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James J. Foster

jjfoster86@gmail.com

University of Konstanz

Jacob M. Graving

University of Konstanz

Keram Pfeiffer

Zoologie II, Julius-Maximilians Universität Würzburg

Research Article

Keywords: vision, navigation, spectral, bees

Posted Date: May 28th, 2026

DOI: https://doi.org/10.21203/rs.3.rs-9827783/v1

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Additional Declarations: No competing interests reported.

High intensity overrides spectral cues in dancing honeybees

James J. Foster[1,2], Jacob M. Graving[2,3,4], and Keram Pfeiffer[5]

[1]Department of Biology, University of Konstanz, Konstanz, Germany
[2]Centre for Advanced Study of Collective Behaviour, University of Konstanz, Konstanz, Germany
[3]Advanced Research Technology (ART) Unit, Max Planck Institute of Animal Behavior
[4]Department of Collective Behavior, Max Planck Institute of Animal Behavior
[5]Zoologie II, Julius-Maximilians Universität Würzburg, Würzburg, Germany
JJF, 0000-0002-4444-2375; JMG, 0000-0002-5826-467X; KP, 0000-0001-5348-2304

Abstract

Foraging honeybees rely on a celestial compass to navigate to and from the hive, using the sun's position as an orientation reference. When the sun is hidden from view, bees can determine its azimuth using skylight patches. The linear polarization, size, and spectrum of a skylight patch contribute to the bee's estimated position relative to the sun. When the light patch is unpolarized, the relative quantities of green and UV light may determine whether it is interpreted as part of the solar or anti-solar sky. How bees combine this information with the intensity gradient across the sky, present across the wavelength spectrum, remains poorly understood. In order to investigate how intensity affects the interpretation of patches of green and UV light by bees, we presented Western honeybees (*Apis mellifera*) with light spots of lower and higher intensity during the 'waggle dance', during which they communicate the direction of a food source relative to the sun. At high intensities, we find that both green and UV light were interpreted as the sun, while for lower intensities we observed an orientation switch between green and UV. We propose that this high-intensity effect may be driven by the combination of beta-band sensitivity of the green photoreceptors to UV light and saturation of the UV photoreceptors. The failure of spectral contrast to influence orientation at high intensities may also be adaptive when the sun is viewed through light cloud that transmits UV.

Keywords

vision, navigation, spectral, bees

Statements and Declarations

All authors declare no competing interests.

Introduction

Central place foragers must accurately navigate between food sources and their home. For foraging honeybees this is a group effort and returning foragers can recruit nest mates to their recently-visited food source, advertising its location by performing a waggle dance (von Frisch, 1967). During this behaviour, the dancer indicates the direction towards the advertised location using the sun as a frame of reference. Inside the hive, during dances on the vertical surface of the combs, the upwards direction relative to gravity substitutes for the sun's direction, so that the angle between the dance and the vertical is that between the sun and the food source. When the comb is arranged horizontally with an open view to the sky, dances are oriented in the geographic direction towards the food source, using available visual cues to estimate the sun's azimuth. In the absence of a direct view of the sun, skylight can be used to infer the sun's position accurately.

Only small patches of skylight are necessary for oriented dances. To infer the sun's position from these patches, the dancing bee must recognise their position within the sky, specifically their azimuth relative to the sun. A light patch's interpretation is thought to depend on a combination of its linear polarization, spectrum and angular size (Brines & Gould, 1979; Wehner, 1989). When the light is linearly polarized, it is primarily interpreted as part of the anti-solar sky (Rossel *et al*., 1978; Brines & Gould, 1979), where the degree of polarization is highest, and its particular azimuth depends on the angle of polarization. Patches of linearly-polarized natural skylight, with a degree of polarization greater than 10% (von Frisch, 1967, pp. 403–404) and angular size in the range from 5°–15°, enable accurate dance

orientation (Rossel *et al*., 1978; Brines & Gould, 1979), and artificial light spots as small as 0.5° permit some orientation (Edrich & von Helversen, 1976). Unlike polarized light, patches of unpolarized light may be identified by dancing bees as either the sun and its surrounding aureole, the 'sun-spot', or part of the sky directly opposite the sun, the 'anti-sun' (Edrich *et al*., 1979; Rossel & Wehner, 1984). This has been demonstrated to depend on the spectrum of the patch of light. White, green, and blue light all elicit sun-spot orientation (von Frisch, 1967; Edrich *et al*., 1979; Rossel & Wehner, 1984). UV light elicits either anti-sun orientation (Brines & Gould, 1979; Edrich *et al*., 1979) or orientation at a range of angles more than 90° from sun-spot orientation (Rossel & Wehner, 1984), the dancer interpreting the patch as falling somewhere within the anti-solar sky, but not necessarily directly opposite the sun.

