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Current Biology

How Ants Use Vision When Homing Backward

Highlights

- Backward-walking ants rely on celestial but not terrestrial cue memories
- Correction of direction based on terrestrial cues occurs after peeking forward
- The retrieved direction can be transferred into a compass frame of reference
- Ants can decouple their travel direction from their body orientation

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In Brief

Schwarz, Mangan et al. show that navigating ants align their body forward to recognize the familiar visual scene and correct their travel direction. However, ants can transfer this egocentric directional information into a compass frame of reference. Subsequently, they can follow this direction independently of their body orientation.

How Ants Use Vision When Homing Backward

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SUMMARY

Ants can navigate over long distances between their nest and food sites using visual cues [1, 2]. Recent studies show that this capacity is undiminished when walking backward while dragging a heavy food item [3–5]. This challenges the idea that ants use egocentric visual memories of the scene for guidance [1, 2, 6]. Can ants use their visual memories of the terrestrial cues when going backward? Our results suggest that ants do not adjust their direction of travel based on the perceived scene while going backward. Instead, they maintain a straight direction using their celestial compass. This direction can be dictated by their path integrator [5] but can also be set using terrestrial visual cues after a forward peek. If the food item is too heavy to enable body rotations, ants moving backward drop their food on occasion, rotate and walk a few steps forward, return to the food, and drag it backward in a now-corrected direction defined by terrestrial cues. Furthermore, we show that ants can maintain their direction of travel independently of their body orientation. It thus appears that egocentric retinal alignment is required for visual scene recognition, but ants can translate this acquired directional information into a holonomic frame of reference, which enables them to decouple their travel direction from their body orientation and hence navigate backward. This reveals substantial flexibility and communication between different types of navigational information: from terrestrial to celestial cues and from egocentric to holonomic directional memories.

RESULTS AND DISCUSSION

Our experiment was conducted near Seville, in the natural environment of the desert ant *Cataglyphis velox*. We buried barriers around an active nest to constrain the foragers to navigate along a one-way route of our design (Figure 1A). The barriers did not interfere with the view perceived by the ants, with the surrounding scenery clearly visible. A feeder with small pieces of cookie

was provided to motivate the ants to run (forward) along our route, which included several 90° turns and baffles to regulate the ant paths. Each forager reaching the feeder was painted with a unique color code and was allowed to travel on the separated outbound and inbound routes to and from the feeder until the full route was learned sufficiently well to avoid collisions with the barriers or baffles. Experienced ants were then subjected to one of three test conditions in which we recorded their heading direction after 40 cm of travel.

Backward-Walking Ants Follow Their Path Integrator Rather Than Their Visual Memories

We first tested how ants walking backward would negotiate a sharp 90° turn along their familiar route. We captured experienced ants after they had run 3 m along the first leg of the outbound route (Figure 1A, CP1). They had thus accumulated a path integrator (PI) homing vector of 3 m pointing southward. Ants were transferred in the dark one by one, provided with either a small or a large food item, and released on a homebound leg of the route in front of a funnel-shaped baffle (Figure 1A, RP1). At the release point, the route pointed southward but, immediately after the funnel, presented a 90° turn right. We recorded their heading direction at 40 cm after exiting the funnel.

Upon release, the ants carrying a small cookie, and thus able to walk forward, initially dashed southward but then displayed a sharp right turn at the exit of the funnel, pursuing the familiar route westward rather than following the direction indicated by their PI (Figure 1B, Forward; see Movie S1). Ants provided with a large cookie behaved differently. The large cookie was too heavy to be lifted, and these ants struggled for several seconds before eventually starting to drag it backward, as observed in other species [3, 4, 7]. We only analyzed the paths where the ants continuously dragged the cookie backward (i.e., ants with antero-posterior orientation within $\pm 45^\circ$ away from the direction of travel). Their initial direction pointed southward, too; however, at the exit of the baffle, these backward-walking ants continued southward, as indicated by their PI, and apparently uninfluenced by their memory of visual terrestrial cues (Figure 1B, Backward; see Movie S1). When looking at their bearings 40 cm after the baffle, the difference between the forward and backward group was striking. In fact, backward-walking ants behaved similarly whether released on their familiar route or in a completely unfamiliar location (Figure S1B). It is known that backward-walking ants can follow their PI [5], but our results additionally suggest that they are uninfluenced by the learned scenery of the route.

