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Report

Visual Scene Perception in Navigating Wood Ants

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Summary

Ants, like honeybees, can set their travel direction along foraging routes using just the surrounding visual panorama [1–5]. This ability gives us a way to explore how visual scenes are perceived. By training wood ants to follow a path in an artificial scene and then examining their path within transformed scenes, we identify several perceptual operations that contribute to the ants' choice of direction. The first is a novel extension to the known ability of insects to compute the "center of mass" of large shapes [6–9]: ants learn a desired heading toward a point on a distant shape as the proportion of the shape that lies to the left and right of the aiming point—the 'fractional position of mass' (FPM). The second operation, the extraction of local visual features like oriented edges, is familiar from studies of shape perception [8, 10–12]. Ants may use such features for guidance by keeping them in desired retinal locations [13, 14]. Third, ants exhibit segmentation. They compute the learned FPM over the whole of a simple scene, but over a segmented region of a complex scene. We suggest how the three operations may combine to provide efficient directional guidance.

Results and Discussion

Ants are thought to set and control their direction toward a goal in a familiar, panoramic scene by turning to match the scene on their retina to one that they previously learned when facing in the direction of the goal (see [15] for review). But the perceptual processes involved in matching a scene to its memory are not well understood. To learn more about the ways in which wood ants (*Formica rufa* L.) perceive scenes and derive directional information from them, we have trained ants to follow indoor foraging routes relative to visual scenes. Ants were released from the center of a cylindrical arena to approach a food reward along a direction specified by a wide shape on the arena wall 150 cm away (Figures 1A and S1A, available online). Once the ants had learned the correct direction relative to the shape, we examined the paths that they took when confronted with new test shapes.

The ants' facing directions in the test scenes allow us to examine whether their performance is consistent with various possible mechanisms of scene matching. The tests suggest that at least two perceptual processes provide cues for the ants' directional guidance. Information comes in part from prominent local visual features of a scene, like oriented edges [8, 10–12]. Guidance by a local feature is indicated when an ant places a feature of a test scene in the same retinal position as the equivalent feature in the training scene [13].

These tests also indicate a novel mechanism of directional guidance. Several insects compute the horizontal and/or vertical center of mass of an extended visual pattern [6–9]. Here, we give evidence that they perform this type of global computation more flexibly. They can encode a learned direction toward a point in a scene as the proportion of the 2D mass of the scene that lies to either side of that point—the fractional position of mass (FPM). To give a concrete example, an ant may set its facing direction by turning to place one-fifth of the mass of the scene on its left retina and four-fifths on its right. Within a relatively distant panorama, the FPM computed at one point on a route can give a robust guidance signal that applies over several meters.

We also test whether the ants' performance in novel scenes is compatible with two other possible mechanisms of scene matching. The first, suggested by findings in *Drosophila* [8] and honeybees [9], is that ants learn a facing direction by storing the retinal azimuth of the center of mass (CoM) of the training pattern when they face in the desired direction. They would then orient to a test pattern by facing so that the CoM of the test pattern coincides with the stored retinal azimuth of the training CoM. The second method, "pixel matching," arose from computational studies [16] that investigated whether views transform smoothly as an animal moves through a natural scene. In this instance, it would mean that an ant can retrieve a learned direction within a scene by rotating until it has minimized the overall luminance difference between corresponding pixels in stored and current views of the scene [17].

Directional Signals from FPM

Behavior that is consistent with the use of FPM would be for ants, when confronted with a test scene, to face toward the FPM that they had previously associated with the position of the feeder in the training scene. Ants starting in the center of the arena were trained to head toward a point 30° inset from the left edge of a 160°-wide (Figure 1A) or a 120°-wide rectangle (Figure S1D), or to the center of a 120° rectangle (Figure S1C). They were then tested with a rectangle of half the width (Figures 1B, S1C, and S1D).