This distinction between sun-spot and anti-solar sky based on spectrum likely corresponds to the broad scale pattern across the sky produced by Rayleigh scattering (Strutt, 1871; Hecht, 1998). Since the probability of scattering p decreases as a function of the wavelength of light λ ($p \propto \lambda^{-4}$), shorter wavelengths are scattered the most, forming a larger proportion of the spectrum in the anti-solar sky than in the solar sky. For the honeybee visual system, consisting of photoreceptors sensitive to UV ($\lambda_{max} = 343$ nm), blue (440 nm) and green (543 nm) light (Menzel & Blakers, 1976; Menzel *et al*., 1986), this effect would be most pronounced comparing UV and green light. Since the probability of scattering also decreases as a function of the scattering angle θ ($p \propto 1 + cos\ cos\ (\theta)^{2}$) between 0° and 90°, under clear conditions the anti-solar sky is also generally darker than the solar sky. An ideal system could take advantage of both intensity and spectrum to more accurately identify the position of a patch of unpolarized skylight, and to distinguish sky from sun. In this study, we recorded the orientation of dancing honeybees viewing green and UV light of equal intensity at two different intensity levels separated by two log units, to investigate whether intensity and spectrum interact in determining the interpretation of an unpolarized light patch.

Methods

Observation Hive

A honeybee colony (*Apis mellifera carnica*) was maintained in an observation hive situated in a small wooden building on the Lahnberge campus of the University of Marburg (50°48'22.7"N 8°48'40.8"E). The building was lined with black plastic sheeting to prevent natural light from leaking into the room. The observation hive consisted of two 'Deutsch Normal' sized frames held between sheets of UV-transparent acrylic (Plexiglas). Bees could enter and exit the observation hive though an opaque 40 cm-long tube that connected the hive to a hole in the wall. A custom support allowed the observation hive to be rotated from vertical to a horizontal position, to remove gravity as an orientation cue during the dances and instead encourage orientation to visual stimuli.

Light Stimuli

To provide dancing bees with an orientation reference two high-power LEDs, one emitting green light (peak wavelength 528 nm; Oslon SSL80, Osram) and one emitting UV light (peak wavelength 365 nm; NCSU276A, Nichia Corporation) were mounted on a rail system above the hive, projecting downwards at 45° to vertical (Fig. 1a), the light spot subtending a visual angle of approximately 10° at the dancing bee's position. An LED driver allowed each LED to be adjusted to irradiances of either 4×10^{12} photons $cm^{-2}\ s^{-1}$ ("dim") or 4×10^{14} photons $cm^{-2}\ s^{-1}$ ("bright") as measured at the position of the dancing bees. Infrared illumination was also provided by high-power IR LEDs, allowing dances to be recorded via a USB camera (DCC1545M, Thorlabs) equipped with a 4 mm- 12 mm lens (12VM412ASIR, Tamron, Saitama, Japan). Both the camera and LED stimuli were mounted on an x-y adjustable rail system, which made it possible to centre the stimuli on the dancing bee during experiments via manual adjustments.

Waggle-dance Recordings

Due to the practical challenges of training foragers to fly between the buildings to a feeder, we chose to focus on the spontaneous waggle dances of foragers returning from unknown locations to maximise data collection. Dances were recorded from returning foragers on rain-free afternoons between the 20th of May and 29th of September 2016, between 12:00 and 18:00 CET, corresponding to solar elevations of 14°–64° and azimuths of 147°–261° (South-East – West). For the longest dances, the dancer was presented first with the dim UV stimulus ("UV dim"), and then the bright UV stimulus ("UV bright"), the bright green stimulus ("green bright") and finally the dim green stimulus ("green dim"). Presentation order was varied on days when large numbers of dances were observed. Dances ranged in length from 14 and 100 waggle runs (median = 33, Q1 = 26, Q3 = 43).

