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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.

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

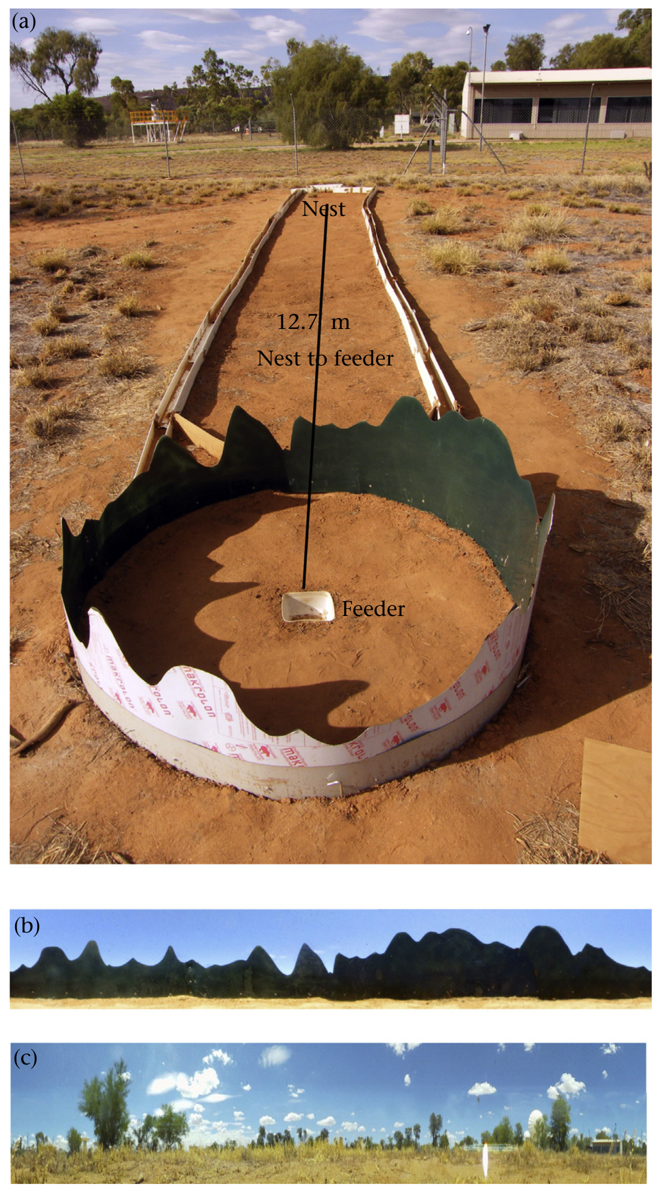

Figure 1. The set-up in experiments 1 and 2. (a) A photo of the arena used in experiment 1 with some of the surrounding scenery, which would not be visible to the ants inside the arena. An enclosure (white plastic) surrounding the nest and leading to the arena kept most of the ants foraging in the corridor 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.

materials in the heat of the day during the summer (Christian & Morton, 1992; Muser et al., 2005; Schultheiss & Nooten, 2013). Ants from one nest took part in experiments 1 and 2, while ants from a different nest took part in experiment 3.

Materials and Set-ups

In each experiment, ants travelled mostly or completely over natural terrain to a plastic tub (15 × 15 and 9 cm deep) sunk into the ground as a feeder. Feeder-to-nest distance was 12.7 m in experiment 1, 5 m in experiment 2 and 10 m in experiment 3. A circular green plastic arena surrounded the feeder in experiments 1 and 3 to provide an artificial terrestrial panorama (reflectance characteristics are shown in Fig. 2b), while in experiment 2 the natural scene provided the terrestrial panorama. The arena in experiments 1 and 3 (diameter 1.4 m) had a uniform green colour but variable height (highest part 0.5 m), providing a panoramic skyline (Fig. 1). A bit of dirt was dug out to provide an entrance into the arena, under the part of the wall between the feeder and the nest.

The feeder was stocked with cookie crumbs (Arnott brand) and pieces of mealworm for the ants to forage. Slippery tape covered the already slippery feeder walls, so that ants could not climb the walls of the feeder. During training, sticks of natural vegetation and cardboard pieces were placed in the feeder as exit ramps.

Around the route between the feeder and the nest in each experiment, we set up an enclosure of plastic or wooden boards that surrounded the nest and extended to the arena wall (Fig. 1). The materials are very hard for ants to climb over, and this increased the number of animals visiting the feeder. This enclosure was wide enough (ca. 1.2 m) so that on the route, the natural scene rose all around above the enclosure for ants travelling away from the walls, which they did most of the time.

Crucial to the study was the use of a transparent UV-blocking plastic (Makrolon brand) a material that blocks (absorbs) UV light. This material filtered out most of the energy below 400 nm (Fig. 2a). It thus blocks much but not all of the wavelengths of light that would excite the UV receptor in *Cataglyphis* ants (Mote & Wehner, 1980). This plastic surrounded the tested ant in some experimental conditions. Its dimensions were 1.4 m (diameter) by 0.61 m (height) in experiment 1, and 0.7 m by 0.63 m in experiment 2. The dimensions were chosen to cover the visible terrestrial panorama in both experiments.

