



Crucial role of ultraviolet light for desert ants in determining direction from the terrestrial panorama



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Ants use the panoramic skyline in part to determine a direction of travel. A theoretically elegant way to define where terrestrial objects meet the sky is to use an opponent-process channel contrasting green wavelengths of light with ultraviolet (UV) wavelengths. Compared with the sky, terrestrial objects reflect relatively more green wavelengths. Using such an opponent-process channel gains constancy in the face of changes in overall illumination level. We tested the use of UV wavelengths in desert ants by using a plastic that filtered out most of the energy below 400 nm. Ants, *Melophorus bagoti*, were trained to home with an artificial skyline provided by an arena (experiment 1) or with the natural panorama (experiment 2). On a test, a homing ant was captured just before she entered her nest, and then brought back to a replicate arena (experiment 1) or the starting point (the feeder, experiment 2) and released. Blocking UV light led to deteriorations in orientation in both experiments. When the artificial skyline was changed from opaque to transparent UV-blocking plastic (experiment 3) on the other hand, the ants were still oriented. We conclude that UV wavelengths play a crucial role in determining direction based on the terrestrial surround.

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Navigating ants use a multifaceted toolkit (Wehner, 2009). Along with path integration (Wehner & Srinivasan, 2003), ants are known to use visual terrestrial cues for navigation (*Temnothorax albipennis*: Pratt, Brooks, & Franks, 2001; *Formica rufa*: Graham & Collett, 2002; Lent, Graham, & Collett, 2013; *Cataglyphis fortis*: Wehner, Michel, & Antonsen, 1996; *Melophorus bagoti*: Wystrach, Beugnon, & Cheng, 2011, 2012; Wystrach, Schwarz, Schultheiss, Beugnon, & Cheng, 2011; *Myrmecia croslandi*: Narendra, Gourmaud, & Zeil, 2013; Zeil, Narendra, & Stürzl, 2014) and as a 'back-up', they also engage in systematic searching (Schultheiss, Cheng, & Reynolds, 2015).

Some properties of the panorama have been shown to guide ants travelling on familiar routes, including fractional position of mass, matching of segments of the scene and the skyline. Fractional

position of mass refers to the amount of the visual scene to one's left versus right as one faces the goal direction. Wood ants, *F. rufa*, use this cue in some conditions in the laboratory (Lent et al., 2013). In other conditions, *F. rufa* might match a salient segment of the scene (Lent et al., 2013). The skyline is a record of where terrestrial objects meet the sky across the 360° panorama (Dyer, 1987; von Frisch & Lindauer, 1954; Graham & Cheng, 2009a, 2009b; Towne, 2008; Towne & Moscrip, 2008). Its use was demonstrated in Central Australian desert ants, *M. bagoti*, when an artificial skyline in black was created to mimic the natural skyline seen from the start of the journey (Graham & Cheng, 2009a). The ants oriented according to the artificial skyline even when it was rotated so that the celestial cues associated with the panorama did not match in test and training conditions.

Here we investigated further the nature of the sensory input used for view-based matching, focusing on the role of ultraviolet (UV) wavelengths of light in the use of the terrestrial panorama. Ants have been found to have two types of visual receptors in their compound eyes and ocelli (*Cataglyphis bicolor*: Mote & Wehner,

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1980), or sometimes three (*M. croslandi* and *Myrmecia vindex*: Ogawa, Falkowski, Narendra, Zeil, & Hemmi, 2015). In these cited cases, one type is most sensitive to light in the green range, with maximum sensitivity at ca. 510 nm or ca. 550 nm. One other type has highest sensitivity in the UV range, peaking at ca. 350 nm or ca. 370 nm. Ground objects typically do not reflect much in the UV wavelengths, far less so than what is found in the sky (Möller, 2002). Theoretically, UV wavelengths are useful for segregating ground objects from the sky.

Two different ways of using UV wavelengths for delineating the skyline have been proposed. Möller (2002) proposed that UV–green contrast, sensitive to the ratio of UV irradiance to green irradiance, might be used to differentiate sky from ground, and thus delineate the skyline. An opponent-process contrast based on the UV:green ratio buys constancy in the face of fluctuating overall intensity both across time and across space. If a cloud covers the sun temporarily and drops the intensity, both the green reflectance of terrestrial objects and the UV irradiance in the sky diminish. But at the local level, the ratios stay fairly constant, as measured empirically by Möller (2002). While UV–green opponent neurons have been found (in locusts: Kinoshita, Pfeiffer, & Homberg, 2007), a proposed UV–green channel for segregating ground objects from the sky remains hypothetical. But such opponent-process systems are well known in other domains of visual processing in which constancy is important, such as colour vision (in primates: Hurvich & Jameson, 1957; in insects: Backhaus, 1991) and polarization vision in insects (crickets: Labhart, 1988, 1996). More recently, UV levels alone have been proposed in two separate studies (Differt & Möller, 2015; Stone, Mangan, Ardin, & Webb, 2014). Stone et al. (2014) used UV levels for segregating the skyline for artificial navigation, and found that it worked better than UV–green contrast. Differt and Möller (2015) also found that UV levels worked well in computational models, with UV–green contrast hardly adding any benefits.

