

certainly tempting. What is noteworthy also is that the spatial scales concerned here are quite substantially beyond the behavioural resolution limit of the animal (Figure 1C,D) [14]. This would imply that the retina could pre-emptively detect defocus long before it becomes behaviourally relevant.

Whether the presumed defocus signal is actually used anywhere in the brain requires further study, for example on the projection patterns of this type. As the spatial sensitivity goes beyond the behavioural limit of the mouse, we might expect these cells not to project to the visual thalamus and cortex, where pattern vision is thought to be formed. Instead, they may project to midbrain structures like area pretectalis, where accommodation is controlled (although like many other small mammals, mice do not accommodate with their huge lenses [14]). Nevertheless, the On-delayed cell might still contribute information for “visual control” of eye growth. Previous work showed that the retina by itself can determine imposed defocus in the projected image, including its sign [15] (which the suggested circuit would presumably not attain). It is therefore conceivable that such a pathway may then signal to adjust axial eye growth rates during emmetropisation [16]. Interestingly, information about the sign of image focus, though present in the retina, is not available when e.g. we try focussing a microscope. Instead, we experience that accommodation uses a trial and error approach which also argues in favour of these type of signals not being part of the ‘conscious’ visual experience. In any case, the new study [10] adds to a growing body of well-characterised retinal output channels in the mouse and thus provides one more puzzle piece in our overall understanding of vision in vertebrates.

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Insect Navigation: What Backward Walking Reveals about the Control of Movement

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Ants often walk backwards to drag large prey to their nest. New experiments show how they can use information from retinotopically encoded views to follow visual routes even while moving backwards. The mechanisms enabling ants to decouple body orientation and the control of travel direction are likely to be shared with other, flying, insects.

Driving a car backwards is a tricky business that many of us find difficult even with the aid of mirrors. Ants also move backwards, not to park in tight spaces but when dragging home items

of food that are too large to carry. Until last year backward navigation in ants was uncharted territory. Now, three papers on desert ants of the genus *Cataglyphis* [1–3] and one on *Myrmecia*



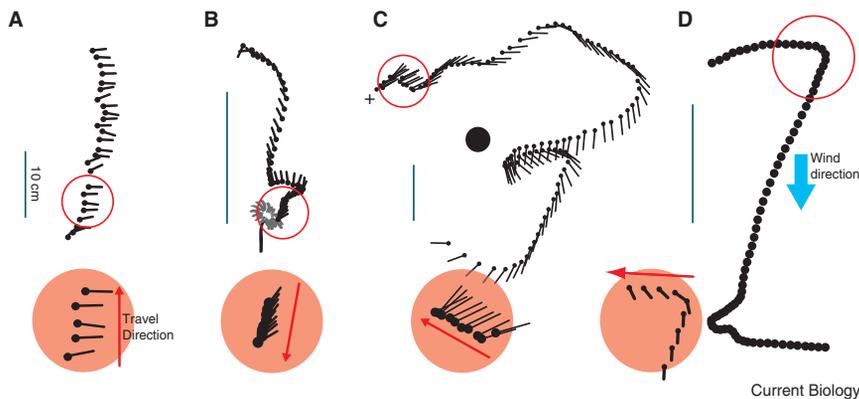


Figure 1. Decoupling body orientation and travel direction in walking and flying insects.

(A) An ant, *C. velox*, dragging prey home [2]. (B) A hoverfly, *Syrirta pipiens*, using visual cues to approach a daisy [17]. (C) A wasp, *Vespula vulgaris*, using visual cues to approach a feeder [13]. (D) *Drosophila* flying up-wind and cross-wind to an odour source [6]. The lollipops indicate the insect's body orientation: A every 500 ms; B and C every 20 ms; and D every 10 ms. All scale bars represent 10 cm. Enlarged areas highlight differences between body orientation and travel direction.

[4] analyse the paths of ants that are steering themselves backwards. In the last issue of *Current Biology*, Schwarz *et al.* [3] report that ants can decouple body orientation and travel direction to move sideways (Figure 1A) as well as backwards in their selected direction. This flexibility may have been inherited from the ants' flying ancestors. Flying insects frequently decouple their body orientation from travel direction, as seen in their manner of approaching a goal (Figure 1B,C). How such decoupling is accomplished is a long-standing problem [5,6] to which these studies on ants add some insight.