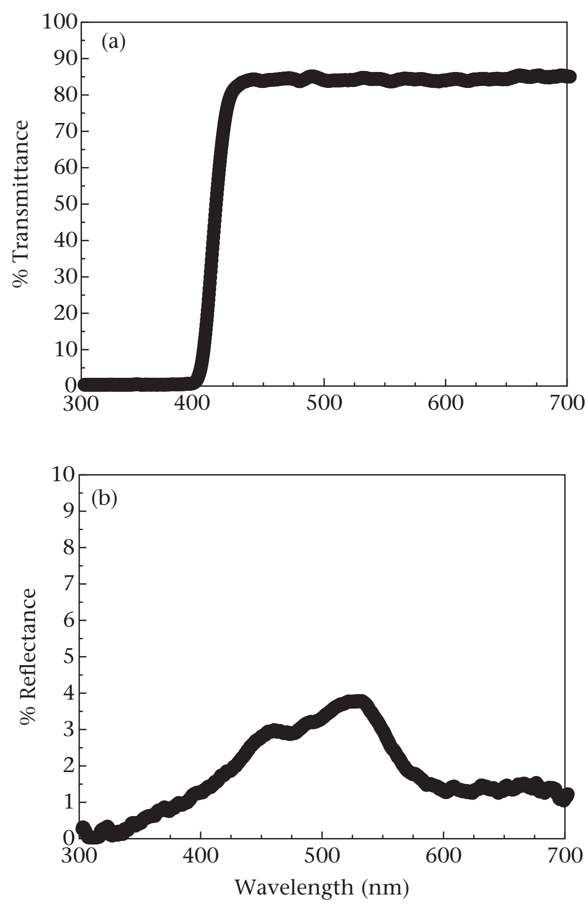

Figure 2. (a) Transmission characteristics of the Makrolon UV-blocking plastic. The photospectrometric measurements were taken with an Ocean Optics Jaz photospectrometer (Ocean Optics, Dunedin, FL, U.S.A.), with the plastic placed in front of a piece of standard white colour, and compared with the reflectance of standard white alone. Thus, in the measurements of the plastic, the light had to go through the plastic twice, to get to the standard white and then to reflect back from the standard white. Only transmittance in the range of 300–700 nm, a reliable range for the instrument, is shown. (b) Reflectance characteristics of the green wall of the arena used in experiments 1 and 3, measured with the same instrument. Note that the scale is reduced 10-fold, with maximum on graph set at 10%.

Training and Test Procedures

During training, ants that arrived at the feeder were painted with nontoxic enamel paint (Tamiya brand) on the abdomen, each with a colour that represented the day of arrival. Thereafter, the ants were left to shuttle back and forth between feeder and nest for at least 2 days before testing.

On a test, an ant might be tested as a full-vector (FV) and or a zero-vector (ZV) ant. An FV ant is so called because it possesses a vector pointing in the nest direction based on path integration on the outbound trip. Such an ant was taken directly from the feeder in a dark (opaque) vial and placed at the release point for a test. A ZV ant is so called because it has run off its vector based on path integration before being tested. We let a ZV ant run home with a bit of food, and captured it just before it entered its nest, using a small plastic enclosure to trap the ant if necessary. Then the ant was taken in the dark to be released for a test.

In testing the use of the terrestrial panorama, tests with ZV ants provide the crucial data. FV ants use the celestial compass cues as well as possible terrestrial cues, and the crucial manipulations should not affect their orientation too much. At most, the direction of their orientation might be off slightly compared with unmanipulated conditions because the UV-blocking plastic cuts out a part of the sky. The oriented behaviour of FV ants would indicate that ants were still motivated to home under the test conditions. FV test conditions were added in experiment 1 because ZV ants were not oriented in the home direction in the key experimental conditions.

On all tests, an ant was released in the centre of a goniometer consisting of a wooden board with a circle drawn on it divided into 24 sectors of 15° each. Location of testing is described in the following subsection. Only ants that held on to a piece of cookie were tested, to ensure homing motivation. We noted the sector in which the ant crossed at 15 and 30 cm from the release point, these distances being drawn on the goniometer. Each ant was tested individually only once, under one of the conditions to be described next.

Australia does not have ethical regulations concerning ants, but the manipulations used in the study are completely noninvasive. From many studies, including this one, we have noted no adverse effects on the ants.

Conditions of Testing

Experiment 1

There were five test conditions in experiment 1 using the dark green arena with a skyline shape. To minimize interference with ongoing training, ants were tested in a replica of the arena of the same construction placed in the same orientation just behind the training arena from the perspective of the nest. The goniometer was placed at the centre of the test arena. In the ZV-control condition, ZV ants were tested in the replica arena, a condition that replicated training conditions. In the ZV-UV-block-inside condition, the transparent UV blocking foil, of a uniform height exceeding the maximum height of the green artificial skyline, was added on the inside of the test arena. In the ZV-UV-block-outside condition, the tall transparent UV blocking foil was added on the outside of the test arena, hugging the walls. Two conditions also tested FV ants. In the FV-control conditions, FV ants were tested in a replica of the training arena oriented in the same direction. In the FV-UV-block-inside condition, the UV-blocking foil was added inside the walls of the test arena.

Having the UV-blocking plastic both inside and outside the test arena provided more than variations on the theme. The ZV-UV-block-inside was important because it reduces the reflectance of the arena wall more than it does the irradiance of the sky. As the plastic was in front of the arena, light had to go through it to reach the wall, and go through it again in bouncing off the wall. This results in a ca. 16% reduction in transmission according to Fig. 2b. Above the wall, the transmission through the plastic is approximately 91% (square root of 84%) in the visible range, a ca. 9% reduction, but wavelengths < 400 nm were cut out as well. The brightness change of course depends on the sensory system of the ant rather than physical parameters. In this regard, data on *C. bicolor* show that their 'green' receptors (with peak sensitivity at ca. 510 nm) are more sensitive by almost two orders of magnitude than their 'UV' receptors (with peak sensitivity at ca. 350 nm; Figure 6 in Mote & Wehner, 1980). Furthermore, in ants' compound eyes, the majority (ca. 75%) of receptors are 'green' receptors (Menzel, 1972). Thus, the 'green' channel, whose contrast is at least preserved in the experimental manipulations, probably dominates brightness perception.

In both these conditions, the biggest change in UV levels, and also in UV–green contrast, was found at the upper border of the uniform transparent plastic. We expected both these UV-block conditions to affect the orientation of ZV ants adversely, while FV ants should not be adversely affected by the UV-blocking plastic.

Experiment 2

Three conditions were tested in experiment 2, all on ZV ants trained with the natural panorama. In the ZV-control condition, ants were tested in training conditions. The goniometer was placed on the feeder, so that the location of testing matched the starting point of the homeward journey on training runs. This condition was used on two replicates from the same nest but at different points in the season, one in mid-November to December and one in February. In the ZV-UV-block condition, ants were again tested at the feeder, but with a UV-blocking foil of uniform height (0.7 m diameter, 0.63 m height) surrounding them. This condition was also used on two replicates at the same two periods in the season. In the ZV-opaque condition, ants were tested at the feeder with an opaque foil (white colour, 0.7 m diameter, 0.63 m height) surrounding them. The foil effectively cut out terrestrial panoramic information, and forced the ants to use celestial sources for directional information.