Analysis

Dance angles were measured manually to the nearest 5° from representative video frames in the middle of each waggle run, assigning the stimulus as the 0° position and measuring increasing angles in counterclockwise direction. To summarise performance for each combination of dance and stimulus, we calculated the mean vector across corresponding sets of waggle runs. Mean vector length was used as a measure of dance consistency and mean angle as a measure of directional bias. Consistency was analysed using beta regression in Bayesian generalised linear mixed-effects models (GLMMs), accounting for effects on mean proportion and concentration (inverse variance), fitted in using Stan version 2.32.2 (Stan Development Team, 2025) via the 'BRMS' package (Bürkner, 2018) in R version 4.5.1 (R Foundation for Statistical Computing). Changes in mean angle between stimulus conditions were fitted with maximum likelihood unimodal and bimodal models using the 'CircMLE' package (Fitak & Johnsen, 2017) and compared via likelihood-ratio tests (Woolf, 1957) with null distributions for no change (mean difference at 0°), fitted using the 'circular' package (Agostinelli & Lund, 2025). Corrections for multiple comparisons used the Benjamini-Hochberg method (Benjamini & Hochberg, 1995). Bayesian circular GLMMs (Graving *et al*., in prep), accounting for individual-differences in directional bias and consistency, were fitted with 'PyMC' (Abril-Pla *et al*., 2023) via the 'Bambi' package (Capretto *et al*., 2022) in Python version 3.12.13, with the circular modulo ($\mathrm{mod}\big((\eta + \pi), 2\pi\big) - \pi$) and softplus ($\log(1 + \exp(\eta))$) inverse links for mean angle and consistency, respectively. Hypothesis tests on Bayesian GLMMs were performed via model comparison using expected log predictive density (ELPD) from leave-one-out cross-validation (LOO-CV; Magnusson *et al*., 2020). Source code for all statistical analysis can be found in the repository github.com/jjfosterlab/GUVdances.

Results

Spontaneous Dance Observations

Over the course of 4 months 6248 waggle runs from 169 dances were observed (Fig. S1). The large inter-dance variability (circular GLMM: SD = 50°) in advertised bearing (relative to sun azimuth) suggests that dances were for a range of locations, with the population mean centred on the nearest edge of the Marburg Botanic Gardens to the South-West (circular GLMM: median estimate = 228°, 95%CI 214°–243°; Fig. S2). Since we were unable to identify dances by the same individual, comparisons were focussed within each continuous dance. This controls for differences in dance direction and consistency that depend on the bearing and distance of the advertised location, respectively, as well as potential individual differences; all of which should remain constant within a dance. Indeed, most individual dances maintained a consistent direction that changed only in response to changes in light stimulus (Fig. 1b).

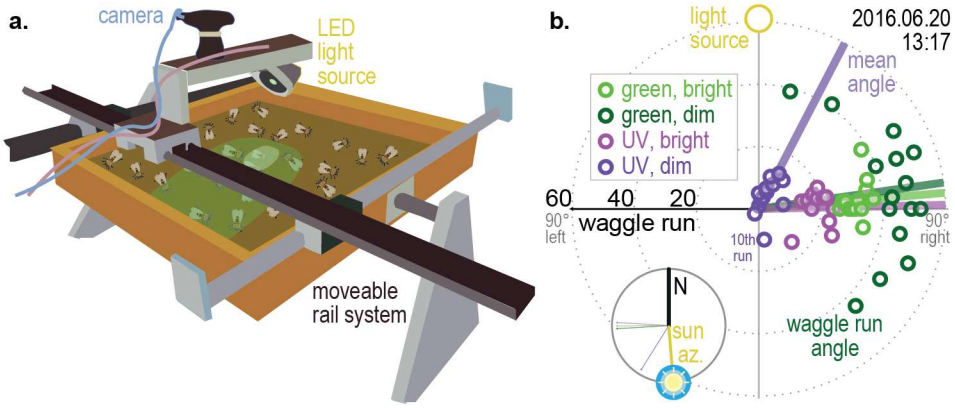


Figure 1. Recording spontaneous waggle dances.

a. To record waggle-dances oriented to visual cues, the observation hive was rotated to horizontal. In this position an adjustable rail system could be used to align the camera (and LED light source) with the dancing bee. **b.** Example dance data for one recording during which all stimuli were presented. Each point shows the direction of an individual waggle run, as viewed from above. Solid lines show mean angles for the waggle runs performed during each stimulus regime. The time and date of each recording were used to determine the true sun azimuth (inset) relative to geographic North, to assess putative advertised directions (Fig. S2). During each waggle dance, the dancer was presented with a series of different light stimuli (green or UV, bright or dim), resulting in up to four different sets of waggle runs.