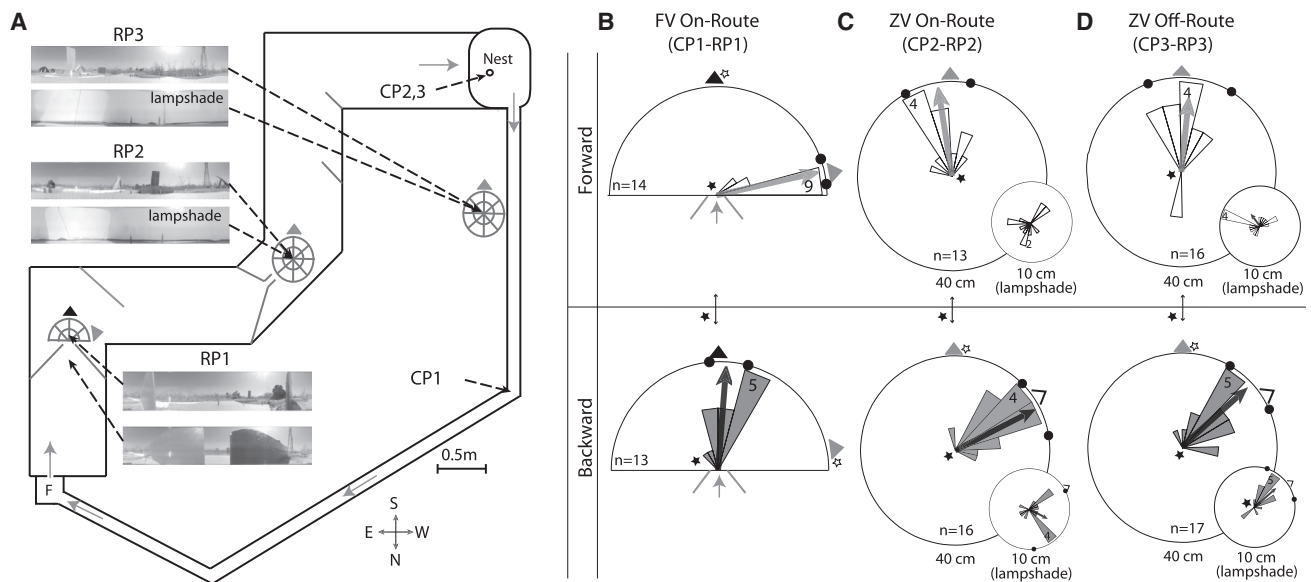


Figure 1. Differences between Forward- and Backward-Walking Ants

(A) Schematic aerial view of the experimental setup. Ants were constrained within a one-way foraging route between the nest and feeder (F). Gray lines within the route depict baffles, and gray goniometer sketches indicate test locations. Arrowheads indicate the theoretical directions tested in (B)–(D), as indicated by the path integration vector (black) and the correct route direction (gray). Note that backward zero-vector (ZV) ants appeared to be oriented toward the feeder-to-nest compass direction (open arrowhead). Dashed arrows indicate capture (CP) or release (RP) points, and the panoramic images illustrate the scenery, as perceived from the RPs. Images were taken with a Sony Bloggie, unwrapped and processed as in [6]. RP1: lower image represents view before baffle and upper image view after baffle. RP2,3: lower and upper images represent views with and without lampshade. Note that the sky was still visible even with the lampshade in place; only terrestrial visual cues were covered.

(B) Circular distribution of heading directions (after 40 cm of travel) of full-vector (FV) ants tested at RP1. Forward ants were oriented and headed toward the route direction (gray arrowhead). Backward ants were oriented and headed along their path integration vector (black arrowhead).

(C and D) Distributions of headings of ZV ants released on-route at RP2 (C) and off-route at RP3 (D). Forward ants showed random headings at 10 cm (lampshade) but were oriented toward the route direction (RP2) or nest direction (RP3) (gray arrowhead) at 40 cm. Backward ants were oriented toward the feeder-nest direction (open arrowhead) at 10 cm (only D) and 40 cm.