Experiment 3

Experiment 3 tested the sufficiency of a clear, UV-blocking cut-out in the shape of the training arena used in experiment 1. In all conditions, ZV ants were tested, with an aim to include at least 100 test individuals in each condition. In the control condition, ants were tested in a replica of the training arena, an exact repeat of the ZV-control condition of experiment 1. In the UV-blocking-foil-cut-out condition, ants were tested in the clear cut-out in the shape of the training arena. This cut-out was placed at a distant test site ca. 143 m away, so that ants would not see a familiar scene through the transparent plastic. In the No-arena condition, ants were tested at the distant test site at which the UV-blocking-foil-cut-out condition took place, but without any arenas, as a test for orientation at that site. Based on suggestive pilot results, we predicted that the control and the UV-blocking-foil-cut-out conditions would produce heading distributions that are significantly oriented, while the No-arena condition would produce an unoriented distribution.

Data Analysis

Circular statistics based on Batschelet (1981) and one test of our own making were used for inferential statistics, calculated using Matlab (Mathworks, Inc., Natick, MA, U.S.A.). We compared headings at 15 cm and at 30 cm in all conditions, and found that in no condition across the experiments did they differ significantly in orientation or scatter. We thus restricted data analysis to headings at 30 cm. For each condition, we tested whether the distribution was significantly oriented in the feeder-to-nest direction by the *V* test (Batschelet, 1981). In addition, we examined whether the 95% confidence interval contained the predicted direction, and conducted the Rayleigh test (Batschelet, 1981) to test whether the distribution was oriented in any direction at all. We set alpha at 0.05 for these tests. Differences in scatter between conditions were tested using the Var test, a test of our own making. The absolute difference of each individual heading from the circular mean of each condition was tabulated. These absolute differences in two conditions were compared using the nonparametric Wilcoxon rank sum test (two-tailed). This test is suitable for any conditions that are oriented, for which a meaningful mean direction can be calculated. Conditions were compared against appropriate control conditions. We compared directions between a condition and its appropriate control using the Watson–Williams test (Batschelet, 1981). In cases of multiple comparisons with a group in experiments 1 and 3, we followed Holm's (1979) method for alpha correction. The first alpha was set to $0.05/k$ (number of comparisons). If the comparison with lowest P value is above that value, no null hypothesis is rejected (all deemed nonsignificant). If the lowest P value falls below $0.05/k$, the associated null hypothesis is rejected. The next P value is set at $0.05/(k-1)$ to test against the next lowest P value, and so on.

RESULTS

Experiment 1

Ants were trained and tested with artificial panoramas in experiment 1. Results showed that the UV-blocking foil had a strong effect on the headings of ZV but not FV ants (Fig. 3, Table 1). FV ants oriented well in the nest direction with or without the UV-blocking foil (Fig. 3a), although surprisingly, control FV ants showed a leftward bias in that the 95% confidence interval did not include the feeder-to-nest direction (Table 1). ZV ants in the control condition oriented well in the nest direction (Fig. 3b, Table 1), also with a leftward bias, but ZV ants with the UV-blocking foil on either the inside or the outside of the arena were not oriented in the nest direction according to the *V* test (Fig. 3b,c, Table 1). The Rayleigh

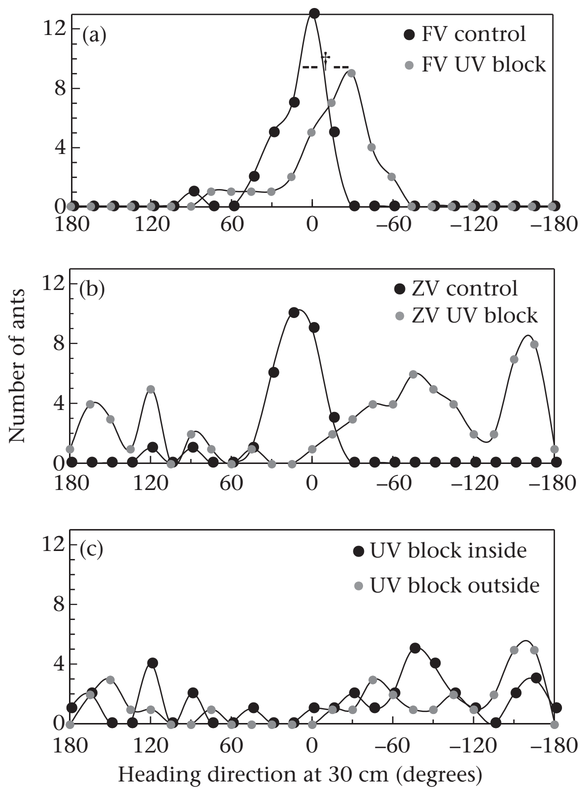

Figure 3. Results of experiment 1. Distributions of heading directions at 30 cm for (a) full-vector (FV) ants under control (training) conditions and with the UV-blocking plastic placed inside the arena, (b) zero-vector (ZV) ants under control (training) conditions and with the UV-blocking plastic placed inside or outside the arena, two conditions combined, and (c) ZV ants with the UV-blocking plastic placed inside or outside the test arena, two conditions separate. Each panel is cylindrical, with $+180°$ and $-180°$ being the same nest-to-feeder direction. Nest direction is at 0°. The line through each distribution is an atheoretical spline that serves only to help readers to visualize the data. The dagger indicates two conditions that differ significantly in mean heading direction. Inferential statistics was not conducted on the combined data in (b).

test showed, however, that these groups were significantly oriented (Table 1). That is because the ants tended to head in the opposite, nest-to-feeder direction (Fig. 3b,c). A V test for this direction showed that this tendency was not significant for the ZV-UV-block-inside condition ($V = 3.18$, $P = 0.220$), but was significant for the ZV-UV-block-outside condition ($V = 11.89$, $P = 0.001$). If the results of these two groups are pooled, the ants were significantly oriented in the nest-to-feeder direction ($V = 15.07$, $P = 0.004$). It should be noted, however, that the 95% confidence interval for either group, or for the two UV-block groups combined, did not include 180°.

In directional scatter, both ZV groups with the UV-blocking foil were more scattered than the ZV-control group (Table 2). Comparing the FV group with the UV-blocking foil on the inside with the FV-control group, the difference in directional scatter was not significant (Table 2).

Comparing mean directions of headings of ZV ants using the Watson–Williams test, both the ZV-UV-block-inside condition and the ZV-UV-block-outside condition differed in mean direction from the ZV-control group (Table 3). For FV ants, the FV-UV-block-inside group differed significantly in mean direction from the FV-control group (Table 3).