Orientation Consistency

The mean vector length was used as a measure of orientation consistency for each dance and stimulus. Our results recapitulate the findings of earlier studies (Edrich *et al*., 1979), that waggle run angles were more consistent for high intensity stimuli (bright green: median = 0.96, Q1–Q3 = 0.88–0.98; bright UV: median = 0.95, Q1–Q3 = 0.93–0.97) than for lower intensities (dim green: median = 0.65, Q1–Q3 = 0.39–0.83; dim UV: median = 0.67, Q1–Q3 = 0.50–0.81). To quantify the joint effects of stimulus brightness and colour, these were modelled as predictors of average consistency and variance in consistency using a beta regression, with dance identity as a random-effects grouping factor. This accounted for differences in consistency between dances for locations at different distances (Weidenmüller & Seeley, 1999). Orientation consistency differed between stimuli within dances (Fig2a–b), and was lower for the dimmer stimuli (total effect: green-dim – green-bright: Δvector-length = -0.21, 95%CI -0.34–-0.10, p = 0.001; UV-dim – UV-bright: Δvector-length = -0.54, -0.70–-0.35, p < 0.001), and higher for the UV stimuli than the green stimuli (UV-bright – green-bright: Δvector-length = 0.08, 0.03–0.15, p = 0.004; UV-dim – green-dim: Δvector-length = 0.22, 0.03–0.39, p = 0.027). Mean vector lengths also varied less across dances for the UV stimuli (UV-bright – green-bright: Δlog(concentration) = 1.91, p = 0.003; UV-dim – green-dim: Δlog(concentration) = 1.45, p = 0.064), but varied more for the dim UV stimulus than the bright one (UV-dim – UV-bright: Δlog(concentration) = 3.70, p = 0.004). Despite condition differences and variability, the majority of dances were sufficiently well-oriented (Rayleigh test p<0.05 for 89% of dances, 94% of dances with the green bright stimulus) to identify a robust mean angle that could be compared across stimuli. Of the 169 dances observed, 19 included all 4 stimulus types in sequence, so these were the focus of direct comparison between stimuli.

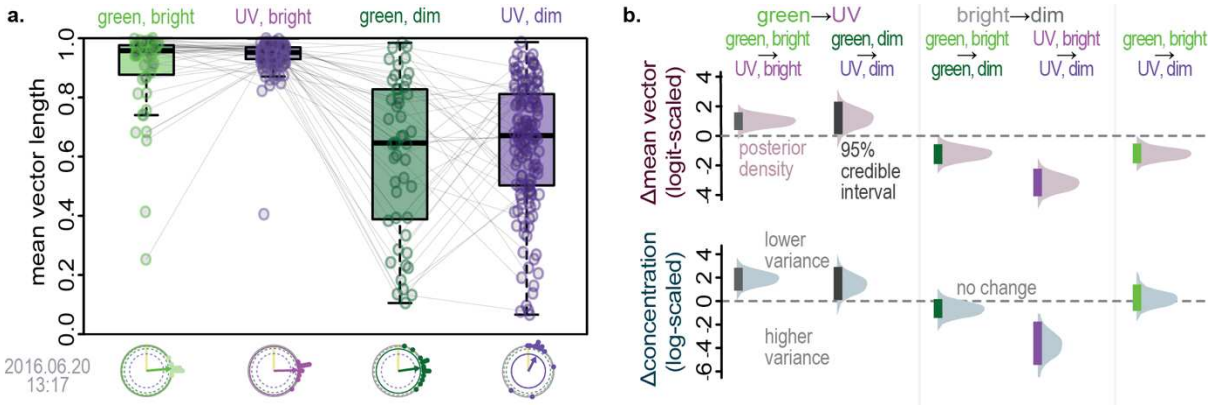


Figure 2. Dance consistency as a function of intensity and wavelength.
Dances were less consistent for lower stimulus intensities, but generally more consistent for UV stimuli at the same intensity. **a.** Orientation consistency, measured as mean vector length within one set of waggle runs, was similar across bright stimuli, but lower and more variable for dimmer stimuli. **b.** Coefficient contrasts for a GLMM accounting for differences in consistency and variance, both within and between individual dances. Mean vectors for dim stimuli were shorter (Δmean vector) and differed in length more between dances (Δconcentration) than for bright stimuli. UV stimuli generally induced longer mean vectors and lower variance across dances.