(B–D) Arrows indicate mean vector and black circles indicated by the 95% confidence intervals of group distributions. Numbers in circular sectors indicate the number of observations for this direction. Filled stars within the histograms depict significantly oriented distributions ($p < 0.01$; Rayleigh test). Open stars near theoretical directions (arrowheads) indicate $p < 0.001$ against this direction as mean of the group distribution (S test, a non-parametric sign test for circular data, MATLAB). Filled stars outside the histograms depict significant differences ($p < 0.001$; WW test) between mean directions of two given distributions.

Details on p values are provided in Table S1; see also Supplemental Experimental Procedures, Figure S1, and Movie S1.

Backward-Walking Zero-Vector Ants Do Not Use the Learned Visual Scenery on a Familiar Route

Our first experiment showed that backward-walking ants are guided by PI and are not influenced by terrestrial cues, but might they rely on the visual scenery in the absence of a PI home vector? We note, for example, that in Ardin et al. [3], displaced backward-walking ants with a somewhat shorter PI vector did not follow their PI, but homed to the nest. To test for this, we captured ants trained to our route a few centimeters before they reached their nest (Figure 1A, CP2)—that is, as zero-vector ants (ZV). We removed the small cookie that these ants were carrying and, as previously, provided them instead with either a big or small piece of cookie to induce backward or forward motion, respectively. This time, the ants were released further along the route within a lampshade that blocked the view of the surrounding scenery (Figure 1A, RP2). Ants were allowed to walk for 10 cm in their chosen direction before the shade was lifted to reveal the familiar scenery. Forward-running ants displayed initially undirected headings but adjusted their course toward the correct route direction as soon as the shade was lifted (Figure 1C). In contrast, the big-cookie backward-dragging ants did

not orient toward the route direction when the shade was lifted (Figure 1C), despite the familiar visual scenery.

Although not the main focus of our study, it is interesting to note that the direction taken by backward-walking ZV ants was not random. We were surprised to find that they aimed, rather consistently, southwest, a direction that corresponds to the feeder-to-nest compass direction. This was clearly apparent after 40 cm of travel, and even seemed to be the case at 10 cm, when they were within the lampshade (Figure 1C) from which only the sky was visible, suggesting that this direction is based on a celestial compass memory. Ants are known to store such celestial compass-based vectors in long-term [8] or medium/short-term memories [9], and it appears that in this unfamiliar situation, the ZV backward ants recovered and used such a vector to set their direction.

Backward-Walking Zero-Vector Ants Do Not Use the Visual Scenery at a Novel Release Point

It has been suggested that ants may use different visual strategies when on route, compared to novel locations off the route [6, 10, 11]. Ants displaced off their route can use the surrounding