Experiment 2

Ants were trained and tested with a natural panorama in experiment 2. In the control condition, ZV ants were clearly oriented in the nest direction (Fig. 4a), but when surrounded with a UV-blocking foil, they appeared less well oriented (Fig. 4b). The UV-block groups in both replicates, however, were in fact significantly oriented in the nest direction (Table 4). Replicate 1 of the UV-block group, however, erred to the right, with the 95% confidence interval not containing the nest direction. Directional scatter between the ZV-control and ZV-UV-block conditions were compared using the Var test. The scatter did not differ significantly for replicate 1, but did differ significantly for replicate 2 (Table 2). When the two replicates were pooled (Fig. 4c), the UV block resulted in more directional scatter in the headings of the ants compared with control conditions (Table 2). ZV ants facing an opaque surround were not significantly oriented (Fig. 4d, Table 4), and not significantly oriented in the nest direction (Table 4).

We compared the mean directions of ZV control groups against the UV-blocking groups using the Watson–Williams test. The mean direction differed for replicate 1 but not for replicate 2 (Table 3). When the two replicates were combined, ZV-control ants did not differ in mean direction from their counterparts surrounded by the UV-blocking foil (Table 3).

In addition, given the differences in behaviour between the ZV ants in experiments 1 and 2, it is of interest to compare groups across experiments in their mean direction, with the usual cautionary note needed about comparing experiments. We compared ZV control groups (two replicates combined for experiment 2) using the Watson–Williams test and found that mean direction differed significantly between experiments ($F = 6.35$, $P = 0.013$). We also compared the UV-blocking conditions (ZV-UV-block-inside and ZV-UV-block-outside combined in experiment 1 versus two replicates of ZV-UV-block in experiment 2) and found that, as expected, they differed significantly in mean direction ($F = 47.96$, $P < 0.001$).

Experiment 3

Ants in experiment 3 were trained in the artificial arena. Experimental groups were tested at a distant location from the

Table 1
Descriptive and inferential statistics for experiment 1

Condition	N	95% CI L (deg)	M (deg)	95% CI R (deg)	R	Rayleigh test		V test	
						z	P	V	P
ZV control	31	25.2	15.3	5.4	0.90	25.21	<0.001	27.04	<0.001
ZV UV block inside	34	−60.0	−106.9	−153.9	0.32	3.49	0.029	−3.18	0.780
ZV UV block outside	32	−111.1	−139.8	−168.5	0.49	7.54	<0.001	−11.89	0.999
ZV UV block, combining ‘inside’ and ‘outside’ conditions	66	−100.9	−126.3	−151.7	0.39	9.75	<0.001	−15.07	0.996
FV control	33	17.7	10.2	2.6	0.94	28.78	<0.001	30.42	<0.001
FV UV block inside	33	−2.0	−14.8	−27.7	0.87	24.79	<0.001	27.73	<0.001

The table shows results for zero-vector (ZV) and full-vector (FV) conditions, including the number of ants tested (N), mean vector direction (M), 95% confidence intervals to the left (95% CI L) and right (95% CI R), mean vector length (R), Rayleigh test results and V test results testing for significant orientation in the fictive nest direction, or exit direction according to the arena.

Table 2
Inferential statistics comparing the directional scatter of conditions in experiments 1 and 2

Experiment	Comparison	Z	P
1	ZV UV block inside versus ZV control	5.36	<0.001
1	ZV UV block outside versus ZV control	3.97	<0.001
1	FV UV block inside versus FV control	1.39	0.163
2	ZV UV block versus ZV control replicate 1	1.92	0.055
2	ZV UV block versus ZV control replicate 2	4.92	<0.001
2	ZV UV block versus ZV control, combining replicate 1 and replicate 2	5.70	<0.001

Comparisons were based on the Var test. Absolute differences of individual headings from the mean circular heading of each of two conditions are computed. The scores for each group are then compared with the Wilcoxon rank sum test, two-tailed. Different zero-vector (ZV) and full-vector (FV) conditions were compared against appropriate control groups.

Table 3
Inferential statistics comparing mean directions of conditions in experiments 1 and 2

Experiment	Comparison	F	P
1	ZV UV block inside versus ZV control	44.74	<0.001
1	ZV UV block outside versus ZV control	104.93	<0.001
1	FV UV block inside versus FV control	14.61	<0.001
2	ZV UV block versus ZV control replicate 1	9.14	0.004
2	ZV UV block versus ZV control replicate 2	3.43	0.068
2	ZV UV block versus ZV control, combining replicate 1 and replicate 2	<1	0.376

Comparisons were based on the Watson–Williams test. Mean directions of different zero-vector (ZV) and full-vector (FV) conditions were compared against appropriate control groups.

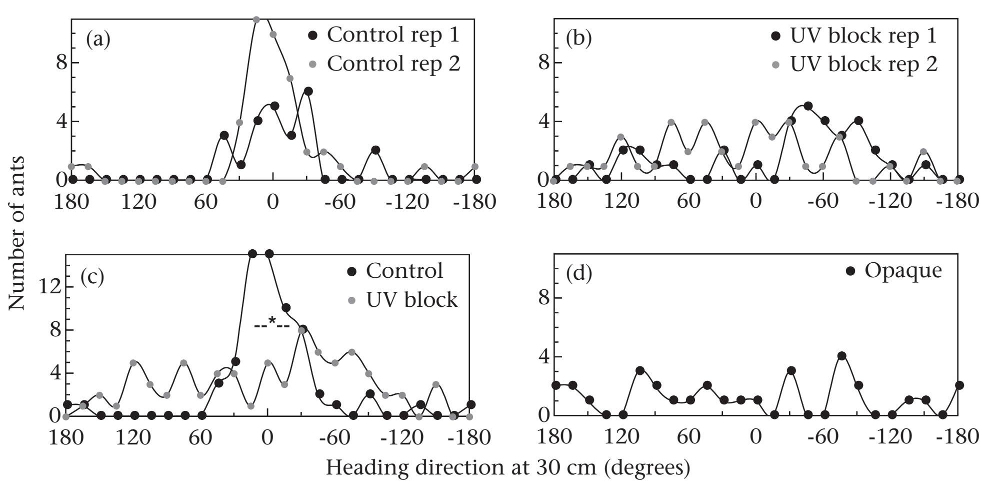

Figure 4. Results of experiment 2. Distributions of heading directions at 30 cm for zero-vector (ZV) ants (a) in control (training) conditions, separately for two replicates, (b) with the UV-blocking foil surrounding them on the test, separately for two replicates, (c) in control (training) conditions and with the UV-blocking foil surrounding them on the test, each with two replicates combined and (d) with an opaque white foil surrounding them on the test. Each panel is cylindrical, with +180° and −180° being the same nest-to-feeder direction. Nest direction is at 0°. The line through each distribution is an atheoretical spline that serves only to help readers to visualize the data. The asterisk indicates two conditions that differ significantly in directional scatter.

