also differ significantly (paired Wilcoxon signed rank test: n = 32, Z = 2.7, p < 0.01).

(D) Left: representation of memory of training panorama with position of each shape's CoM stored in a bar code (azimuth memory) and linked to its visual features (shape memory). Right: directional vectors activated by the training pattern.

(E) Left: rectangle in one-shape tests activates both CoM components. Black arrow indicates CoM linked to rectangle; gray arrow indicates CoM linked to triangle. Right: activation of vectors associated with both CoMs. Both vectors originate at the position of the test rectangle's CoM. Length of arrow represents relative angular separations between feeder and each shape's CoM.

(F) As in (E), with one-shape triangle test. Black and gray arrows indicate respectively vectors linked to the triangle and rectangle.

See also Figure S1.

we mean by bar code in this context, imagine a ring of 100 beads of which a few, each corresponding to a bar, are decorated and that the ring is fixed on top of the insect's head. Each decorated bead, just two in this case, represents the center of one of the panorama's component shapes memorized when the ant heads toward a goal. The ant can then aim at the goal by aligning the decorated beads with the shapes' CoMs.

With the two-shape panorama reduced to one shape, the ant may be uncertain in which position to place each decorated bead and may try to align both decorated beads with the test shape. In other words, with no bar code pattern to support identification, the ant activates memories of both training shapes and their associated headings (heading vectors). As both heading vectors originate at the CoM of the test shape, they no longer agree in pointing to the same CoM-defined direction. Instead

they pull the ants in opposite directions (Figures 1E and 1F). It may help to think of interactions between the two heading vectors not as the outcome of an internal computation, but rather as a consequence of ants turning rapidly between placing a single shape first in the remembered retinal position of the rectangle's CoM and then in that of the triangle so that the resultant heading lies somewhere between these CoM positions.

In the experiments shown in Figure 1, the rectangle dominates the triangle. Given just the rectangle, the ant is pulled more in the direction defined by the rectangle (Figures 1B2 and 1C2). Vertical edges are particularly attractive in several insects [15, 16] and may also make the rectangle potent here. However, in tests with the triangle alone (Figures 1B3 and 1C3), the heading vector associated with the rectangle is likely to be activated more weakly so that the resultant heading is aimed roughly toward
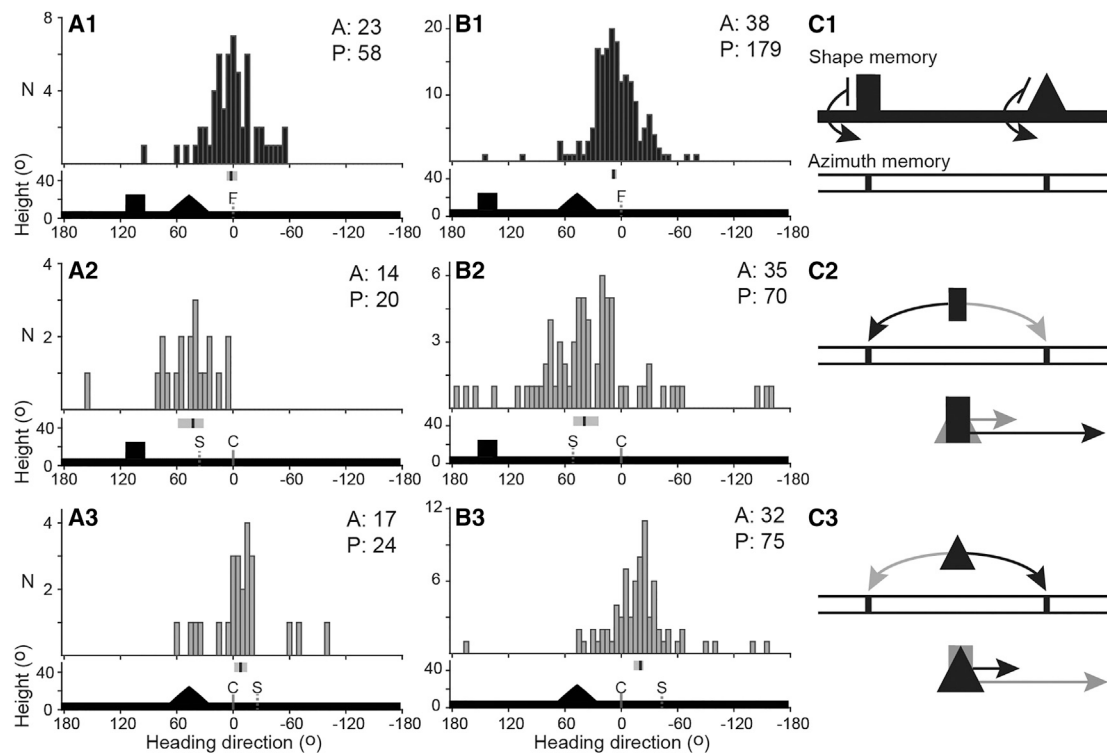
Figure 2. Headings with Feeder to One Side of Two Training Shapes

(A1 and B1) Distribution of headings with training panorama. CoMs of rectangle and triangle are separated by 57° (A1) and 95° (B1), respectively.