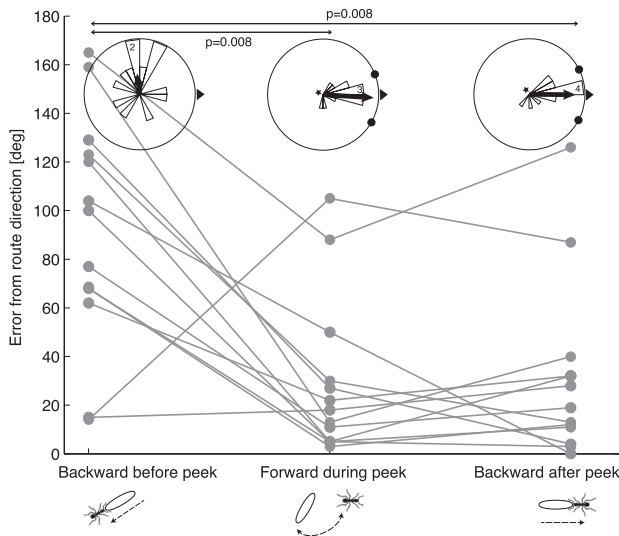


Figure 2. Peeking Behavior Enables Ants to Adjust Their Direction of Travel

Angular error (angle away from the homing direction) of the direction of backward travel 10 cm before and 10 cm after the peeking behavior. “Forward during peek” corresponds to the direction of the furthest location away from the dropped cookie reached by the ant during peeking behavior. Each line corresponds to an individual ant (p values correspond to a paired sign tests). Circular histograms show travel directions relative to the route direction (arrowhead), with mean vector of the distribution (arrow) and 95% confidence intervals (black circles). Numbers in circular sectors correspond to the number of observations for this direction. Filled stars within the histograms depict significantly oriented distributions (Rayleigh tests: before peek, $p = 0.159$; peek, $p < 0.001$; after peek, $p < 0.001$). Lower sketches illustrate an example of a peeking behavior sequence (dashed arrows depict direction of travel; see also [Movie S2](#)).

scenery to guide their path directly toward the nest (or the familiar route) across novel terrain [6, 12, 13], as in models of visual homing [6, 14, 15]. Perhaps backward-walking ants cannot use on-route strategies because it requires forward body alignment [2, 16–19] but can nonetheless use off-route strategies. To test this, we repeated the previous experiment with the lampshade, but this time ZV ants were released off route, at a novel location (relative to their normal return route) ~ 2 m to the side of their nest (Figure 1A, RP3). Again, small-cookie forward-walking ants corrected their heading toward the nest when the lampshade was lifted (Figure 1D), showing that they could use their memory of visual terrestrial cues to home from this novel location. Backward-walking ants, however—as before—did not move in the correct home direction but instead walked in the feeder-to-nest compass direction and maintained that direction when the visual scenery was revealed (Figure 1D). That is, they failed to use the visual scenery to correct their heading toward the nest.

Ants Can Peek Forward to Set a Direction, Which They Then Maintain Backward

If backward-walking ants do not use their memory of the visual terrestrial cues, how can we explain their ability to home successfully after being displaced to novel locations [3]? Pfeffer and Wittlinger [5] noticed that ants walking backward on unfamiliar

terrain occasionally dropped their food and searched around before grabbing the food again. The authors noted that after these searches some ants were more precisely oriented along the feeder-to-nest direction. We were interested in investigating whether ants might obtain information from the visual scenery during such maneuvers. In our various experiments, roughly one-third of our recorded ZV ants dropped their food items and hence were not included in our previous analysis. These ants ($n = 13$) displayed on our recording board what we will call here a “peeking behavior”: they stopped dragging, dropped their cookie, turned around, took a few steps forward, turned around, came back, grabbed the cookie again, and resumed their backward motion—but this time along the route direction, as taken by the forward ants (Figure 2; see [Movie S2](#)).

The peeking behavior is not stereotypical but varies across situations. Within the familiar surroundings of our setup, ants left their cookie only for a short period of time (mean \pm SD = $3.5 \text{ s} \pm 1.9 \text{ s}$) and displayed only a few steps forward (maximum distance: mean \pm SD = $4.2 \text{ cm} \pm 1.7 \text{ cm}$). In contrast, ants display longer and tortuous searches in unfamiliar terrain, as observed in *Cataglyphis fortis* [5]. Ants also sometimes attempted to face forward with the food still in their mandibles, which, it appears, also enables them to use their visual memories to adjust their walking direction (Figure S1C). Such “glances back” could explain how *Myrmecia* ants achieved “backward” homing [3] (Figure S2). Note that none of the full vector (FV) ants we observed dropped their cookie. This is different to Pfeffer and Wittlinger’s observation and might be due to our short period of observation. In general, it seems clear that ants with shorter PI homing vectors are more prone to display peeking behavior ([5] and [Figure S2](#)). This could be because of the greater angular uncertainty of short PI vectors [20] or because information from the visual scene (or odors) is needed to pinpoint the exact nest location. Exactly how many peeks would be required to recapitulate a route or pinpoint the nest remains unknown.

Interestingly, the few steps forward displayed during the peeking behaviors (in familiar surroundings) were oriented along the correct route direction (Figure 2). Such a need to turn around and face the route direction supports the idea that obtaining directional information from terrestrial cues is an egocentric process [2, 6, 10, 13, 17, 18, 21–25], where ants must align their view to match their egocentric memories of the visual landscape. Crucially, however, the direction obtained by this egocentric process while facing forward can subsequently be maintained while going backward (Figure 2). Thus, ants must somehow be able to transfer the directional information based on terrestrial cues into a different frame of reference, which we investigate next.