Table 4
Descriptive and inferential statistics for experiment 2

Condition	N	95% CI L (deg)	M (deg)	95% CI R (deg)	R	Rayleigh test		V test	
						z	P	V	P
ZV control replicate 1	24	10.0	−6.1	−22.2	0.84	16.76	<0.001	20.00	<0.001
ZV control replicate 2	40	12.0	−1.2	−14.5	0.80	25.33	<0.001	31.92	<0.001
ZV control, combining replicate 1 and replicate 2	64	7.0	−3.1	−13.2	0.81	42.00	<0.001	51.92	<0.001
ZV UV block replicate 1	34	−23.0	−54.8	−86.6	0.44	6.41	0.001	8.52	0.019
ZV UV block replicate 2	40	61.1	26.3	−8.6	0.37	5.56	0.003	13.42	0.001
ZV UV block, combining replicate 1 and replicate 2	74	17.2	−14.0	−45.2	0.31	6.87	<0.001	21.94	<0.001
ZV opaque	28	–	42.2	–	0.07	0.14	0.868	1.50	0.345

The table shows results for zero-vector (ZV) conditions, including the number of ants tested (N), mean vector direction (M), 95% confidence intervals to the left (95% CI L) and right (95% CI R), mean vector length (R), Rayleigh test results and V test results testing for significant orientation in the fictive nest direction, or exit direction according to the arena.

training site, either with a clear cut-out having the shape and orientation of the training arena (UV-blocking-foil-cut-out) or in the open at the unfamiliar site (No arena). Experiment 3 was high in power, with over 100 individuals tested in each condition. The ants (all ZV ants) appeared well oriented, somewhere in the vicinity of the feeder-to-nest direction, in the Control and UV-blocking-foil-cut-out conditions, but it is difficult to discern a clear peak in the heading distribution from the No-arena condition (Fig. 5a,b). The *V* test, however, revealed significant orientation in the nest direction in all three groups (Table 5). Both the UV-blocking-foil-cut-out group and the No-arena group erred to the left, in that the 95% confidence interval did not contain the feeder-to-nest direction. The Var test for directional scatter revealed significant differences between all pairs of groups by Holm's (1979) correction method: control condition versus No-arena condition ($Z = 5.62$, $P < 0.001$), UV-blocking-foil-cut-out condition versus No-arena condition ($Z = 3.41$, $P < 0.001$), control condition and UV-blocking-foil-cut-out condition ($Z = 2.29$, $P = 0.022$). These latter two conditions differed significantly in mean direction (Watson–Williams test: $F = 8.54$, $P = 0.004$). The No-arena condition was too scattered in heading distribution to compare with other conditions. The headings in each condition were smoothed by a running average of three bins in Fig. 5c,d. That is, the count in each bin consisted of the average of the raw count in that bin and its two immediate neighbours. These figures might show the trend of the data better, but were not used for analyses.

DISCUSSION

To summarize the experimental findings, in experiment 1, the terrestrial cues consisted of a skyline in a uniformly coloured arena, offering a form of ‘pure skyline’, while in experiment 2, ants homed under natural conditions. When wavelengths < 400 nm were greatly reduced at a uniform height surrounding the test ant, ants trained and tested in the arena without directional information from path integration (ZV ants) did not orient in the nest direction. Rather, they tended to orient in the opposite nest-to-feeder direction. When ZV ants homing in natural conditions had wavelengths < 400 nm knocked down at a uniform height surrounding the test ant, they were still oriented in the nest direction, but the performance was more scattered compared with control ZV ants homing under unaltered conditions. These results point to the importance of UV wavelengths in using the terrestrial panorama to orient. Reducing UV wavelengths up to a uniform height alters the UV:green ratio and the overall UV level found in the skyline. In effect, the test skyline under such conditions would be the uniformly tall top border of the surrounding clear plastic, where the greatest change in either UV:green ratio or UV level was found. Disruption of orientation would show that one of these parameters (or both) plays a major role in defining the skyline.

In experiment 3, a clear cut-out of the shape of the training arena, made with the UV-blocking plastic foil, was placed at a distant test site. The ZV ants used this cut-out readily to home, albeit less precisely and with a distortion in the initial direction compared with controls. This shows a form of sufficiency of the contour of maximum UV–green contrast or maximum change in UV levels in the face of many changes in spectral composition, two theoretically proposed ways of extracting the skyline (Differt & Möller, 2015; Möller, 2002; Stone et al., 2014).

The most serious alternative interpretation to consider is that a slight reduction in brightness contrast, between ground objects (arena wall or the natural scene) and the sky, might have caused the ants' performance to deteriorate in the UV-blocking-foil conditions in experiments 1 and 2. The UV-blocking foil has the same physical effects on ground objects and sky in experiment 2 in the natural surround, but physiologically, the sky might show a greater reduction in overall brightness (sum of ‘green’ and ‘UV’ receptor stimulation) because it contains more intensity than ground objects in the UV wavelengths, which are knocked down by the UV-blocking foil. In experiment 1, this is compensated for to some extent because the foil reduced the intensity of the wall more (light had to pass through the foil twice in reaching the wall through the foil and then bouncing back out through the foil). It seems, however, that passing clouds covering the sun would have a greater effect in reducing intensity contrast. Such an event might change intensity levels by an order of magnitude (see Möller, 2002). Geophysically, clouds covering the sun block transmission of visible (to humans) light more so than transmission of UV wavelengths (Blumenthaler, Ambach, & Salzgeber, 1994), meaning that cloud cover tends to reduce brightness and green contrast of the skyline