(A2 and B2) Rectangle tests. Ants' median heading was significantly further from the rectangles' CoM with the 95° separation than with the 57° separation (two-sample Wilcoxon rank-sum test: n = 14, 35; Z = −3.9; p < 0.001).

(A3 and B3) Triangle tests. Angles between triangles' CoM and median heading did not differ significantly between the 95° and 57° separations (two-sample Wilcoxon rank-sum test: n = 17, 32; Z = −1.8; p = 0.07).

(C1) CoM positions of each training shape memorized as a bar code with linked visual features.

(C2 and C3) Suggested activation of memories and directional vectors in one-shape tests (cf. Figures 1E and 1F).

The black line and gray bar below each histogram indicate respectively the median heading direction and its 95% confidence interval. Abbreviations and conventions are as in Figure 1.

the triangle in both tests. The similar headings in Figures 1B3 and 1C3, despite the very different angular separations between the triangles and the feeder during training, suggest also that the heading vectors may be weighted more strongly the closer the feeder is to the CoM of a shape.

The model depicted in Figures 1D–1F can be probed with an experiment in which ants are trained to a route with the two shapes on the left side of the food (Figure 2). The headings associated with the two shapes will then be in the same direction. Consequently, ants in one-shape tests generating a weighted average of the two headings should aim too far to the right of the right-hand shape (Figure 2C3) and not far enough from the left-hand shape (Figure 2C2). For training, a triangle was placed to the left of the food and a rectangle to the left of the triangle. In one experiment, the angular separation between the shapes' CoMs was 57° (Figure 2A1), and in a second experiment, it was 95° (Figure 2B1), with the separation between the triangle and the food kept constant.

The ants' headings in the one-shape tests fulfil the model's predictions. Ants tested with the rectangle alone (Figures 2A2 and 2B2) undershot and went significantly to the left of the CoM-defined direction (paired Wilcoxon signed rank test

comparing training and test distributions aligned on the CoMs of the shape; Figure 2A2: n = 14, Z = 2.42, p = 0.0157; Figure 2B2: n = 35, Z = 2.78, p = 0.0054). Ants trained with the smaller separation and tested with the triangle alone (Figure 2A3) headed just to the right of the CoM-defined direction, and the median heading was not significantly different from it (paired Wilcoxon signed rank test: n = 17, Z = 1.21, p = 0.2274). With the larger separation (Figure 2B3), the median heading in tests with the triangle was significantly to the right of the CoM-defined direction (paired Wilcoxon signed rank test: n = 32, Z = 4.02, p < 0.0001).

