

View-based Homing

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Places in the natural world are uniquely defined by the panoramic views seen from these locations. Provided orientation remains constant, views change in a systematic and smooth fashion with distance from a location. These image differences are mainly due to the depth structure of the environment: Views change faster in densely cluttered environments than in open country (Zeil et al. 2003; Stürzl & Zeil 2007). We review the information content of panoramic images with regard to finding a location in space, both under natural conditions and in experimental arenas (Stürzl et al. 2008). We then go on to discuss the way in which insects learn and use views for homing. Homing insects are known to be guided by visual memories of the goal environment. They acquire these visual representations during highly structured and elaborate learning flights on departure. The organization of these learning flights is surprisingly similar across different species of wasps and bees, indicating that they reflect fundamental requirements of view-based navigation. Using high-speed stereo cameras we show that ground-nesting wasps employ a saccadic gaze strategy during both learning and homing, in which gaze is stabilized along consecutive segments of linear flight. To understand what wasps are looking for during their learning flights and how they use what they see during learning to guide their return, we have used a robotic gantry to move a panoramic imaging device along the flight paths of learning and homing wasps (Zeil et al. 2007). We then determined how image differences develop throughout a learning flight and identified which views guide the insect's return. We discovered that learning wasps move in such a way as to systematically acquire a series of boundary snapshots that define a V-shaped flight corridor leading to the nest. When they encounter these boundary views upon homing, they move away from the left or the right boundary towards the centre line of the V-shaped flight corridor.

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Allometry of dung beetle eyes in relation to their ecology and behaviour.

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The true dung beetles – Scarabaeini – are all characterised by their use of detritus as a nesting material. However, among the 5000 species in the subfamily, two methods of handling dung predominate. It is either rolled away and buried, or buried directly beneath the pat in a concealed tunnel. Remarkably, gross eye structure was found to vary widely across 26 species examined in the taxon, and in the extent to which the eye is divided by a structure called the canthus.

Eye size was measured by creating castes of the cornea, and then correlated to body size. Diurnal ball rollers, despite using celestial cues for orientation, show little allometric increase in eye size, whereas crepuscular and nocturnal species reveal evidence of pronounced pressure to increase eye size in relation to body size. Atypically, diurnal tunnelling species have far larger eyes than predicted by their body size, which may be related to their requirements for accurate flight rather than dung sequestering or diel flight activity (Fig. 1).

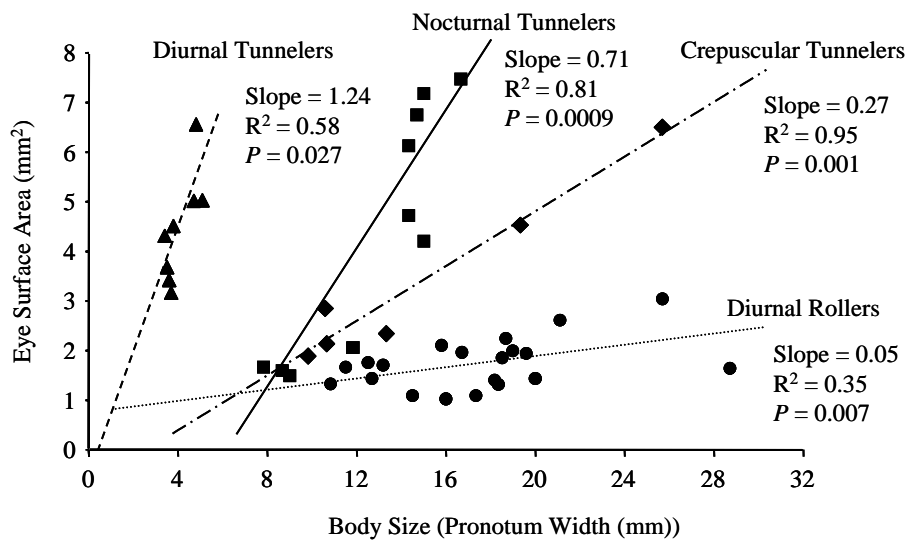


Fig. 1 Correlation of eye size and body size in different groups of dung beetles

All species however have the eye divided to some extent by the canthus, which remains an enigmatic but costly structure because it apparently reduces the available area for light capture. The dung beetle eye is shown to be a plastic organ which varies in response to ecological pressures rather than phylogenetic history.