The ants' trajectories in the training situation (Figure 1A1) are in the approximate direction of the food, but on a fine scale their trajectories are often sinuous. We obtain estimates of the ants' heading direction with respect to the training (or test) shape from the endpoints of the saccade-like turns that ants make to help adjust their path [18]. The ants' facing directions at these endpoints are projected onto the shape, and the distribution of these facing directions is presented in two ways (e.g., Figure 1A2). The contour plot shows how facing directions are distributed along the initial 30 cm path to the feeder. The histogram at the top pools all the facing directions along this initial path. In every experiment we describe, the pooled distribution of facing directions has one major mode and we focus on the position of this mode relative to the training and test shapes. In training, the mode coincides with the direction of the food (e.g., Figure 1A2)

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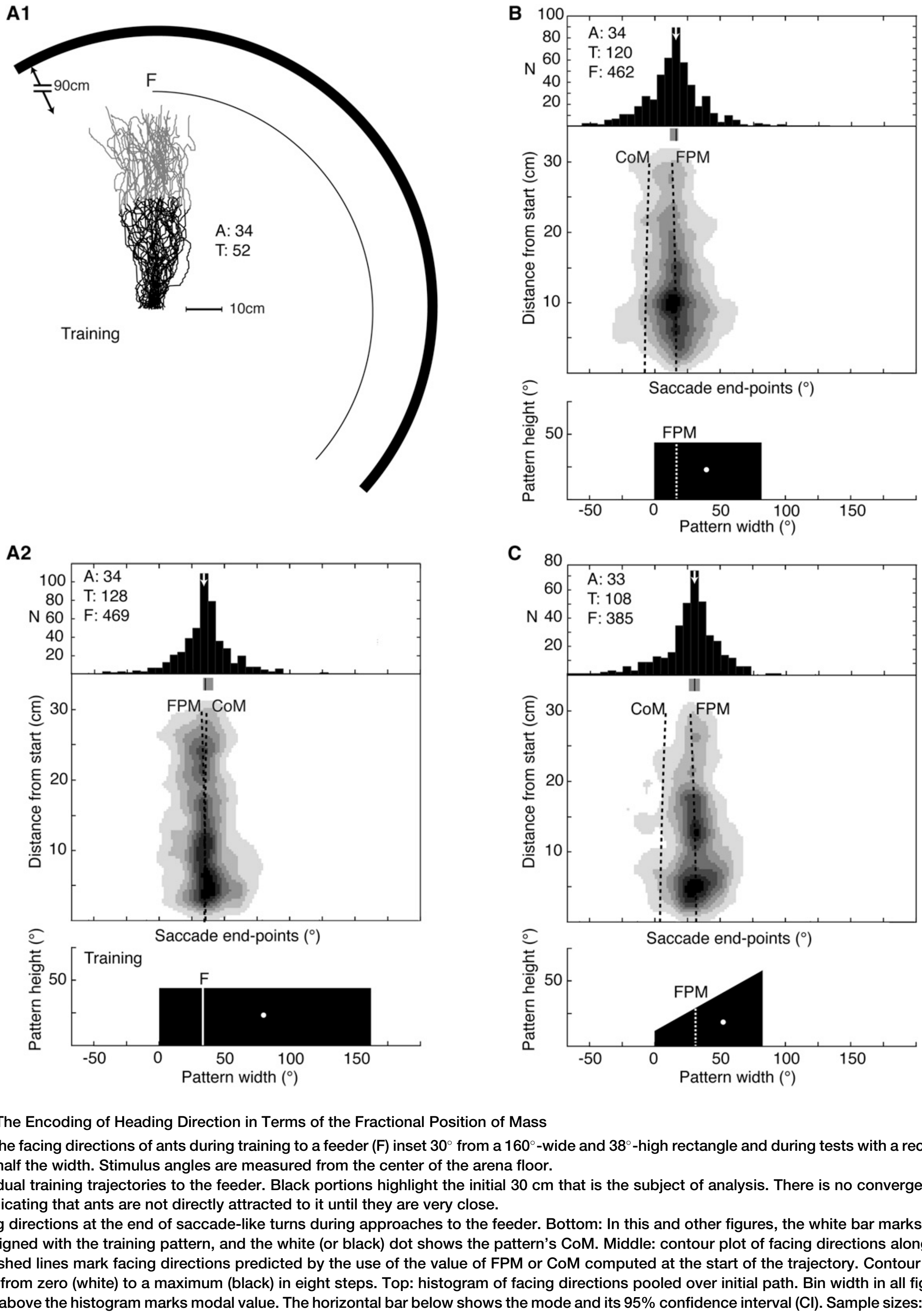

Figure 1. The Encoding of Heading Direction in Terms of the Fractional Position of Mass

We show the facing directions of ants during training to a feeder (F) inset 30° from a 160°-wide and 38°-high rectangle and during tests with a rectangle or a wedge of half the width. Stimulus angles are measured from the center of the arena floor.