These tests also show that the ants discriminate between the two shapes. For the 95° separation (but not for the smaller separation), the angle between the CoM of the test shape and the ants' median heading was significantly larger in tests with the rectangle than with the triangle (Figures 2B2 and 2B3; paired Wilcoxon signed ranks test: n = 31, Z = 4.37, p < 0.0001). Thus, ants presented with one shape seem to retrieve the memories of both shapes, but their heading is more strongly influenced by the memory corresponding to the presented shape. A further inference from the data (supported by the data of Figure 1) is that vectors associated with shapes close to the feeder are more strongly weighed than those of shapes that are further from the
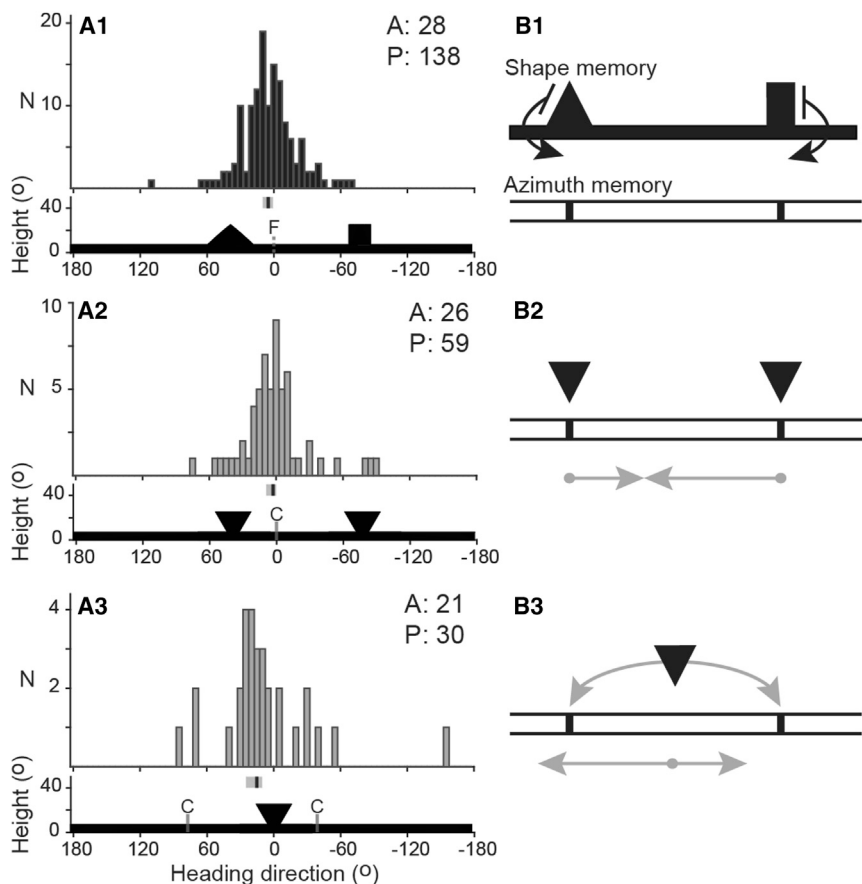
Figure 3. Training Headings Are Maintained when Unfamiliar Shapes Replace Familiar Ones

(A1) Distribution of headings with training panorama.

(A2) Tests with two inverted triangles. Median heading does not differ significantly from the median headings during training (paired Wilcoxon signed rank test: n = 26 and 26, Z = 0.37, p = 0.7127).

(A3) Tests with one inverted triangle. Line labeled C shows CoM-defined directions of rectangle and triangle. Median heading differs significantly from both these CoM-defined directions (paired Wilcoxon signed rank test; rectangle: n = 21, Z = 4.01, p < 0.0001; triangle: n = 21, Z = 3.74, p = 0.0002).

(B1) CoM positions of each training shape memorized as a bar code with linked visual features.

(B2) Memory activation in tests with two inverted triangles. Each inverted triangle activates memory of one CoM component and its associated directional vector. Origins of component vectors are as in training.

(B3) Single inverted triangle activates memories associated with both bar code positions. Associated vectors originate at the shape's CoM leading to a compromise heading.

The black line and gray bar below each histogram indicate respectively the median heading direction and its 95% confidence interval. See also Figure S2 and Table S1.

feeder or possibly separated from the feeder by an intervening shape.

The different headings relative to the triangle and rectangle in one-shape tests (Figures 2B2 and 2B3) argue against an alternative explanation of the results in which direction is set relative to a CoM computed across the two shapes of the training scene. If ants were to compute a CoM from the left edge of the left-hand shape to the right edge of the right-hand shape, they should head 92° to the right of each test shape (S in Figures 2B2 and 2B3). In fact, the headings relative to the CoM of both the triangle and the rectangle differ significantly from 92° (paired Wilcoxon signed rank test comparing test with training distributions; Figure 2B2: n = 35, Z = 2.36, p = 0.0183; Figure 2B3: n = 32, Z = 3.68, p = 0.0002). These differences are less clear when the separation between the shapes in the training scene is smaller (Figure 2A1). Headings relative to the test triangle differ significantly from S (72°) (paired Wilcoxon signed rank test; Figure 2A3: n = 17, Z = 2.3, p = 0.0217), but this is not the case for headings relative to the test rectangle (paired Wilcoxon signed rank test; Figure 2A2: n = 14, Z = 0.91, p = 0.3627).

The headings in one-shape tests on ants trained to a feeder that lay between the triangle and rectangle (Figure 1) also cannot be explained by a CoM computed over both shapes. Again ants in one-shape tests tend to take different headings relative to the triangle and rectangle. Furthermore, there are significant differences between the ants' headings in one-shape tests and the

angular distance between the CoM computed over the two shapes and the feeder (S). The value of S is 20° for the training arrangement of Figure 1B1 and 16° for that of Figure 1C1. The headings relative to the test rectangle differ significantly from S in the test shown in Figure 1B2 but not in those shown in Figure 1C2 (paired Wilcoxon signed ranks test; Figure 1B2: n = 41, Z = 4.5, p < 0.0001; Figure 1C2: n = 37, Z = 1.92, p = 0.0544). The headings relative to the test triangles differ significantly from S in the tests of Figure 1B3, but not in those of Figure 1C3 (paired Wilcoxon signed ranks test; Figure 1B3: n = 39, Z = 2.14, p = 0.0328; Figure 1C3: n = 34, Z = 1.77, p = 0.0768).