Backward-Walking Ants Use Their Celestial Compass to Maintain a Straight Course

It is notable in all the above experiments that ants walking backward maintained a straight course, even after peeking. Moving straight is not a trivial task [26–28], particularly given the chaotic step movements involved in ant backward locomotion [4]. In theory, maintaining a straight path can be achieved in multiple ways: by using proprioceptive information, rotational optic flow, or celestial cues, or by memorizing the scene perceived (on adopting the backward course) to hold a good match while moving. We decided to test whether ants maintain their backward

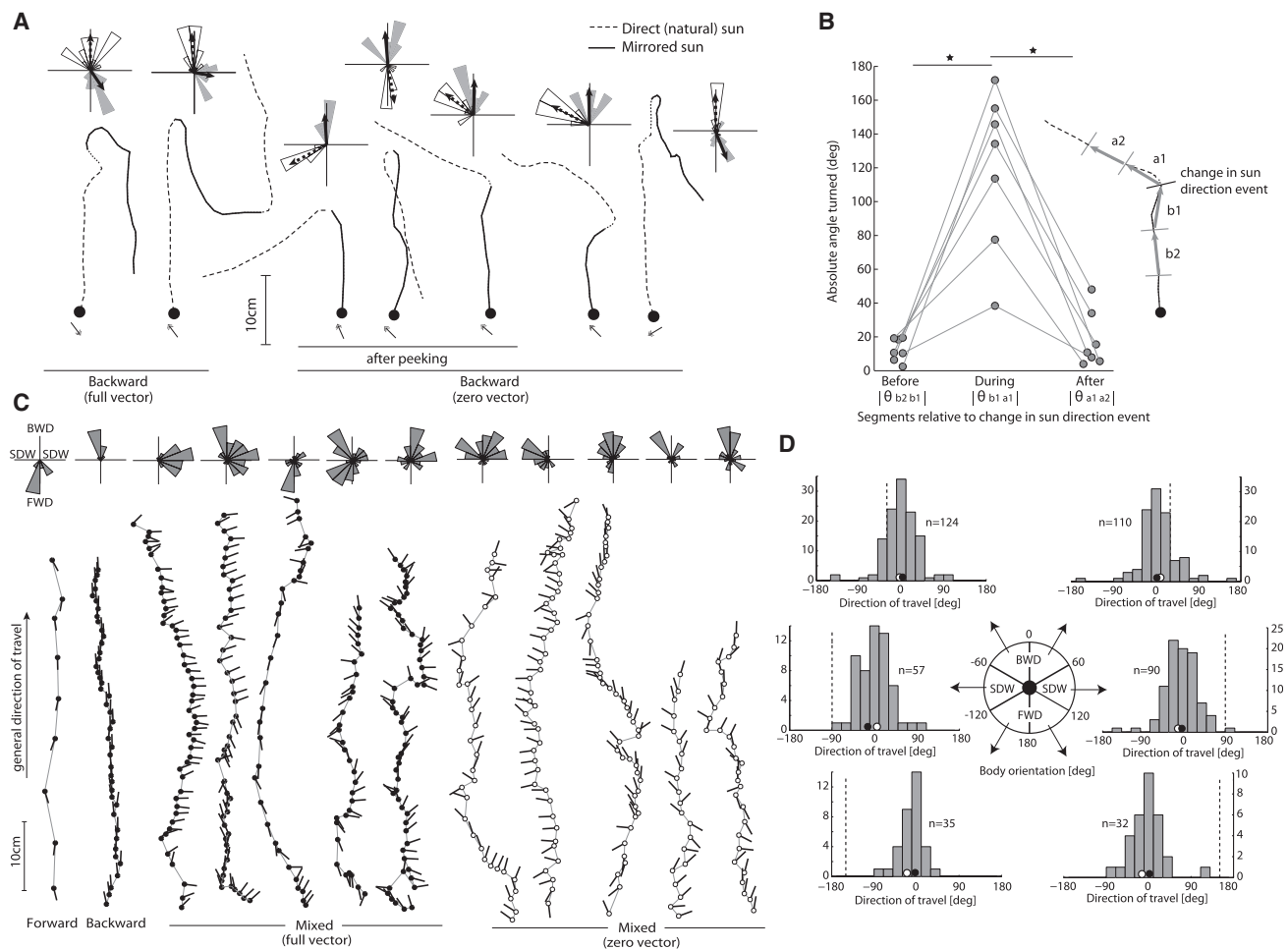


Figure 3. Ants Can Maintain a Direction of Travel Independently of their Body Orientation

(A) Mirror experiment. Recorded paths were digitized and the ant's location was extracted at two frames/s. Dashed lines represent path sections under direct (natural) sun conditions, and solid lines represent path sections with the sun mirrored by 180° compared to the ant position. Small arrows indicate the direction of the sun's position in the sky, and black circles the start of the paths. The mirror manipulation was applied in backward-walking full-vector ants (vector direction indicated by open arrowhead) and zero-vector ants before or after the ant had displayed a peeking behavior. The circular histograms show the relative distribution of the travel direction of path segments sampled at two frames/s under direct natural sun (gray) and mirrored sun (white). The two associated vectors indicate the mean vector of the circular distributions; the x and y axis length indicate a vector norm of 1.

(B) The angle turned by each individual (gray dots) is greater as a response to the manipulative change in sun direction than it is before or after the change, indicating the use of a celestial compass. As depicted, individual paths were divided into four successive vectors of 8 cm each: two before the manipulation (b2, b1) and two after (a1, a2). Angles turned correspond to the absolute angular difference between the vectors (before: $|\theta_{b2\ b1}|$; during: $|\theta_{b1\ a1}|$; after: $|\theta_{a1\ a2}|$). * $p < 0.015$, nonparametric "sign test" test (MATLAB) for paired individual data.