If UV level or UV–green contrast is used by insects in segregating the skyline, light in the UV range should prove important for navigation based on the panoramic scene. Evidence for this claim is still lacking. We tested the importance of the UV wavelengths in the terrestrial scene for the Central Australian *M. bagoti* (Cheng, Narendra, Sommer, & Wehner, 2009; Muser, Sommer, Wolf, & Wehner, 2005; Schultheiss & Nooten, 2013) by using a clear plastic that filtered out most of the energy from UV wavelengths. The material cut out most wavelengths under 400 nm, as spectrometric measurements indicated. This obliterated most, although probably not all, of the sensitive range of the ant's UV receptor. It was a serious 'knock-down' manipulation, if not a total 'knock-out' one. Key manipulations consisted of surrounding the scene viewed by homing ants with a tall cylinder of this clear plastic. Overall brightness is reduced a little by this manipulation, and in some cases, for both ground objects and the sky. The greatest change in UV levels or in UV–green contrast, however, would be at the top border of the clear plastic. Because it is at a uniform height, a skyline defined in terms of either parameter would be uninformative. The necessity of the UV wavelengths for orientation was tested both in an impoverished artificial arena defining a skyline and in the natural panorama. The efficacy of UV wavelengths was tested by replicating the skyline of a training arena with an identical skyline using clear UV-blocking plastic.

METHODS

Location and Setting

Field work took place at a private property ca. 10 km south of the town centre of Alice Springs, Australia, in a region of semiarid

climate with an average annual rainfall of 282.6 mm. The field site is dominated by the invasive buffel grass, *Cenchrus ciliaris*, mixed with bushes of *Acacia* and *Hakea* genera, and tall eucalypts. Low buildings were also scattered around the premises, adding to the panoramic terrestrial cues (Fig. 1a). Experiments took place in three southern summers from November to March, from 2012 to 2015.

Test Animals

The red honey ant, *M. bagoti*, is widespread in the area. It occupies the niche of a thermophilic diurnal scavenger (Wehner, 1987), looking for desiccated arthropod remains and plant

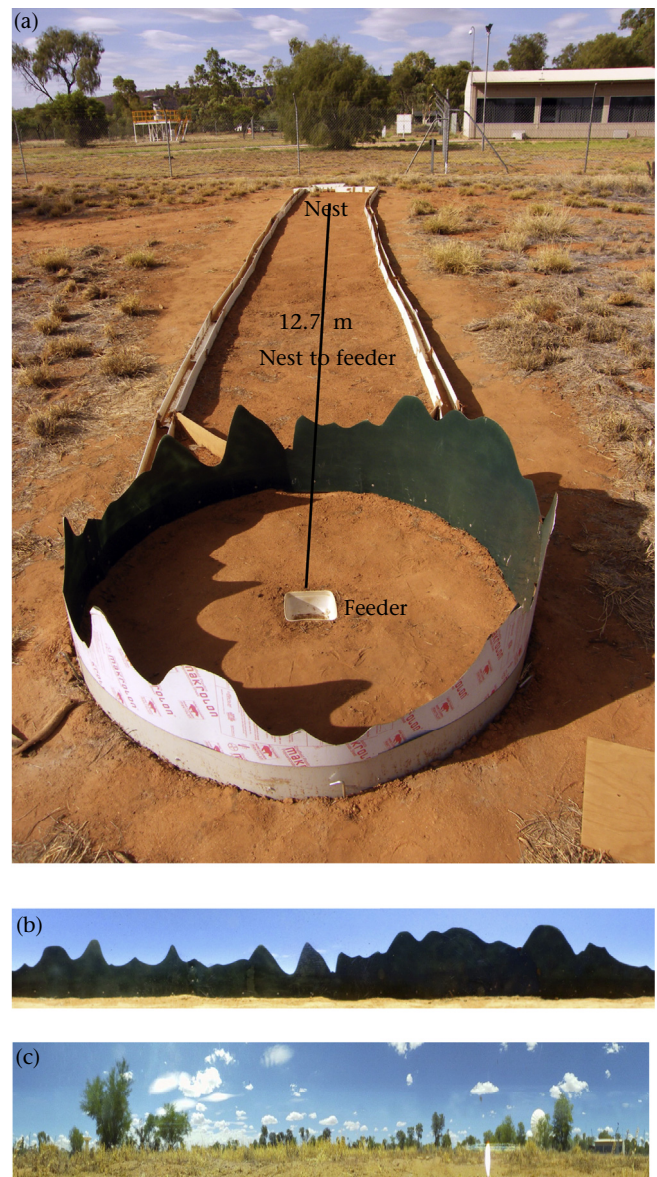


Figure 1. The set-up in experiments 1 and 2. (a) A photo of the arena used in experiment 1 with some of the surrounding scenery, which would not be visible to the ants inside the arena. An enclosure (white plastic) surrounding the nest and leading to the arena kept most of the ants foraging in the corridor and increased the number of foragers arriving at the feeder. (b) The panoramic view provided by the arena. The photo was taken with a panoramic lens and rendered into cylindrical form. The photo 'wraps around', in that the right side of the photo coincides with the left side. (c) The panoramic view at the feeder in experiment 2, with again the right side of the photo coinciding with the left side.

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