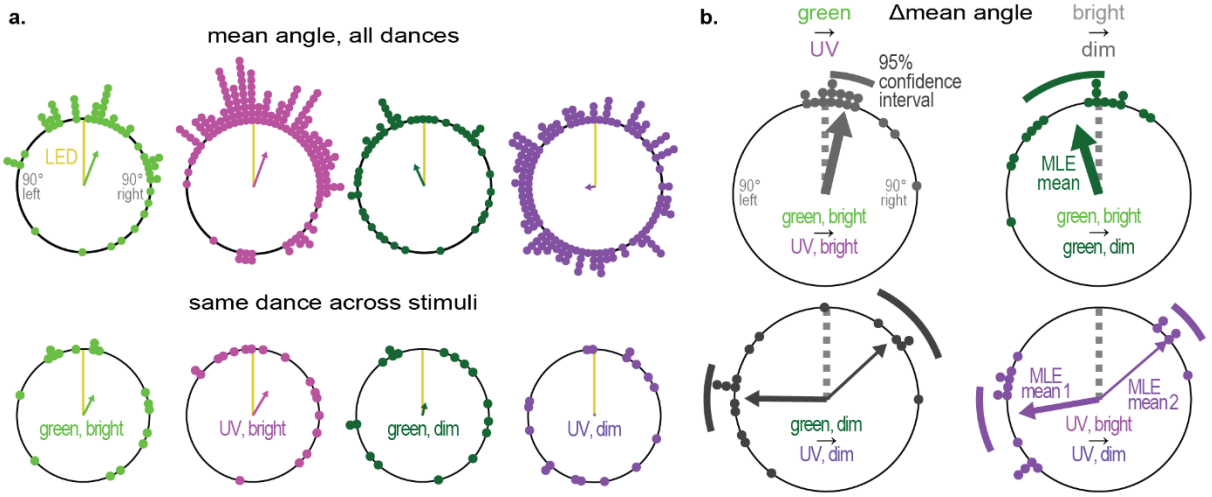


Figure 3. Bright UV light elicits sun-orientation.
The bright UV stimulus evoked behaviour equivalent to the sun-orientation induced by the bright and the dim green stimulus, unlike the sky orientation evoked by the dim UV stimulus. **a.** Individual dances varied in angle relative to the LED stimulus, with a bias towards the LED light source for the brighter stimuli, corresponding to locations to the South-West of the hive (Fig. S2). To compare dance angles across stimuli, we focussed on the set of 19 dances for which all stimuli were presented sequentially. **b.** Differences in mean dance direction (Δmean angle) were used to assess stimulus-induced changes in mean dancing direction. Mean angles did not differ significantly between the bright UV and green stimuli or the two green stimuli, both producing distributions of Δmean angles centred close to 0° (stippled grey line indicating no change). Dance directions for the dim UV stimulus differed from the other stimuli, producing a bimodal distribution of leftwards and rightwards differences that suggests interpretation as a patch of sky ≈90° from the sun. The plotted arrows show the modes of the best fit maximum-likelihood unimodal or bimodal models. Each arrow's length shows the kappa (inverse variance) parameter converted to an equivalent mean vector length, and thickness is scaled by the weighting (proportion of data) for each mode. Arcs outside the unit circle indicate 95% confidence intervals estimated numerically for the corresponding sample size (data proportion).

Dance Direction

The total population of dance mean angles exhibited a moderate bias towards the stimuli (Fig. 2c), likely corresponding to sun-spot orientation for locations at the nearest edge of the Botanic Gardens situated South-West of the observation hive (Figure S2). This trend was weaker for the dim green stimulus and absent for the dim UV stimulus, for which mean angles were approximately uniformly distributed. In

the longer dances during which all four stimuli were presented, population-level biases were weaker, but similar in direction (Fig. 2c). Differences between mean angles within these dances were used to assess the effects of each stimulus on dance direction (Fig. 2d).

The main result of this study is that the mean dancing direction in relation to the bright UV stimulus did not differ from the mean dancing direction in relation to the bright green stimulus, suggesting that the bees interpreted the bright UV stimulus as the sun (likelihood ratio test: Δdeviance = 5.044, d.f. = 1, p = 0.074; Bayes factor = 3.020). Furthermore, the mean angles did not differ significantly between the two green stimuli (likelihood ratio test: Δdeviance = 3.312, d.f. = 1, p = 0.081; Bayes factor = 1.271) suggesting that both are interpreted as the sun despite different intensities. Conversely, orientation to the dim UV stimulus was dramatically different from both the bright UV (likelihood ratio test: Δdeviance = 20.21, d.f. = 3, p < 0.001; Bayes factor = 349.098) and dim green stimuli (likelihood ratio test: Δdeviance = 12.27, d.f. = 3, p = 0.010; Bayes factor = 19.342), resulting from both leftwards and rightwards reorientations between stimuli. Although more dances were to the left of the UV-bright dances (13 *versus* 6) there was no significant difference in frequency between leftwards and rightwards turns (binomial p = 0.167; bootstrapped proportion: 0.71, 95%CI = 0.41–0.75). Many dances were also bimodal (secondary mean weighting >0.25 in 29% of dances; Fitak & Johnsen. 2017), with modes for both a leftwards and rightwards turn within a single dance. Combining both modes, the mean difference was unimodal (concave Beta distribution, $p(\phi < 2) < 0.01$) and centred close to 90° (mean absolute difference = 86°, 95%CI 69°–102°; Bayesian GLM: ΔELPD = -1.0, ΔSE = 0.6). This clear difference in dance behaviour suggests that dancing bees interpret the dim UV stimulus differently from the others, likely a switch from sky-patch orientation (dim UV) to sun-spot orientation (other stimuli).