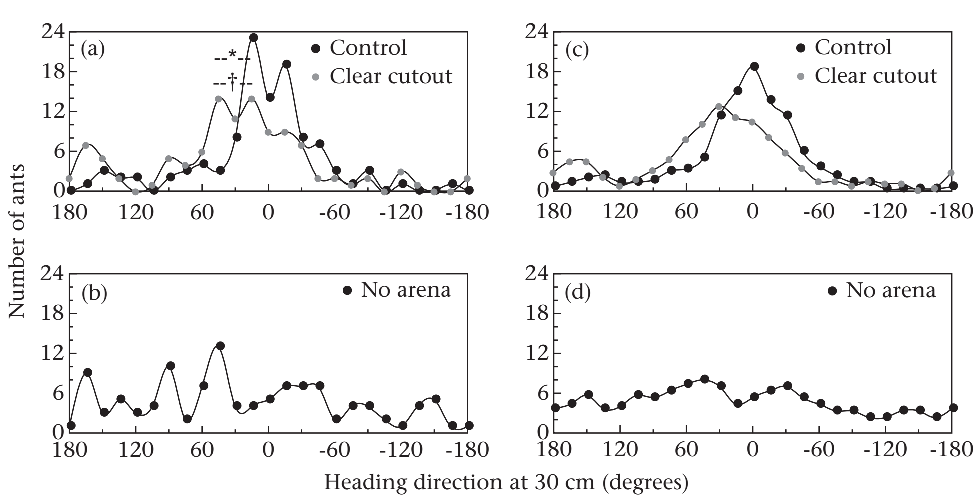

Figure 5. Results of experiment 3. (a, b) Distributions of heading directions at 30 cm for zero-vector (ZV) ants in (a) the control condition and with UV-blocking foil cut out to the shape of the training arena (clear-cutout) and (b) the No-arena condition. (c, d) Smoothed data for (c) the control condition and with UV-blocking foil cut out to the shape of the training arena and (d) in the No-arena condition. Data in (c) and (d) were transformed from those in (a) and (b) by averaging each bin with its two immediate neighbours. Each panel is cylindrical, with $+180°$ and $-180°$ being the same nest-to-feeder direction. Nest direction is at 0°. The line through each distribution is an atheoretical spline that serves only to help readers to visualize the data. The asterisk indicates two conditions that differ significantly in directional scatter. The dagger indicates two conditions that differ significantly in mean heading direction. Inferential statistics were not performed on (c) and (d).

Table 5
Descriptive and inferential statistics for experiment 3

Condition	N	95% CI L (deg)	M (deg)	95% CI R (deg)	R	Rayleigh test		V: nest direction	
						z	P	V	P
Control	108	13.0	3.0	−7.1	0.67	48.9	<0.001	72.80	<0.001
UV blocking foil cut-out	107	42.7	27.8	13.0	0.49	25.8	<0.001	15.51	<0.001
No arena	114	79.5	41.5	3.6	0.21	5.0	0.007	6.52	0.009

The table shows for each condition the number of zero-vector ants tested (N), mean vector direction (M), 95% confidence intervals to the left (95% CI L) and right (95% CI R), mean vector length (R), Rayleigh test results and V test results testing for significant orientation in the fictive nest direction.

more so than it does UV contrast and the UV:green ratio. Our observations from working with this species, albeit not formally documented, have suggested that cloud cover does not affect the orientation of ZV ants adversely. More formal investigations along these lines, however, would be illuminating and should be carried out.

In experiment 1, the ants homed in a uniformly coloured arena that proffered a skyline. The uniform coloration impoverishes spectral cues, but does not eliminate them. While the wall would have the same reflectance characteristics everywhere, the position of the sun would still provide spectral cues (Wehner, 1997). Thus, it was obvious to human observers (without a UV receptor) that one side of the arena looked brighter because the sun was shining on it. The UV-blocking plastic would not alter such a brightness gradient substantially, lowering the brightness on both the sun and the opposite sides. Polarization compass cues in the sky would also be left largely intact. The ZV ants did not orient in the home direction, but some evidence indicates that they did orient opposite the home direction. This backtracking behaviour may parallel what Wystrach, Schwarz, Baniel, and Cheng (2013) found in this species. In that study, *M. bagoti* backtracked when they were captured near their nest after homing from a familiar site (feeder) and then displaced to a distant, unfamiliar location. These ants must have been using their celestial compass to head in the nest-to-feeder direction because the distant site had no useful terrestrial information. Evidence that ZV ants of this species use celestial cues for orientation has been found in some circumstances (Legge, Spetch, & Cheng, 2010; Legge, Wystrach, Spetch, & Cheng, 2014; Wystrach & Schwarz, 2013; Wystrach et al., 2013). In our ants homing with the UV-blocking shield in place, we tentatively interpret the manipulation to have rendered the scene unfamiliar to the ants, unfamiliar enough that they too exhibited backtracking behaviour. The interpretation is uncertain because the 95% confidence interval of the mean direction did not include 180°. The distortion, if it is that, could arise because the UV-blocking foil changed the pattern of polarized light visible to the ants. The polarization compass in ants depends on UV-sensitive receptors in the dorsal rim area (Wehner, 1994). It remains possible, however, that ants in the key experimental conditions were simply disoriented.

FV ants in experiment 1 facing the UV-blocking plastic were oriented in the feeder-to-nest direction, albeit with a bias (Table 1). This shows that ants facing the UV-blocking plastic were motivated to home. Their mean direction, however, differed from that of FV controls facing the replica of the training environment. Again, changing the amount of UV wavelengths perceptible at different azimuths, compared with training conditions, might have distorted the information based on the polarization compass.

FV and ZV ants facing a replica of the training environment showed a leftward bias. Two explanations, not mutually exclusive, might account for this pattern. The first is that just to the left of the feeder-to-nest direction, the arena presented a distinctive undulating cue, a near-vertical segment (see Fig. 1a,b), which might provide a more distinct cue for approaching. This explanation assumes that well-trained FV ants use both the celestial cues and the terrestrial panorama in orientation, and evidence for this claim has been found in this species (Legge et al., 2014). A second, perhaps related reason is that in training, only a small opening allowed exit from the arena. Some of the ants might have erred strategically to one side (and why not the more distinct side?) so as to determine the direction to turn when they arrive at the wall. These, however, remain post hoc explanations in need of confirmation.

Under natural conditions (experiment 2), obliterating UV wavelengths (<400 nm) at a uniform height did not knock out homeward orientation. Unlike the arena, the ants were both motivated to and could orient homewards, but their performance was worse, in being more scattered in initial heading. We thus conclude that UV wavelengths provide an important cue for the ants. We can only speculate at this point on what other cues are available. Assuming the UV receptor to be effectively taken out of play by the UV-blocking plastic, brightness contrast or contrast in the green channel between ground objects and sky remain possibilities. Of course, the cues linked to the sun, polarized light and spectral patterns were not blocked, and were, in principle, available as well.