(A1) Individual training trajectories to the feeder. Black portions highlight the initial 30 cm that is the subject of analysis. There is no convergence on the feeder, indicating that ants are not directly attracted to it until they are very close.

(A2) Facing directions at the end of saccade-like turns during approaches to the feeder. Bottom: In this and other figures, the white bar marks the feeder position aligned with the training pattern, and the white (or black) dot shows the pattern's CoM. Middle: contour plot of facing directions along the initial 30 cm. Dashed lines mark facing directions predicted by the use of the value of FPM or CoM computed at the start of the trajectory. Contour plots in all figures go from zero (white) to a maximum (black) in eight steps. Top: histogram of facing directions pooled over initial path. Bin width in all figures is 5°. The arrow above the histogram marks modal value. The horizontal bar below shows the mode and its 95% confidence interval (CI). Sample sizes: A, number of ants; T, number of tracks; F, number of endpoints.

(B and C) Facing directions during tests. (B) represents 80° by 38° rectangle. (C) represents wedge of similar width. The dashed bar on test patterns marks FPM corresponding to FPM of feeder on training pattern. Format is as in (A).

and is consistent with the use of FPM, CoM, or pixel matching (see Supplemental Experimental Procedures for details of computations).

The modal facing direction of ants in tests with half-sized rectangles coincides with the training FPM computed over the test rectangle (Figure 1B, S1C, and S1D). Do ants