Sun (and moon) identification in *T. saltator*

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The sandhopper *Talitrus saltator* uses the sun and moon to return to the band of wet sand of the beach (Papi & Pardi, 1953, Ugolini et al., 1999). Although the ability to compensate for azimuthal variations of the sun and moon are well known, the factors by which sandhoppers identify the moon and the sun are not yet understood. Previous studies hypothesized that identification of the sun depends on the L:D rhythm and the sky/sun illumination intensity: below an intensity threshold, the sun compass no longer operates and the animals show positive phototaxis (Ugolini et al., 2005). On the other hand, identification of the moon seems to be independent of the intensity of illumination (Ugolini et al., 2005).

Our recent findings showed that *T. saltator* uses the skylight intensity gradient (i.e. the nonhomogeneity of light intensity between solar and antisolar hemidomes) as a compass cue in ecologically correct direction finding. Animals tested in a confined environment with the possibility to perceive only the skylight intensity gradient (altered skylight polarization and spectral gradient, and no direct vision of the sun) clearly used this factor as an orienting cue. In order to identify the parameters on which sun and moon identification are based, we carried out experiments with adult individuals of *T. saltator* under artificial (laboratory) conditions. Groups of about 10 sandhoppers were released at night in a transparent Plexiglas bowl placed horizontally on a tripod and surrounded by a white Plexiglas dome internally illuminated by an optic fibre bundle (artificial sky); a second fibre bundle was used to simulate the sun or moon. To reproduce the light intensity gradient of the sky in the dome, we used grey gelatine filters. A Xenon lamp (150 Watt) was used as the artificial sun/moon.

In the laboratory releases, identification of the moon was independent of the intensity of the artificial moon and sky. Indeed, the animals maintained a correct moon orientation even under a "sun compass" level of illumination or with only the presence of the false moon (with the artificial sky illumination switched off). Use of the Xenon lamp seems not to have affected the (moon) orientation of the animals. However, significant deviations from the direction based on the moon compass were obtained in two conditions: 1) with the Xenon lamp simulating the sun/moon and an illumination external to the dome, 2) with the grey filter placed above the false sky toward the antisolar hemidome. In both cases, the sandhoppers were oriented in agreement with the *T. saltator* model for sun compensation at night (Pardi, 1954, Ugolini et al., 2002). Therefore, identification of the sun in sandhoppers seems to be based on a sun and sky illumination threshold, on the L:D rhythm, and also on the presence /absence of the skylight intensity gradient.

Therefore, identification of the sun in sandhoppers seems to be based on a sun and sky illumination threshold, on the L:D rhythm, and also on the presence/absence of the skylight intensity gradient.

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**Visually-mediated stabilizing reflexes dictate the direction of
the path-integrated egocentric home vector**
-Or-
Home is where the eyes are.

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This study investigates the relationship between the spatial sense derived from path integration and the modulation of spatial perception by stabilizing reflexes such as the optokinetic response. The psychobiology of such modulation has been well-studied in humans, in which two separate visual representations in the brain have been identified, one governing spatial perception and one governing visually-guided behavior (e.g., Bridgeman, 1986). However, these studies relate stabilizing reflexes to perception of local object direction; stabilizing reflexes have never been related to larger-scale spatial perception/memory systems involved in navigation.