In experiment 3, a cut-out made of the UV-blocking plastic mimicking the shape of the green arena was presented on the crucial test at a distant test site. Given that the plastic eliminated most wavelengths of light < 400 nm, we hypothesized that the skyline defined by the cut-out would still be the top border of the arena, matching training conditions. The biggest jump in UV levels or in UV–green contrast would still be found at the top of the clear cut-out. With a sample size >100, the ants were oriented in the nest direction, although less precisely and with a deflection in mean direction compared with controls. With regard to the deflection in mean direction, one possibility is the natural panorama viewed through the clear plastic. We conducted a pixel-by-pixel comparison of the natural skyline at the test site and the skyline defined by the training arena: the best match was at about 85° (results not shown). Perhaps the ants in the clear-cut-out test perceived two skylines, one at the top of the test arena and one through the cut-out. Combining those two cues would deflect the mean direction to the left relative to controls.

In reducing substantially the UV wavelengths with the plastic, we of course changed the amount of UV light reaching the ants as well as the UV:green ratio. If either parameter is used to segregate the skyline, similar patterns of results would be found. Navigation based on a skyline defined by measuring the amount of UV light has been demonstrated in autonomously navigating vehicles (Stone et al., 2014). Stone et al.'s vehicles, however, were navigating in environments altered by humans: streets in urban neighbourhoods. Human alterations do not change the UV levels found in the sky, but make the green channel noisier, with some human-made objects reflecting little in the green wavelengths. For biological navigational systems evolving in natural habitats unaltered by humans, some form of UV–green contrast based on opponent processes may be theoretically more likely (Möller, 2002). Evidence supports such an opponent-process system in the polarization compass (Labhart, 1988, 1996). Such opponent processes buy constancy in the face of changing overall illumination levels and alleviate the need to adjust the threshold on the basis of overall light levels, a by no means trivial problem. It would be good to carry out a similar knock-down manipulation targeting the green wavelengths as well. The UV:green ratio would also be distorted if green wavelengths are substantially reduced, and similar deficits should be found. If the ants use the amount of UV light (or stimulation of the UV receptor) for segregating the skyline, the green knock-down manipulation should have little effect.

Sensitivity to UV wavelengths serves navigation in other ways in insects. Sensory neurons sensitive to UV wavelengths in the dorsal rim of the eyes of desert ants and honeybees serve as receptors for polarized light (Wehner, 1994, 1997). Dung beetles, *Scarabaeus zambesianus*, use polarized moon light in order to roll a ball of dung away from the dung pile in a straight line (Dacke, Nilsson, Scholtz, Byrne, & Warrant, 2003). This polarization channel is also mediated by sensitivity to UV wavelengths (el Jundi et al., 2015). In the desert locust, *Schistocerca gregaria*, the polarization channel is mediated by blue receptors (el Jundi, Pfeiffer, Heinze, & Homberg, 2014), but intriguingly, UV–green opponent-process neurons have been found in the anterior optic tubercle (Kinoshita et al., 2007). These neurons are excited by unpolarized light in the green wavelengths and inhibited by unpolarized light in the UV wavelengths, or vice versa. They are thought to serve the celestial compass in locusts. Whether such opponent-process neurons can be found in circuits in insects that encode terrestrial cues remains an open question.

In sum, this study has shown that light in the UV range plays an important role in ant navigation based on the terrestrial panorama. Knocking it down by blocking UV wavelengths made ZV ants not orient in the nest direction when navigating out of a uniformly coloured arena providing a skyline (experiment 1), but instead if anything in the opposite nest-to-feeder direction. With UV wavelengths blocked, the ants did not orient as well in the nest direction under natural conditions, although they were still significantly oriented in this direction (experiment 2). With an opaque artificial arena replaced with a UV-blocking but clear arena of the same shape, the ants managed to orient significantly in the nest direction.

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References

Backhaus, W. (1991). Color opponent coding in the visual system of the honeybee. *Vision Research, 31*, 1381–1397.

Batschelet, E. (1981). *Circular statistics in biology*. New York, NY: Academic Press.

Blumenthaler, M., Ambach, W., & Salzgeber, M. (1994). Effects of cloudiness on global and diffuse UV irradiance in a high-mountain area. *Theoretical and Applied Climatology, 50*, 23–30.

Cheng, K., Narendra, A., Sommer, S., & Wehner, R. (2009). Traveling in clutter: navigation in the Central Australian desert ant *Melophorus bagoti*. *Behavioural Processes, 80*, 261–268.

Christian, K. A., & Morton, S. R. (1992). Extreme thermophilia in a Central Australian ant, *Melophorus bagoti*. *Physiological Zoology, 65*, 885–905.

Dacke, M., Nilsson, D. E., Scholtz, C. H., Byrne, M., & Warrant, E. J. (2003). Insect orientation to polarized moonlight. *Nature, 424*, 33–33.

Differt, D., & Möller, R. (2015). Insect models of illumination-invariant skyline extraction from UV and green channels. *Journal of Theoretical Biology, 380*, 444–462.

Dyer, F. C. (1987). Memory and sun compensation by honey bees. *Journal of Comparative Physiology A, 160*, 621–633.

von Frisch, K., & Lindauer, M. (1954). Himmel und Erde in Konkurrenz bei der Orientierung der Bienen [Sky and Earth in competition in the orientation of bees]. *Naturwissenschaften, 41*, 245–253.

Graham, P., & Cheng, K. (2009a). Ants use the panoramic skyline as a visual cue during navigation. *Current Biology, 19*, R935–R937.

Graham, P., & Cheng, K. (2009b). Which portion of the natural panorama is used for view based navigation in the Australian desert ant? *Journal of Comparative Physiology A, 195*, 681–689.

Graham, P., & Collett, T. S. (2002). View-based navigation in insects: how wood ants (*Formica rufa* L.) look at and are guided by extended landmarks. *Journal of Experimental Biology, 205*, 2499–2509.

Holm, S. (1979). A simple sequentially rejective multiple test procedure. *Scandinavian Journal of Statistics, 6*, 65–70.

Hurvich, L. M., & Jameson, D. (1957). An opponent-process theory of color vision. *Psychological Review, 64*, 384–404.

el Jundi, B., Pfeiffer, K., Heinze, S., & Homberg, U. (2014). Integration of polarization and chromatic cues in the insect sky compass. *Journal of Comparative Physiology A, 200*, 575–589.

el Jundi, B., Warrant, E. J., Byrne, M. J., Khaldy, L., Baird, E., Smolka, J., et al. (2015). Neural coding underlying the cue preference for celestial orientation. *Proceedings of the National Academy of Sciences USA, 112*, 11395–11400.