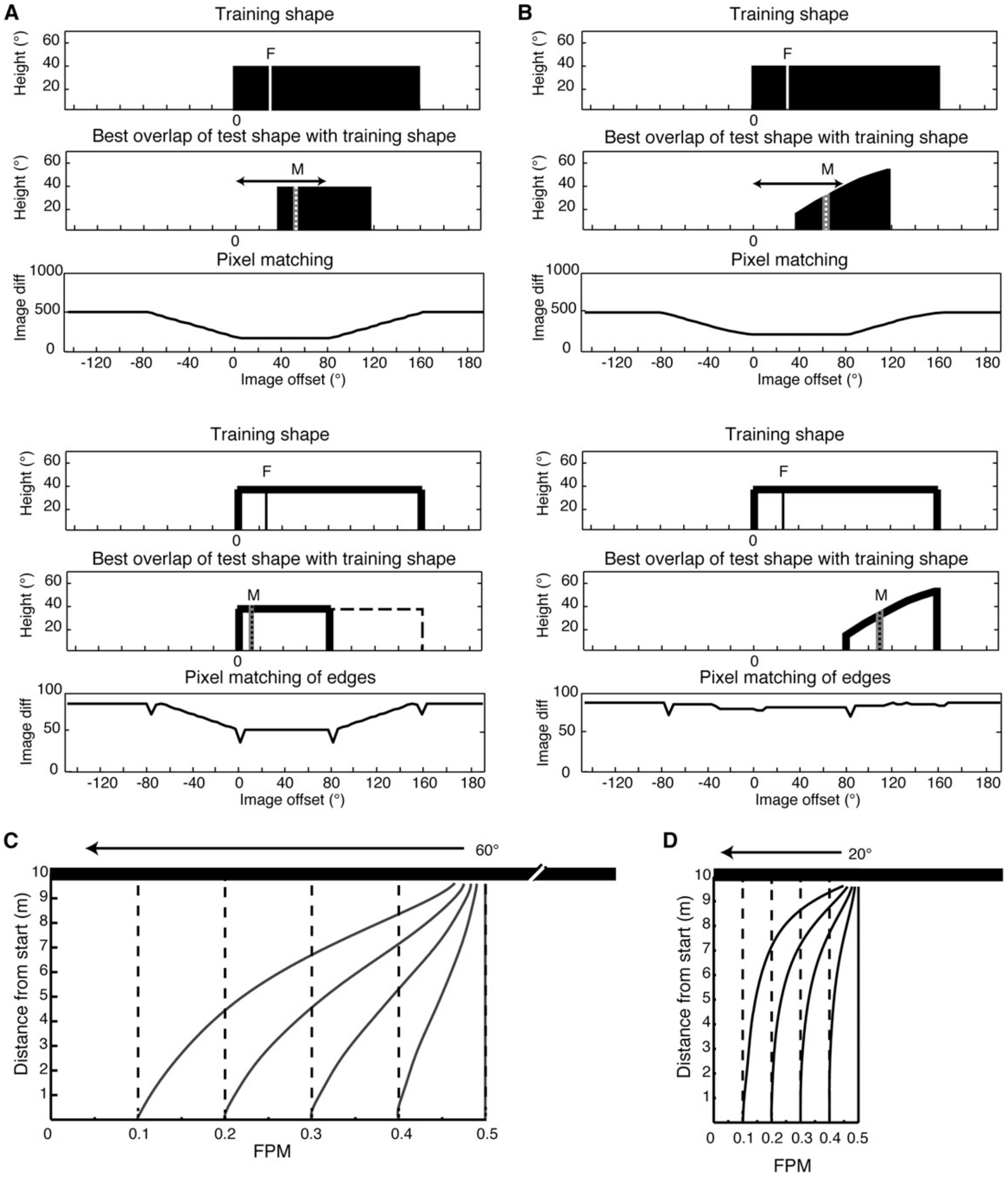

Figure 2. Simulations

(A and B) Image differences from pixel matching for the training and test patterns of Figure 1. Solid and outline patterns show the results of pixel matching over the whole pattern and the pattern edges, respectively. The top of each panel shows the training shape projected spherically onto a point in the center of the arena. The center shows the same projection of a test shape aligned so that it is at the position of minimum image difference between the training and test shapes or in the middle of a flat valley when the minimum is not well defined. Position of food is marked relative to training pattern (F) and the ants' modal facing direction with CI relative to test pattern (M). If ants were to rely on pixel matching, F and M would be aligned. The bottom shows the image difference between test and training patterns as the test pattern is shifted in 1° steps across the training pattern. The zero point on each abscissa indicates the left-hand edge of the training pattern.

(C and D) Simulations of the changing value of the FPM associated with five 10 m straight paths to different points along a rectangular pattern. Dashed lines are the top views of the paths to a 120°-wide (C) or 40°-wide pattern (D), as shown by horizontal bars. The FPM at the start of the route lies between 0.1 and 0.5. The curved line associated with each straight path shows the way in which FPM shifts from its starting value toward 0.5 during the approach.

compute the FPM across the width and height of the pattern? To find out, we tested ants with a wedge (Figure 1C). Their modal facing direction shifted rightward as expected given the assumption that their estimates of FPM integrate width and height.

Because of the varying shapes of the training and test distributions, our first step in a statistical test of this conclusion is to analyze whether the distributions of facing directions in Figures 1B and 1C differ when aligned on their modes. If the Mann-Whitney U test reveals no significant difference, as is