Modelling Dance Direction

To confirm that the pattern of dance direction changes observed in the dances that included all stimuli was also found across the data as a whole (and could not be explained by changes in dance consistency alone) we fitted a circular generalised linear mixed-effects model (circular GLMM; Graving *et al*., in prep.) with stimulus brightness and colour as categorical predictors and dance identity as a grouping factor (random effect). As was the case for the mean dance directions within the subset including all four stimuli (Fig. 3), differences in direction between the two bright stimuli (Fig. 4b) were centred close to no change (UV – green: posterior median = 4°, 95%CI = 0°–8°). There was some evidence for a leftward shift for the dim green stimulus (dim – bright: -31°, 95%CI = -46°– -18°), as well as a generally wider spread across individual mean dance angles (dim – bright: $\Delta\kappa_\mu$= -0.534, 95%CI = -0.769– -0.316, equivalent Δvector-length= -0.166, -0.257– -0.091) after accounting for reduced consistency. At the population level, average mean directions for the dim UV stimulus were ≈90° leftwards from the other stimuli (UV-dim – UV-bright: -86°, -100°– -72°; UV-dim – green-dim: -51°, -68°– -34°), with estimated individual changes in mean angle covering a wide range to both the left and right ($|\Delta\mu|$ UV-dim – UV-bright: median = 90°, 95% in 12°–171°; UV-dim – green-dim: 54°, 4°–147°). Dance consistency was generally greater for the two bright stimuli (UV – green: $\Delta\kappa$= 2.06, 95%CI = 1.46–2.61, equivalent Δvector-length= 0.024, 0.015–0.033) but considerably lower for the two dim stimuli (dim – bright: $\Delta\kappa$= -3.70, -4.26– -3.16, Δvector-length= -0.176, -0.260– -0.118; UV-dim – green-bright: $\Delta\kappa$= -3.82, -4.52– -3.15, Δvector-length= -0.193, -0.272– -0.135). Model comparisons (Fig. 4c) suggested effects of stimulus brightness (ΔELPD = 3014.3, ΔSE = 60.9), colour (ΔELPD = 180.9, ΔSE = 15.3) and their interaction (ΔELPD = 63.5, ΔSE = 14.2) best explain variation in direction (μ) and consistency (κ) across waggle runs.

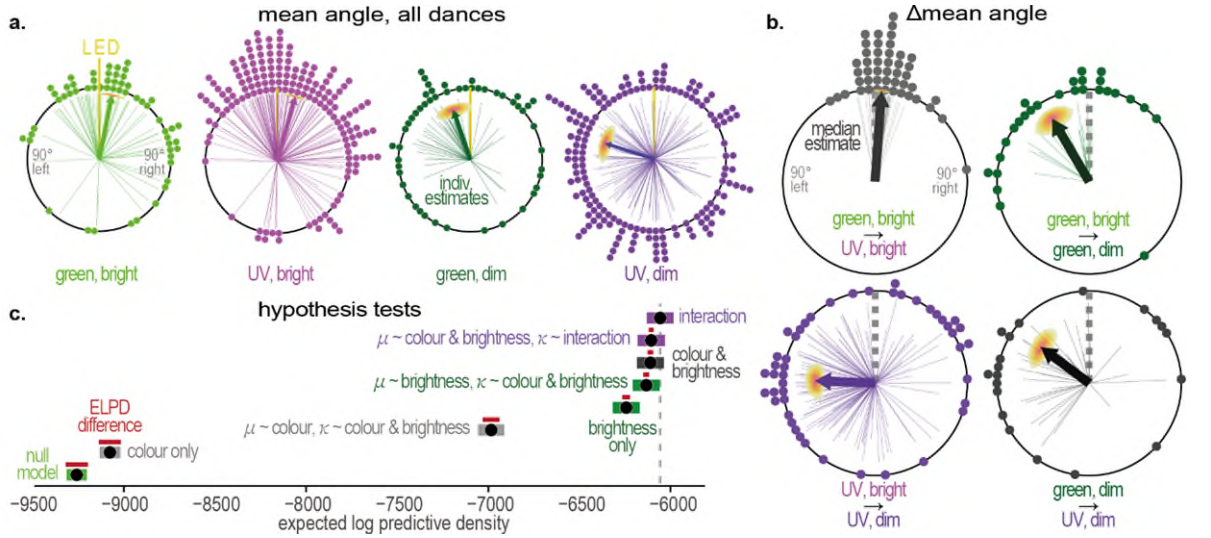


Figure 4. Circular GLMM results.