Kinoshita, M., Pfeiffer, K., & Homberg, U. (2007). Spectral properties of identified polarized-light sensitive interneurons in the brain of the desert locust *Schistocerca gregaria*. *Journal of Experimental Biology, 210*, 1350–1361.

Labhart, T. (1988). Polarization-opponent interneurons in the insect visual system. *Nature, 331*, 435–437.

Labhart, T. (1996). How polarization-sensitive interneurones of crickets perform at low degrees of polarization. *Journal of Experimental Biology, 199*, 1467–1475.

Legge, E. L. G., Spetch, M. L., & Cheng, K. (2010). Not using the obvious: desert ants, *Melophorus bagoti*, learn local vectors but not beacons in an arena. *Animal Cognition, 13*, 849–860.

Legge, E. L. G., Wystrach, A., Spetch, M. L., & Cheng, K. (2014). Combining sky and earth: desert ants (*Melophorus bagoti*) show weighted integration of celestial and terrestrial cues. *Journal of Experimental Biology, 217*, 4159–4166.

Lent, D., Graham, P., & Collett, T. S. (2013). Visual scene perception in navigating wood ants. *Current Biology, 23*, 684–690.

Menzel, R. (1972). The fine structure of the compound eye of *Formica polyctena* – functional morphology of a Hymenopteran eye. In R. Wehner (Ed.), *Information processing in the visual systems of arthropods* (pp. 37–47). Berlin, Germany: Springer-Verlag.

Möller, R. (2002). Insects could exploit UV-green contrast for landmark navigation. *Journal of Theoretical Biology, 214*, 619–631.

Mote, M. I., & Wehner, R. (1980). Functional characteristics of photoreceptors in the compound eye and ocellus of the desert ant, *Cataglyphis bicolor*. *Journal of Comparative Physiology A, 137*, 63–71.

Muser, B., Sommer, S., Wolf, H., & Wehner, R. (2005). Foraging ecology of the thermophilic Australian desert ant, *Melophorus bagoti*. *Australian Journal of Zoology, 53*, 301–311.

Narendra, A., Gourmaud, S., & Zeil, J. (2013). Mapping the navigational knowledge of individually foraging ants, *Myrmecia croslandi*. *Proceedings of the Royal Society B: Biological Sciences, 280*, 20130683.

Ogawa, Y., Falkowski, M., Narendra, A., Zeil, J., & Hemmi, J. M. (2015). Three spectrally distinct photoreceptors in diurnal and nocturnal Australian ants. *Proceedings of the Royal Society B: Biological Sciences, 282*, 20150673.

Pratt, S. C., Brooks, S. E., & Franks, N. R. (2001). The use of edges in visual navigation by the ant *Leptothorax albipennis*. *Ethology, 107*, 1125–1136.

Schultheiss, P., Cheng, K., & Reynolds, A. M. (2015). Searching behavior in social Hymenoptera. *Learning and Motivation, 50*, 59–67.

Schultheiss, P., & Nooten, S. S. (2013). Foraging patterns and strategies in an Australian desert ant. *Austral Ecology, 38*, 942–951.

Stone, T., Mangan, M., Ardin, P., & Webb, B. (2014). Sky segmentation with ultraviolet images can be used for navigation. *Proceedings of the 2014 Robotics: Science and Systems Conference, X*. http://dx.doi.org/10.15607/RSS.2014.X.047. http://roboticsproceedings.org/rss10/index.html.

Towne, W. F. (2008). Honeybees can learn the relationship between the solar ephemeris and a newly-experienced landscape. *Journal of Experimental Biology, 211*, 3737–3743.

Towne, W. F., & Moscrip, H. (2008). The connection between landscapes and the solar ephemeris in honeybees. *Journal of Experimental Biology, 211*, 3729–2736.

Wehner, R. (1987). Spatial organization of the foraging behavior in individually searching desert ants, *Cataglyphis* (Sahara desert) and *Ocymyrmex* (Namib desert). In J. M. Pasteels, & J. M. Deneubourg (Eds.), *From individual to collective behavior in insects* (pp. 15–42). Basel, Switzerland: Birkhäuser.

Wehner, R. (1994). The polarization-vision project: championing organismic biology. *Fortschritte der Zoologie, 39*, 103–143.

Wehner, R. (1997). The ant's celestial compass system: spectral and polarization channels. In M. Lehrer (Ed.), *Orientation and communication in arthropods* (pp. 145–185). Basel, Switzerland: Birkhäuser Verlag.

Wehner, R. (2009). The architecture of the desert ant's navigational toolkit (Hymenoptera: Formicidae). *Myrmecological News, 12*, 85–96.

Wehner, R., Michel, B., & Antonsen, P. (1996). Visual navigation in insects: coupling of egocentric and geocentric information. *Journal of Experimental Biology, 199*, 129–140.
Wehner, R., & Srinivasan, M. V. (2003). Path integration in insects. In K. J. Jeffery (Ed.), *The neurobiology of spatial behaviour* (pp. 9–30). Oxford, U.K.: Oxford University Press.
Wystrach, A., Beugnon, G., & Cheng, K. (2011). Landmarks or panoramas: what do navigating ants attend to for guidance? *Frontiers in Zoology, 8*, 21.
Wystrach, A., Beugnon, G., & Cheng, K. (2012). Ants might use different view-matching strategies on and off the route. *Journal of Experimental Biology, 215*, 44–55.
Wystrach, A., & Schwarz, S. (2013). Ants use a predictive mechanism to compensate for passive displacements by wind. *Current Biology, 23*, R1083–R1085.
Wystrach, A., Schwarz, S., Baniel, A., & Cheng, K. (2013). Backtracking behaviour in lost ants: an additional strategy in their navigational toolkit. *Proceedings of the Royal Society B: Biological Sciences, 280*, 20131677.
Wystrach, A., Schwarz, S., Schultheiss, P., Beugnon, G., & Cheng, K. (2011). Views, landmarks, and routes: how do desert ants negotiate an obstacle course? *Journal of Comparative Physiology A, 197*, 167–179.
Zeil, J., Narendra, A., & Stürzl, W. (2014). Looking and homing: how displaced ants decide where to go. *Philosophical Transactions of the Royal Society B, 369*, 20130034.