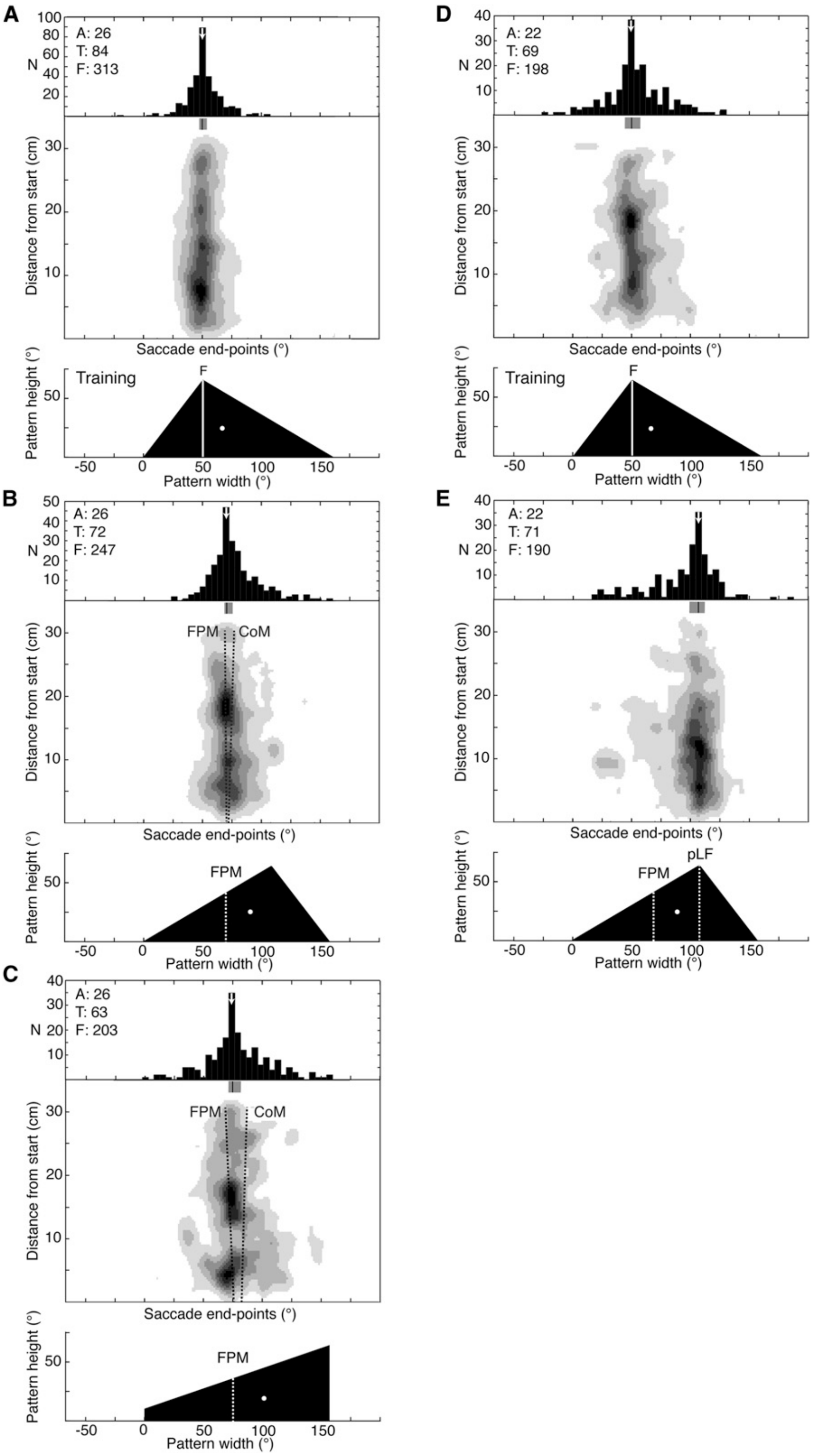

Figure 3. Training to a Triangle

We show facing directions of ants from two colonies trained to a feeder below the peak of a 160°-wide and 65°-high scalene triangle and tested with different shapes of the same width.

(A) Facing directions of first colony with training pattern.

(B and C) Tests with reflected triangle and wedge. Modal facing directions in (B) and (C) correspond to position of the predicted FPM on the test pattern. Test distributions in (B) and (C) did not differ when aligned on their modes (Mann-Whitney U test, $p = 0.425$) or on the FPMs of the test patterns ($p = 0.425$). They did differ when aligned relative to the peaks ($p < 10^{-6}$) or the edges ($p < 0.00001$) of the test patterns.

(D) Training triangle for second colony.

(E) Tests with reflected triangle. The modal facing direction is in line with the peak of the triangle (pLF). Because of varying skew in D and E, distributions of facing directions differ significantly when aligned on their modes. ($p < 10^{-6}$). Other conventions are as in Figure 1.

the case here ($p = 0.746$), we apply the same test to assess the significance of any shifts between distributions associated with various experimental conditions. The distributions in Figures 1B and 1C also do not differ when aligned on the predicted FPMs (Mann-Whitney U test, $p = 0.746$). They do differ when aligned relative to the vertical edges of the patterns (Mann-Whitney U test, $p < 10^{-6}$). These tests suggest that the vertical edges of the pattern were not the major guiding cue and that the shift in the position of the mode results from differences in the shapes of the test patterns.

CoM (Figures 1B and C) and pixel matching (Figures 2A and 2B) also do not predict the ants' modal facing directions toward these test shapes (see Figure S2 for simulations of pixel matching between the training and test shapes of Figures 3, S3, and 4). The direction predicted by the CoM lies outside the modes' 95% confidence intervals (Figures 1B, C, S1C, and S1D). A pixel-matching algorithm using solid shapes generates image differences between test and training patterns without a well-defined minimum (Figure 2A). Pixel matching using edges [19] gives minima that do not correspond to the ants' behavior (Figure 2B).