Circular GLMMs confirm patterns of mean angle change across all dances. **a.** Predictions of mean direction and vector length from the circular GLMM for each individual dance (thin lines) and population posterior density (yellow–red shaded area) and median estimate (thick arrows) for the average dance, shown with mean dance angles (points; as in Fig. 3a). **b.** Model predictions for mean dance angle changes. Points show the difference in mean angle within all dances that included both stimuli (bright stimuli: n=45; green stimuli: n=27, UV stimuli: n=154, dim stimuli: n=20). Individual and population-level mean resultant vector shown as in **a** (vector length scaled by concentration across individuals). Most dance angle changes were small between the bright green stimulus and the bright UV stimulus, and modest for the dim green stimulus, as indicated by the high posterior density (yellow–red shaded area) near 0° difference (dashed line). A wide variety of left and right turns were observed between the dim UV stimulus and the other stimuli. **c.** Model comparison to investigate effects shared across dances. Points show expected log predictive density (ELPD) for models with the specified effects and error bars indicate ±standard error, with the ELPD difference (±standard error; red line) from the model with highest ELPD (best predictions) shown directly above it. Model comparison suggests population-level effects of stimulus colour, brightness, and their interaction (deviation of dim UV from combined effects of bright UV and dim green) on both dance direction and consistency.

Discussion

Bright UV Light Induces Sun-Spot Orientation

In this study we tested how light intensity influences spatial orientation to light spots of different wavelengths in honeybees during waggle-dances on a horizontal comb. Our data show that at high light intensities both green and UV light spots are interpreted in the same way, while dance directions differed between UV and green stimulation at lower light intensity. This suggests that a high intensity light spot is always interpreted as the sun, irrespective of the wavelength content. In previous studies all UV stimuli elicited ‘anti-sun’ dances, at either precisely 180° (Edrich *et al*., 1979; Brines & Gould, 1979) or a broad range of positions >90° (Wehner *et al*., 1984) from sun-spot dances; oriented as if the stimulus were part of the anti-solar sky. This behaviour would match the prospective position of these stimuli within the spectral-gradient across the sky (Fig. 5a) from sun to anti-sun (Coemans *et al*., 1994). Bees have been proposed to assign the position of a patch of unpolarized skylight either by its relative proportion of bee-visible photons in the UV (Brines & Gould, 1979), or specifically the ratio of UV to green light (Edrich *et al*., 1979; el Jundi *et al*., 2014). Our UV stimuli have a narrow emission spectrum producing exclusively UV photons so by either measure would count as anti-solar sky.

The difference in interpretation of UV stimuli between our experiments and other studies may instead lie in the particular combination of angular size and brightness. With the exception of brighter source of approximately 10^{13} photons cm^{-2} s^{-1}, which did not induce celestial orientation (either sun-spot or sky orientation) when presented to bees dancing on a 27° tilted observation hive (Edrich, 1977), the brightest

UV light-spots previously used to elicit dance orientation were approximately 1.7×10^{12} photons cm^{-2} s^{-1} (Edrich *et al*., 1979), similar in brightness to our dim UV stimulus (4×10^{12} photons cm^{-2} s^{-1}). These were presented with a visual angle of 2.3°, approximately the field of view of a single ommatidium. Dance consistency reached a plateau for those stimuli (Fig. S3; Edrich *et al*., 1979), although the particular brightness at which this began reportedly differed across days and individuals. Indeed, typical dance consistency for our dim UV stimulus was qualitatively similar to this peak performance (Fig. S3; Edrich *et al*., 1979). Light-adapted UV-sensitive photoreceptors ('UV receptors') in the main retina reliably reach saturation between 10^{13} and 10^{14} photons cm^{-2} s^{-1} (Kolyfetis *et al*., 2025) such that increases in brightness above this level do not produce increases in response strength. Green-sensitive photoreceptors ('green receptors') also detect UV light via the beta-band of their opsin (Stavenga, 2010), which has a peak sensitivity in the UV around one third of the maximum in the green (Fig. 5c). Negative interactions between the UV receptors and green receptors have also been reported (Menzel & Blakers, 1976), particularly the hyperpolarization of UV receptors in response to green light, so at higher UV intensities responses of green receptors may partially suppress the responses of UV receptors. At moderate intensities these interactions can suppress beta-band sensitivity of green receptors to UV (Menzel & Blakers, 1976), so that beta-band responses of green receptors become more pronounced as UV receptors saturate. Hymenopteran green receptors are also typically less sensitive (Skorupski & Chittka, 2010). Correspondingly, previous work (Fig. S3; Edrich *et al*., 1979) suggests that a green stimulus would need to be around 3–10 times as bright as a UV one to elicit as similar level of consistency. In combination, these effects would allow the responses of green receptors to continue to increase at intensities of UV light for which UV receptors saturate, narrowing the gap in response strength between the two receptor classes above 10^{13} photons cm^{-2} s^{-1} (Fig. 5d). The result would be an increase in the ratio between the responses of green and UV photoreceptors at high UV intensities. Intriguingly, some polarization-sensitive neurons in the locust anterior optic tubercule (LoTu1) presented with ipsilateral unpolarized light respond with excitation to green and inhibition to UV at 1.7×10^{12} photons cm^{-2} s^{-1}, but with excitation to both at 1.7×10^{13} photons cm^{-2} s^{-1} (Kinoshita *et al*., 2007), so it is possible that a similar switch for bright UV stimuli is also present for locusts.