During path integration the home vector stored in memory may be considered allocentric if its angular component is referred to a stable external cue (celestial cues, earth's magnetic field). In this case, an animal returning home retrieves the vector from memory, measures its directional component relative to the external cue, and travels in the computed direction regardless of current location or orientation. In contrast, the home vector may be considered egocentric if it is referred to the animal's body axis, and takes no account of external cues. The ideal test of the allo- or egocentric nature of the home vector is to re-orient the animal in its natural habitat. Such a test may prove problematic if there is a strong counter-rotation – the optomotor reflex. However, in this study I exploit this reflex to demonstrate the relationship between the memory-stored home vector and stabilizing reflexes. Fiddler crabs readily form burrows in a dish of mud, and appear to exhibit all relevant natural behaviors. A dish containing crabs (*U. pugilator*) was placed on a platform inside a surround which could be rotated. The surround had vertical stripes or a panoramic scene from the crab's own mudflat, to provide visual contrast. When the surround was rotated it induced the counter-rotational response by the eyes, which was usually followed later by body rotation. For small rotations of the surround (<40°) quite often only the eyes responded, and on average the eyes counter-rotated about 12° more than the body. A homing error follows, which is less than the rotation of the surround. This shows the home vector was not referred to the sky, surround or burrow, and indicates an egocentric home vector. The main finding is that the homing error is nearly identical to the change in eye orientation, and not change in body orientation. For example, if the surround rotated by 20°, the eyes by 15° and the body not at all, the startled crab quickly rotated its body beneath the eyes, which remained stable, to realign the two and made a 15° homing error. When the body rotated very little, and the eyes tracked the surround through several saccades, it was the eyes' final deviation from their original orientation, excluding all inter-saccade movements, which dictated the homing error. Thus, eye position dictates the current direction sense, which I interpret to mean that *the home vector is referred not to the body axis per se, but to the current state of the stabilizing control loop as indicated by eye position.*

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Vision, behaviour and information: Fiddler crabs use a multi-stage response strategy to gather information on predation risk

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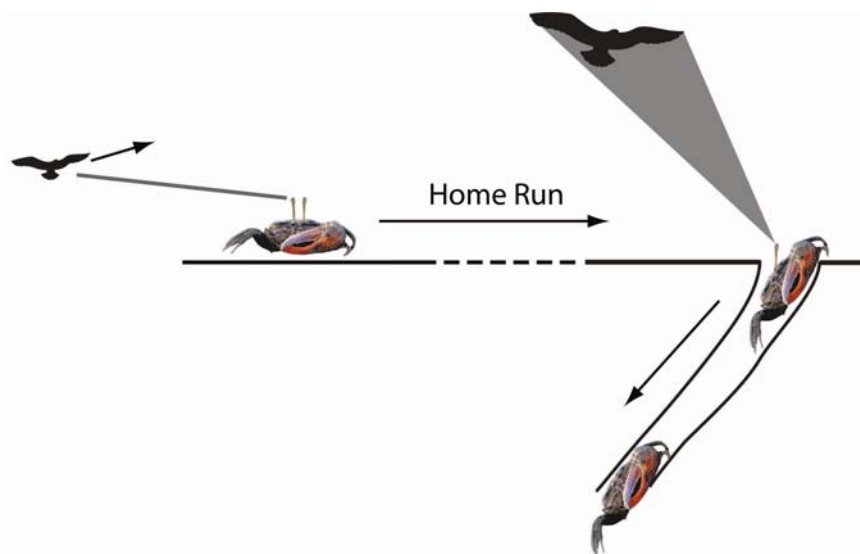
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The structure of an animal's behaviour is an important factor to consider if we are to understand the visual processing taking place in their daily life. We show here that predator avoidance behaviour of fiddler crabs living in their natural environment is optimised to aid the gathering and processing of relevant visual information.

We have previously explored the escape behaviour of fiddler crabs in response to avian predators. Results showed that at the time of first response (the decision of whether to run home towards the burrow or not) the crabs information about the predator's distance and direction of approach was limited. Fiddler crabs are forced to base their decision on incomplete information that does not accurately predict the actual risk of predation.