The case that FPM is computed across the width and height of a pattern and is used to control direction is supported by a further experiment in which ants were trained to face a point below the peak of a scalene triangle (Figure 3A). In tests with the triangle reflected about the peak (Figure 3B) and with a wedge (Figure 3C), the modes of the distributions of facing directions coincided with the FPM acquired during training. Repetition of this experiment on a second colony of ants indicated that ants can also use local features to set direction.

Directional Signals from Local Features

On approaches to the training scene, the acquired FPM and familiar local features signal the same desired direction. But, in test scenes, the two cues may indicate different directions

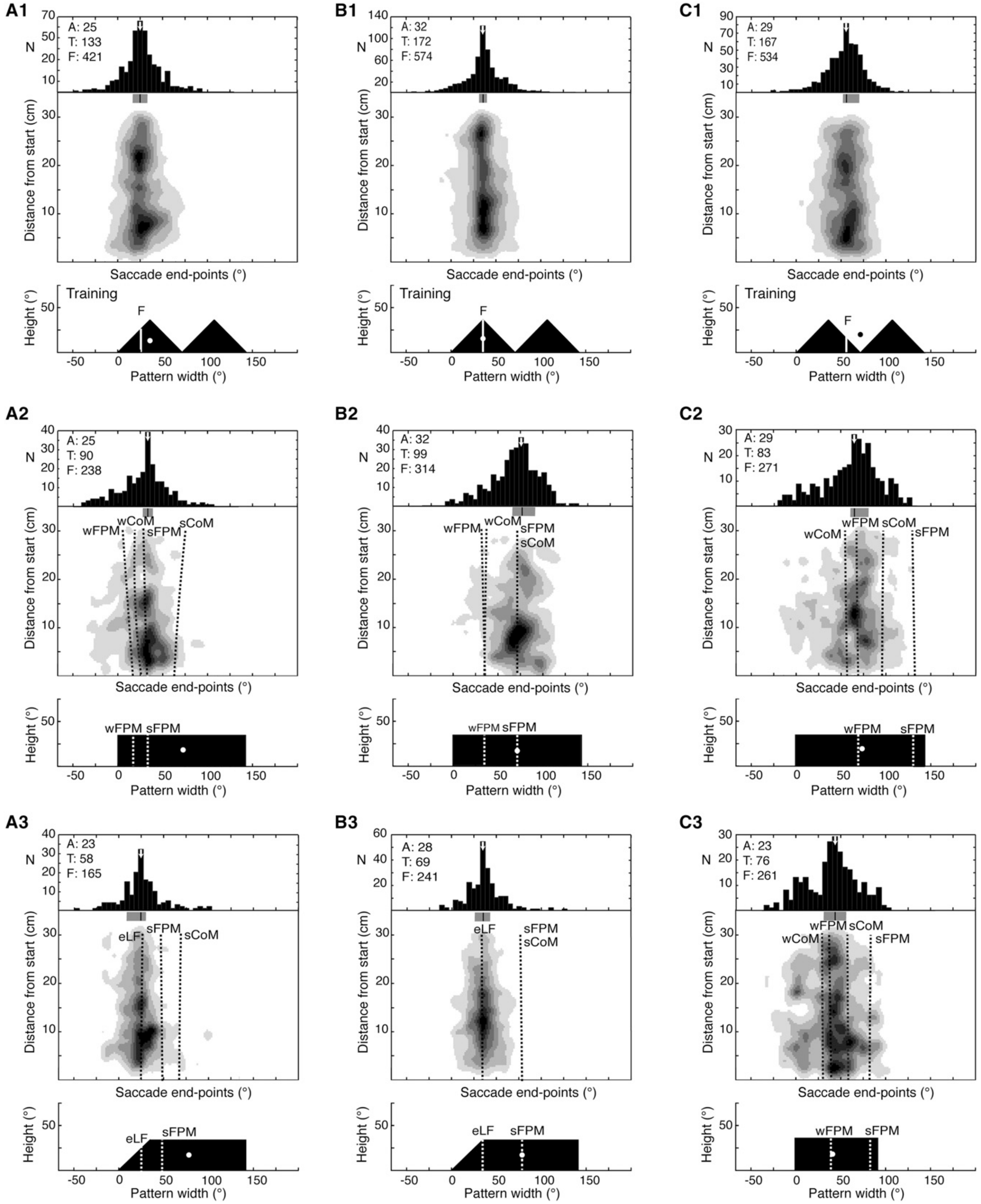

Figure 4. Facing Directions of Ants Trained with a Pattern Composed of Two Abutting Triangles

(A1–C1) three groups of ants, each trained to a different point (F) on the base of the left-hand triangle.