Foraging ants normally travel forwards with their olfactory and visual sensors at the front and, like cars, their movements are most efficient when travelling in this direction [2]. Ants travelling between their nest and a foraging site rely on a combination of visual route memories, path integration and olfactory cues [7]. The visual route memories are thought to be the views, encoded in retinotopic form, that are experienced while ants travel the route in a forward direction [8,9]. These memories appear to work by eliciting rotations of the insect's body that bring the ant's current view into retinotopic alignment with the remembered view [10]. The second guidance system, path integration, is most important when a habitual route has not yet been established. As an ant moves, it continually monitors its direction of

travel and the distance that it covers, integrating this information so that it always knows its current direction and distance from its nest [11]. Ants assess travel direction with a sun compass and they estimate the distance covered by monitoring their stepping movements. Once food is found, the ant can use information from path integration as a 'home vector' to return directly to the nest.

Pfeffer and Wittlinger [1] analysed the paths taken by *Cataglyphis fortis* when dragging food items backwards in a direction set by path integration. They collected ants at a food site and took them to a distant test site where the visual panorama was unfamiliar so that the ants would rely on their path integration system. Here the ants found either a small food item, which they carried forwards, or a large food item, which they dragged backwards. Remarkably, walking backwards did not appear to impair the accuracy of the guidance from path integration. The forward and backward walking ants took the same directions and travelled for similar distances before beginning to search.

While following path integration, Pfeffer and Wittlinger's [1] backward moving ants periodically let go of their food and performed an inspection loop that was sometimes several metres long. They then picked up the food again and resumed their backward paths. The greater the ants' distance

from the start, the larger and more frequent were these loops. The increasing time spent on these foodless inspection loops could reflect a search for visual information since the directional uncertainty of the signal from path integration grows as the home vector shortens. Had the ants been travelling over familiar ground, then these loops might have allowed the ants to obtain visual information for locating the nest.

The two other studies examined how in familiar terrain ants can use their visual memories to walk backwards. In one case ants were released from an arbitrary location near the nest [4] and in the other along a familiar route [3]. If the visual memories are indeed retinotopic, using them while facing backwards presents a puzzle, as backward facing ants cannot align their current view with views that they have stored when moving forwards. Schwarz *et al.* [3] have offered an ingenious solution that involves what they call 'peeking' during short inspection loops — possibly abbreviated forms of those observed in *C. fortis* [1] — when backward walking ants briefly drop their food. The ants (*C. velox*) were trained along a multistage route in which the direction of each route segment differed from the nest direction dictated by path integration. Ants were taken for testing either when they were partway along the food-ward route with an active home vector (HV ants), or they were allowed to complete the homeward route and were collected just before entering the nest (zero vector or ZV ants). The ants were then released back on the route with a small or large food item to make them walk respectively either forwards or backwards.

The forward walking ants (those carrying small items) all set out in the direction specified by their visual route memories. In contrast, the backward walking ants (those with large food items) set out in a different direction, apparently not using the visual cues. The HV ants behaved similarly to the ants that Pfeffer and Wittlinger [1] had released on an unfamiliar test ground, setting out in the direction prescribed by path integration. Curiously, the backward-walking ZV ants (which didn't have the same information from path

integration) also set out in a similar direction. Schwartz *et al.* suggest tentatively that this direction may be set by a (possibly short-term) memory of the feeder-to-nest direction. What is clear is that the use of visual memories depends on viewing direction.

The neat part of the story comes from those ZV ants that, like the *C. fortis* observed by Pfeffer and Wittlinger [1], let go of their food item and looked around. Because these ants were on familiar terrain, the function of the foodless inspection loops [1], or peeking [3], becomes clear. After obtaining a forward view along the route, the ants grabbed the item again and were then able to follow the direction given by the route memories even whilst walking backwards. That this change in travel direction occurs only after peeking suggests that the visual route memories do indeed need to be matched retinotopically.

How do the ants transform the route information acquired during forward peeking into directed backward movements? Schwarz *et al.* [3] propose that while the ants are oriented forwards, in the familiar direction determined by view-based route memories, they update a desired course direction in terms of celestial cues that can be used independently of the ants' body orientation. Thus, while walking backwards, they would be guided by the same cues as Pfeffer and Wittlinger's [1] ants. Evidence supporting this explanation comes from repeating a century's old experiment [12]. Reversal of the apparent azimuthal position of the sun with a mirror changed the travel direction of backward-walking ants. This result also raises the possibility that, in forward walking ants too, celestial cues may participate in maintaining a straight path along a route.

There are at least two situations in which flying insects also employ a behavioural sequence of first setting a course by aligning the body and its sensors in a desired travel direction, but then decoupling the body orientation and travel direction. In both cases, the orienting cues are patchily distributed and the decoupling occurs when the insect searches for further information. In one of these, when a

flying hoverfly (Figure 1B) or wasp (Figure 1C) uses visual cues to pinpoint a goal, it intersperses periods of travelling forwards towards the goal, when it is thought to be matching precise retinotopic views [13], with transverse sweeps during which its body orientation is decoupled from the flight direction [14].