(C) Example paths of single ants, traveling forward (with a small food item), backward, or in a combination of different body orientations ("mixed," with a big food item). Head position (black dots) and head-to-tail orientation (black dashes) were extracted from the recorded paths (GoPro cameras) at five frames/s. Circular histograms show distributions of the ants' body orientations relative to their direction of travel (travel direction – body orientation), computed as the change in location of the ants' head from the current frame to the next (i.e., backward: BWD; forward: FWD; sideways: SWD; see also Movie S3). No correlation between body orientation and direction of travel could be found for the mixed ants (circular-circular correlation, $0.13 < r < -0.11$, $p > 0.324$).

(D) Distributions of directions of travel (path segments sampled at five frames/s of mixed ants shown in Figure 3C) for different categories of body orientations show that ants can maintain an overall path direction (aligned at zero) independently of their body orientation. Dashed lines indicate the mean direction expected if the ants were pulling backward. Filled and open dots indicate the means for the FV and ZV ants, respectively (see also Figure S2 for a similar analysis and result with *Myrmecia* data).

direction through celestial cues, as do dung beetles when pushing their dung ball backward with their hind legs [29–31]. We used a century-old method: mirroring the sun so that it appeared to be in the opposite half of the sky while hiding the direct sun with an opaque board [32]. We waited for a rather overcast day to limit the effect of blue sky polarization [33, 34] and performed

the manipulation when the sun was clearly visible. As soon as the sun was mirrored, backward-walking ants displayed a turn and moved in a different direction (Figure 3A). This was true for both FV and ZV ants and whether before or after peeking, as long as ants were not walking forward. As observed in previous sun mirror manipulations [32, 34], the turns displayed here by

backward-walking ants were not exactly 180°. This may be due to the conflicting influence of the remaining blue sky polarization, which suggests that a variety of celestial cues are involved.

It seems clear that backward-walking ants use their celestial compass to maintain a straight course. This does not refute the possibility that self-motion or stabilization based on terrestrial cues can be used too; however, celestial cues dominate.