(A2, B2, and C2) Tests with rectangles. Dashed bars on patterns show the FPM of F when triangles are segmented and FPM is computed over the left-hand triangle (sFPM) or not segmented and computed over both triangles (wFPM). Modal facing directions in (A) and (B) are aligned with sFPM. In (C3), mode is just left of the FPM of the two triangles (wFPM). Because of the differing skew, distributions aligned on their modes differ significantly between (A1) and (A2) (Mann-Whitney U test, $p < 0.01$) and between (B1) and (B2) ($p < 0.001$). A3, B3: tests with trapezoid, with sloping left edge to match that of the triangles.

(legend continued on next page)

and, if ants can be guided by either, their responses to the scene may be uncertain. Ants from a second colony were also trained to a point below the peak of the scalene triangle (Figure 3D). When tested with the reflected triangle, these ants faced its peak rather than the training value of the FPM (Figure 3E) suggesting that they were guided principally by the position of the peak.

The varied behavior of the two colonies is puzzling. Individual ants may well differ in the readiness with which they accept differently shaped peaks as similar local features and so may aim at the reflected peak, the FPM, or some compromise. We cannot account for this consistent variation between colonies, except to note that the colony responding to the peak, rather than to the FPM, had been housed in the lab for longer than the other and its members moved more slowly.

Guidance by local features or by FPM computed over width and height was also found in a more complex experiment designed to test whether ants compute the FPM over an outline pattern (Figure S3). In this experiment, the same ants are guided by the pattern's vertical edges or by FPM, depending on the details of the test shape. The ants seem to have learned both the FPM and the desired retinal positions of the vertical edges.

Overall, experiments with simple shapes (Figures 1, S1, 3, and S3) indicate that ants control their desired heading direction with signals derived from at least two visual mechanisms operating in retinal coordinates. The FPM used for directional control seems to be estimated across the width and height of a shape. Heading direction can also be set by placing local features (peaks or edges, see Figure 4) in a desired retinal position. Despite uncertainty over which directional cue might dominate the ants' behavior in particular cases, it is striking that the modal facing directions indicate the use of one or other of these cues and not a mixture. But the varying skew seen in the distributions of endpoints toward test scenes warns that additional factors are likely to be involved.

Segmenting Patterns for FPM

If FPM is to play a significant role in directional guidance within a natural 360° scene, rules are needed for deciding where in the scene the computation of FPM starts and ends. We approach this question by asking how ants treat a shape consisting of two abutting triangles. Do they compute the FPM over both triangles, or over one and segment the shape at the trough? Three groups of ants were trained to approach the triangles. For a given group, the feeder was placed in line with a point to the left of the left-hand triangle (Figure 4A1), below its peak (Figure 4B1), or to its right (Figure 4C1).

The behavior of the first two groups (Figures 4A and 4B) suggests that during training ants segmented the pattern at the trough and computed the FPM across the left-hand triangle. Thus, when tested with a 140°-wide rectangle, the modal facing directions of the two groups (Figures 4A2 and 4B2) were consistent with an FPM derived from the left-hand triangle (sFPM), but inconsistent with an FPM computed over the whole pattern (wFPM). In these tests, the vertical edges of the test pattern differ from the oblique edges of the triangles and do not encourage the matching of local features.

In contrast, when ants were tested with a trapezoid of which the left-hand edge was slanted to correspond with the left edge of the triangle (Figures 4A3 and 4B3), they placed the obliquely oriented edge in the same retinal position as the left edge of the pair of training triangles. They matched a fragment of the test pattern to the training pattern and ignored signals from the FPM. This behavior resembles the results of earlier experiments [13] in which wood ants were trained to approach food at the base of an upright or upside-down cone and then tested with a trapezoid, one side of which matched the edge of the cone. Ants in this case also placed the edge in a learned position on the retina and ignored the bulk of the trapezoid.

The third group, trained close to the trough of the triangles (Figure 4C1) and tested with 160° and 80° rectangles, behaved in a way that is consistent with no segmentation. Their modal facing direction was just left of the center of both rectangles (Figures 4C2 and 4C3), suggesting that they computed the FPM across the two triangles.