A second example involves a different modality, but is remarkably similar. Flying insects locate an odour source with a 'cast and surge' strategy. Turbulence in the air can mean that odours arrive in discontinuous packets. When the insect encounters a packet of attractive odour, it orients its body into the wind and travels forwards. This 'surge' direction is subsequently maintained by stabilising visual cues such as visual texture on the ground, and possibly also celestial cues. Thus, as in the ants' peeks along the route, information is transferred from the orienting cues (view-matching or wind) to the course direction. After losing contact with the odour, the insect 'casts' for a new odour packet, switching to travel in roughly the crosswind direction (Figure 1D). During these casts, the body orientation and travel direction are often decoupled by up to 90° [6].

The decoupling of travel direction from body orientation is possible in both crosswind casting and backward walking because the initial orienting cues, which to be effective depend on aligning body orientation, are translated into sensory cues that can be used irrespective of body orientation or travel direction. This ability raises the problem of how to transform the desired course direction, set with respect to the external cue, into egocentric commands for the motor ganglia. Recent studies in *Drosophila* indicate that a group of neurons in the central complex may perform this crucial transformation. The central complex has long been implicated in orienting behaviour, and its columnar structure spanning three distinct sub-regions appears to be highly conserved between different orders of insects [15]. A circular network of one set of neurons seems to have the necessary properties for the transformation: there is a peak of firing activity consistent with a desired

course direction, and the position of the peak is updated appropriately both by cues from self-motion and by visual rotations of the outside world [16]. This peak could thus drive the egocentric thrust commands to travel in a direction defined by, for instance, celestial cues.

Decoupling body orientation and travel direction can allow considerable flexibility in manoeuvring. First, as when an ant rotates to travel backwards after peeking, an insect can change its body orientation while maintaining its course direction. More generally, an insect could align its body with a visual memory (Figure 1C), or turn and attend to a visual stimulus [17] or possibly an odour, without having to travel in that direction. Second, and conversely, an insect can change its travel direction without the sensory disruption caused by turning, giving the possibility of maintaining a retinotopic view or an upwind orientation. This two-way independence of body orientation and course direction suggests that, in addition to neurons controlling the translational course direction, there may also exist an additional set of neurons still waiting to be described that transform the sensory input into the rotational commands for setting body orientation.

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Circadian Rhythms: The Price of Electric Light

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A new study demonstrates that modern electric lighting has caused the near-24-hour biological clock to be set to a later time and that humans physiologically respond to seasonal changes in day length under conditions of natural light exposure.

You can learn a lot from camping. Charles Darwin's experience of "living in the open air, with the sky for a roof, and the ground for a table" [1] during the voyage of the Beagle is perhaps one of the better known camping trips in the annals of science but there have been others. In 1938 the great American physiologist and sleep researcher Nathaniel Kleitman camped out with a student in Mammoth Cave in Kentucky for over a month [2]. By living on a self-imposed 28-hour day they offered one of the first glimpses into the workings of the human 24-hour biological clock: Kleitman's experiment demonstrated that humans spontaneously generate a near-24-hour rhythm in body temperature that isn't evoked by the environment. In the nearly 80 years since Kleitman's experiment, these endogenous, near-24-hour, or circadian, rhythms have been found to be central to human biology. In this issue of *Current Biology*, Stothard and colleagues [3] report on the findings

of their own camping trip which demonstrated that the timing of the near-24-hour clock is shifted later under conditions of modern electric lighting and that humans are responsive to seasonal changes in day length under conditions of natural light exposure.

A wide range of human biology has been shown to be under the purview of the near-24-hour biological clock: endogenous circadian rhythms exist in numerous physiological and behavioral variables [4]. These rhythms are ultimately the product of transcriptional-translational feedback loops that form the underlying 'gears' of the clock and this molecular clock-work is found in most tissues, with a central clock existing in suprachiasmatic nuclei of the hypothalamus [5]. The suprachiasmatic nuclei function to internally synchronize the various rhythms and are themselves synchronized to the external 24-hour day by light [6]. Intrinsically photosensitive retinal ganglion cells

transmit the light information to the central clock via a monosynaptic connection [5]. Importantly, the magnitude and direction of the resetting effect of light is dependent on the biological time of exposure [4].

For millions of years, humans and their more immediate ancestors lived under a relatively consistent pattern of light exposure: from day to day the variability in the timing of sunset and sunrise was on the order of minutes while greater variation might only occur over the course of a year. The introduction of widespread electrical lighting in the 20th century [7] upended the pattern of light exposure to which the circadian system had adapted. Stothard and coworkers set out to quantify the impact of this electrical light exposure on the timing of the 24-hour biological clock in humans using two separate experiments.

The first experiment was an extension of their previous work. In their earlier study, they demonstrated that a week of