Ants Can Maintain a Direction of Travel Independently of their Body Orientation

Some of the ants dragging their large food item backward managed nonetheless to rotate their body around while keeping the food in their jaws (Figure 3C). These were removed from our previous analysis because they did not travel solely backward. Interestingly, these ants revealed their ability to decouple their direction of travel from their current body orientation (see Figure S1C for the direction taken by these ants). That is, they could maintain an absolute direction of travel whether moving backward, forward, or sideways or rotating in any other intermediary body orientation (Figure 3C; Movie S3). In other words, this shows that ants' directional memories can be stored and retrieved within a holonomic frame of reference. In robotics, "holonomic" means that all degrees of freedom (x,y and the body orientation θ) are controllable, so the system can be reduced to its position in space (the body orientation θ is integrable). For instance, holonomic wheels are wheels that, like ants, can move in any direction independently of their orientation. In the vertebrate literature, this may be referred to as an "allocentric directional" reference frame [35]. We performed a similar analysis using a dataset from previously published work on the distantly related *Myrmecia* ants [3] and obtained comparable results (Figure S2D). Similarly, flying hymenoptera can fly sideways to maintain a compass direction despite cross-wind [36], suggesting that this ability has evolved before the origin of the ant taxa.

Such a holonomic system is ideal to integrate multiple sources of directional information, as any directional input added to the system can be taken into account independently of the insect's current body orientation. This not only explains how a direction obtained when facing forward (e.g., during peeking) can subsequently be followed backward using celestial cues, but also how ants can integrate egocentrically perceived wind directions [37] or steer an intermediate course when the direction indicated by terrestrial cues and path integration are set in conflict [20, 38–41].

Neurobiological Implication

It is interesting to consider the implications for the neural circuitry underlying navigation [42]. The central complex has been closely implicated in storing directional memories [43], tracking body orientation from self-motion cues [44, 45], and using celestial cues as an external frame of reference [43, 46, 47]. The central complex thus possesses all the ingredients necessary to integrate directional memories into a holonomic frame of reference [42]. By contrast, a current hypothesis for visual scene orientation is that it involves the comparison, by retinotopic alignment, of the current egocentric view to egocentric visual scene memories [2]: a function that can be plausibly mapped to the mushroom bodies [42, 48]. The ability of ants, as

shown here, to recover a direction using egocentric visual route memories (when peeking forward) and subsequently follow that direction using celestial cues independently of their body orientation would then require a transfer of information, whether direct or indirect, from the mushroom body to the central complex. To date, surprisingly few connections between these distinctive neuropils have been observed, but they could be crucial to understanding navigation. Indeed, it may be more appropriate to consider these brain areas as supporting complementary computational processes, which can flexibly interact to achieve complex navigational tasks, rather than distinct behavioral competencies [42].

Conclusions

Ant navigation is often described as a tool kit of distinct behavioral strategies, in which the use of celestial and terrestrial cues (apart, perhaps, from wind [37, 49, 50]) are processed by independent modules weighted by simple rules and gated by simple motivational control [51–53]. The current results depict a different story: ants walking backward must assess their accumulating uncertainty and eventually drop their cookie to peek forward for the time necessary to recover a direction; and this direction, obtained by egocentric, rotationally dependent processes based on memories of terrestrial visual cues, can be integrated (together with other directional information such as the PI vector) in a holonomic frame of reference and followed independently of the body orientation using the celestial compass. Whether these two processes (i.e., peeking forward to gather information using memories of the visual scene or moving along the computed direction using the celestial compass) are always achieved sequentially, or can be achieved simultaneously and continuously, remains to be seen. In any case, strategies of different kinds mingle, and navigational behavior appears to be a product of remarkably flexible control.

SUPPLEMENTAL INFORMATION

Supplemental Information includes Supplemental Experimental Procedures, two figures, one table, and three movies and can be found with this article online at <http://dx.doi.org/10.1016/j.cub.2016.12.019>.

AUTHOR CONTRIBUTIONS

Conceptualization: S.S., M.M., B.W., and A.W. Investigation and Methodology: S.S., M.M., and A.W. Formal Analysis: S.S. and A.W. Writing – Original Draft: A.W. Writing – Review & Editing: S.S., M.M., J.Z., B.W., and A.W. Supervision: B.W. Data and Analysis for Figure S2: J.Z.

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