While it is clear that ants are able to discriminate between the rectangle and the triangle, it is uncertain how they do it. Since ants can distinguish very cleanly between a vertical and an oblique edge (Figure 4 in [9]), the outputs of filters sensitive to edge orientation may contribute to identifying a shape. The vertical positions of the rectangle and triangle also differ, and neurons sensitive to this feature [3] may also contribute to distinguishing one shape from another.

If the failure to take the CoM-defined direction in one-shape tests occurs because an isolated shape lacks a neighbor in the expected position, we should find evidence that ants memorize the angular separation between two training shapes. Accordingly, we examined whether two unfamiliar shapes placed the right distance apart can substitute for the training configuration. Ants trained with a triangle and rectangle (Figure 3A1) were tested with both shapes replaced by inverted triangles
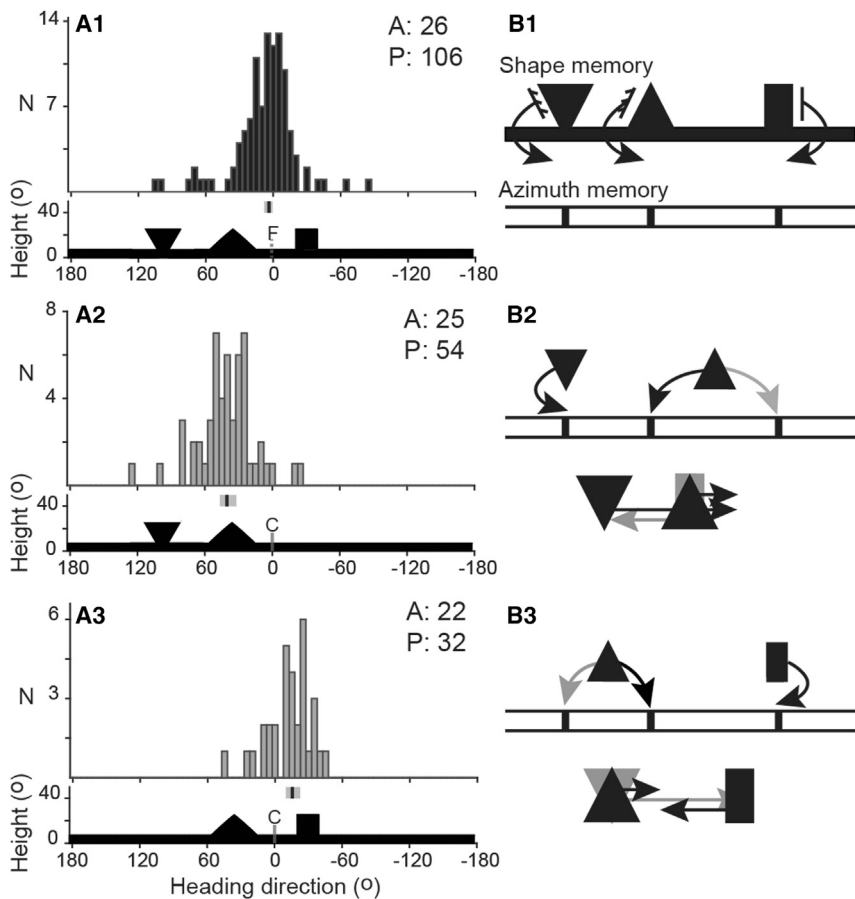
Figure 4. Headings with Three-Shape Scenes

(A1) Headings with training panorama.

(A2) Tests without the rectangle. Median heading differed significantly from the CoM-defined direction (paired Wilcoxon signed rank test comparing training and test distributions; n = 25, Z = 4.32, p < 0.0001).

(A3) Tests without inverted triangle. Median heading differed significantly from the CoM-defined direction (paired Wilcoxon signed rank test; n = 22, Z = 3.3, p = 0.001).

(B1) CoM position of each training shape memorized as a bar code with linked visual features.

(B2 and B3) Suggested activation of memories and heading vectors during tests. One shape in each test is recognized unambiguously by its context (see text); the other shape activates memories associated with the other two shapes. Hatching on shape memory edges emphasizes that the edge polarity is reversed between the inverted and normal triangle.