The same pattern of segmentation occurred in two more groups of ants trained with a pair of unequally sized triangles and tested with a 120°-wide rectangle (Figure S4). The modal facing direction of the first group, trained to a point below the peak of the small triangle, was in the center of the test rectangle (Figure S4A), suggesting that this group segmented the scene at the trough. The modal facing direction of the second group, trained closer to the trough, was significantly to the left of the test rectangle and is consistent with a FPM computed across both triangles (Figure S4B). Whether the triangles in the pair are of equal or unequal size, segmentation occurs when the trained direction is toward the outer edge of the pair and does not occur when the trained direction is nearer to the trough.

These findings suggest that ants can segment complex patterns at clear break points and compute the FPM over a segmented region. They also suggest that patterns are segmented in a way that depends upon the ants' desired heading relative to the pattern. With a distant panorama, a single value of FPM can guide an ant along a straight path over relatively long distances. But in scenes composed of objects that are nearby, the useful range of a single value of FPM is shorter, particularly when the FPM is computed over a wide segment and the aiming point is close to the pattern or segment boundary (Figures 2C and 2D). Appropriate segmentation could, in principle, mitigate these effects to some degree. Thus, in each training condition, the outcome of the ants' decision of whether or not to segment the triangles placed the FPM closer to the center of mass than had the ants done the reverse.

The ability to compute FPM over a segment of a scene brings with it the problem of identifying a segmented region. Because ants can learn the FPM of a training pattern and then extract the same FPM from a test pattern of a novel shape and size, recognition of a segment is likely to be distinct from computing its FPM. Recognition may be accomplished through the use of local visual features to pick out fragments of a pattern.

The finding that local features can dominate FPM in controlling direction (Figures 4A3 and 4B3) raises the hypothesis that

Modal facing directions are predicted by the retinal position of the left edge of the test triangles relative to F (eLF). Distributions in (A1) and (B1) do not differ significantly from those in (A3) and (B3), if aligned on their modes (A, $p = 0.191$; B, $p = 0.870$) or on the left edges of the patterns (A, $p = 0.496$; B, $p = 0.870$). They do differ if aligned on their sFPM (A, $p < 10^{-6}$; B, $p < 10^{-6}$). C3: test with 80°-wide rectangle. Modal facing direction is close to wFPM. Distributions of (C2) and (C3) do not differ significantly when aligned on their modes ($p = 0.119$) or on wFPM ($p = 0.762$). They do differ if aligned on sFPM ($p < 10^{-6}$).

directional signals associated with local features and FPM might act sequentially. First, directional signals from local features orient the ant's body in the direction of the correct segment. Placement of this segment in the ant's frontal visual field then makes it an appropriate segment over which to extract the acquired FPM for a signal that can guide the ant over an appreciable distance.

Conclusions

These results suggest that local and global visual features combine in the control of direction. One method of control is to rotate until the current view on the retina is in register with the view learned when facing in a desired direction. Ants are likely to be more sophisticated. They perform saccade-like turns to place scenes in desired retinal positions. The initial speed of a turn increases with the size of the visual error to be eliminated, indicating that ants compute in advance the approximate magnitude of the turn needed for accurate placement of a learned feature on the retina [18]. A problem associated with such feature matching is the possibility of making errors when pairing features between stored and current views. Because global features can provide a sparse encoding of a scene, their use in image matching may reduce the number of false matches.

Here, we have been concerned with image matching for the control of direction along a familiar route. The same general principles—the partitioning of scenes into identified segments and guidance by the sparse global features associated with each segment—could apply to a related task: the use of image matching for returning to a specific location. Views stored at a location [20–22] can, in principle [16, 20, 23, 24], guide approaches to that location from novel directions [25–27]. Modeling studies with artificial [28] or naturalistic [29] environments show that guidance to a goal can be accomplished by storing the direction of the azimuth and elevation of the CoM of the whole scene at the goal and deriving direction to the goal from the differences in azimuth and elevation between the current and stored views of the scene. In a similar vein, insects could be guided by differences between the widths and CoM azimuths of identified segments of the current and stored views of a scene (cf. [20]).

Supplemental Information

Supplemental Information includes Supplemental Experimental Procedures and four figures and can be found with this article online at http://dx.doi.org/10.1016/j.cub.2013.03.016.

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