Fiddler crabs employ two tactics to deal with this issue. The first involves the use a multi-stage escape sequence. Breaking up their response into stages means that they can gather additional, more risk-sensitive information about the approaching object without exposing themselves to too much danger. This allows them to cut some of their responses short and avoid the most costly part of their escape sequence, the underground response. This suggests that we need to interpret the quite commonly found multi-stage anti-predator responses not only as a tool to successively reduce the animals' exposure to the predator, but also in light of the animals' visual information processing limits.

The second involves the crabs' ability to selectively habituate to certain repeated events in their natural environment while remaining responsive to others. We are in the process of determining the sensory information that underlies this learning process.



Two stages of the crabs' escape response to avian predators: the home run and the underground response

Bumblebee Learning Flights

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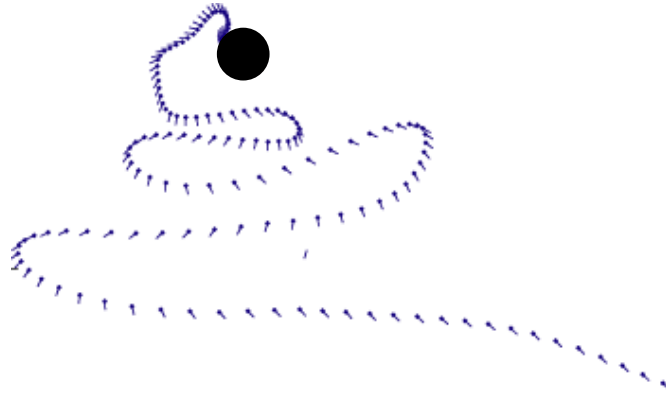


Figure 1: A characteristic scanning return flight when a single landmark is placed over the nest

When bees and wasps leave the nest to forage they perform learning flights [1]. Analysis of the learning flights of solitary and social wasps has identified several components of the flights which seem to be adapted for the active acquisition of visual information [2, 3, 4, 5]. Here we present a similar analysis of the learning flights of bumblebees when they are close to their nest. A colony of bumblebees was located under a textured white carpet with various configurations of between one and four black cylinders 0, 8 or 20 cm from the nest hole. We have videoed the flights at high speed and definition to examine head and body movement and at lower speed and definition to capture the geometry of the flight over a larger area. Outward and return flights are analysed and the impact of the landmark configuration assessed. We also identify common strategies used by the bees (for instance, scanning return flights, Figure 1) and assess correlations between outward and return flights. In particular, we show that the bees' headings when leaving the nest are strongly correlated with the headings on their return, and that the mean heading is largely independent of landmark configuration.

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What visual information do Australian desert ants use for navigation?

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Ants that forage in non-barren environments often develop idiosyncratic routes between their nest and a profitable foraging ground. These routes are guided by stored views of local landmarks (Wehner et al., 1996). Displacement studies have shown that these route memories are independent of path integration and can be accessed out of the habitual sequence (Kohler and Wehner, 2005). Therefore, these ants with their low resolution vision are able to recognise their location and recall the appropriate navigational instruction. Here we ask which components of natural scenes ants use to recognise location.

The Australian desert ant *Melophorous Bagoti* provides an excellent opportunity for the study of visually guided navigation. Foragers of this species rapidly learn idiosyncratic foraging routes and, although their habitat contains grass tussocks, shrubs and trees, these objects are sparse enough to make analysis of the natural images tractable.

We captured successful *Melophorous Bagoti* foragers after they had returned to their nest from a feeder and these ants accurately oriented toward the nest when released at locations about 4m away. This simple release paradigm can be used to investigate visual place recognition by monitoring the accuracy of nestwards orientation when parts of the ants' visual field are systematically obscured. We therefore released ants after placing walls of various heights around the experimental release point. Preliminary results indicate that the lower portion (up to 20° above the horizon) of the visual field is more important for place recognition and homing than upper portions. Panoramic images were captured from the release location and the nest. Analysis of these images should indicate what visual information is available within the necessary portion of the ants' visual field.

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