The black line and gray bar below each histogram indicate respectively the median heading direction and its 95% confidence interval. See also Figure S3.

(Figure 3A2). Headings in this test did not differ from those during training.

In contrast, ants presented with a single inverted triangle did not adopt a CoM-defined direction and seemed to take some compromise direction. Taken together, the data in Figure 3 suggest that, when component shapes are properly positioned with respect to each other, ants are able to match the test pattern to the two learned CoM positions (Figure 3B).

This conclusion gains support from tests in which the angular separation between the rectangle and triangle is increased from the training value (Figure S2). The ants' headings become more variable (Table S1) and are slightly biased toward the rectangle (Figure S2). There are at least two possible explanations of the increased variance. First, recognition of individual shapes degrades when the separation between the shapes is larger than in training, resulting in more variable headings. A second possibility is that the shapes are correctly identified, despite the increased separation, but that the separation causes disagreement between the heading directions activated by the two shapes and that this conflict is resolved differently by different ants.

To check whether the conclusions derived from experiments with two shapes might hold for more complex panoramas, we explored the ants' ability to head in the CoM-defined direction when they were trained with three shapes and tested with one shape removed. The many-shape problem that emerges once scenes are enlarged beyond two shapes means that we only test whether the results are consistent with a plausible hypothe-

sis. We cannot discard alternative accounts of the three shape data.

The training panorama was a triangle and rectangle placed either side of the feeder, with an additional inverted triangle to the left of the pair flanking the food (Figures 4A1 and S3). In tests, the shape at either the right or the left end of the trio was removed. Ants did not take the CoM-defined direction in either test. Without the right-hand shape, the ants headed just to the left of the triangle, i.e., significantly to the left of the CoM-defined direction (Figure 4A2). In tests with the left-hand shape removed (Figures 4A3 and S3A2), the ants' heading was significantly to the right of the CoM-defined direction and just to the left of the rectangle.

One account (Figure 4B) of the two-shape tests has a similar logic to the explanation of the one-shape tests in Figures 1 and 2. The inverted triangle in Figure 4A2 and the rectangle in Figure 4A3 are identified unambiguously because their immediate surroundings—the triangle on one side and nothing to the other—are as in training. The unusual position of the triangle, at one or the other end of the panorama, makes its identity uncertain. Its visual features and its accustomed neighbor on one side suggest that it is the triangle, but it could be mistaken for the missing neighbor on the other side. Consequently, both component vectors are activated. The combination of the three component vectors evoked by the two test shapes (Figures 4B2 and 4B3) will replicate the ants' heading. The necessary weighting of the three components is similar to the one-shape tests of Figure 2. Namely, the component vector associated with the inverted triangle, both separated by a shape from the feeder and distant from it, is weaker than the vectors associated with the two shapes immediately flanking the feeder.

Several computational papers (e.g., [17–20]) have suggested how an insect might set its direction of travel along a route by

matching a current view to a memorized view that it stored when first taking the route. These studies have suggested computationally plausible mechanisms [17–19] that could underlie alignment image matching [21] and have demonstrated that in principle hundreds of independent images can be stored [20]. However, how insects actually implement alignment image matching remains unclear. We hope that our current findings will contribute to answering this question. From these and earlier experiments [9, 10], we conclude that ants segment a scene into component shapes, probably at troughs in the skyline [9]. For navigation, the CoM of each component shape aims to be placed in its memorized retinal position [10] and thus contributes a signal to the ant's heading (cf. [22, 23]). A component shape is identified both by the relative position of its CoM within a bar code pattern and also by its intrinsic visual features [9], although the experiments of this paper do not establish what these features are.

More generally, the current data indicate that ants encode and remember a panorama as the positions of the component shapes' CoMs laid out in a ring. This parsimonious memory is enhanced by attaching details of each shape to its CoM position. Although for navigation within a panorama, CoMs are encoded retinotopically [10], there may be parallel encodings of the bar code in, for instance, relative or compass coordinates [24]. These memories could be realized in the neural circuits of the mushroom bodies [20, 25–27] and/or in the fan-shaped body of the central complex [3]. However, the visual processing involved may well originate in mechanisms with a primary role in allowing insects to approach specific objects like grass stalks [15] and to aim at the CoM of single objects [28].

SUPPLEMENTAL INFORMATION

Supplemental Information includes Supplemental Experimental Procedures, three figures, and one table and can be found with this article online at http://dx.doi.org/10.1016/j.cub.2016.06.005.

AUTHOR CONTRIBUTIONS

MATLAB scripts were written by J.L.W. All three authors contributed equally to this work.

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