Although sun-spot orientation to bright UV light was induced under artificial conditions in our experiments, there are likely some natural situations in which this mechanism would be adaptive. Indeed, initial interest in orientation to unpolarized UV was inspired by the observation that honeybees could sometimes orient their dances under uniform cloud cover (von Frisch, 1967, pp. 366–372); remaining oriented when covered by a filter blocking visible light but transmitting UV, and becoming disoriented when a UV-blocking filter was introduced. It was suggested that these bees could detect the sun's aureole, which, in the UV, often remains brighter than the rest of the sky under cloud cover (von Frisch, 1967, pp. 373–377; Brines & Gould, 1982). Mie scattering, which occurs in clouds, is mostly wavelength independent (Hecht, 1998) and therefore eliminates the spectral gradient, redistributing light between the solar and anti-solar sky. This more uniform spectrum does not provide enough information on its own for spectral-gradient orientation. Under these circumstances, the sky patch with the most UV is located around the sun, so that interpretation of the sky patch with the most UV as antisolar sky (Fig. 5a) would result in incorrect orientation, whereas interpretation as the sun would result in correct orientation (Fig. 5b). In this case, our proposed mechanism, could be beneficial if it results in appropriate orientation to both the dimmer clear-sky spectral gradient from the cloudy-sky's (UV) intensity gradient.

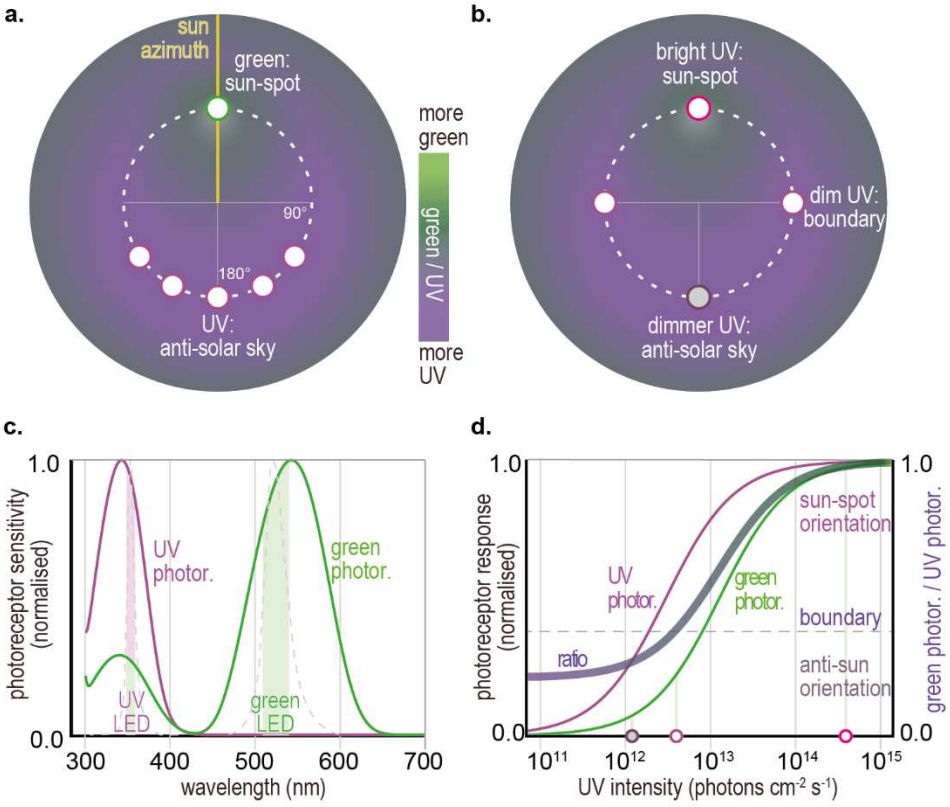


Figure 5. Effects of brightness on apparent spectral contrast.
a. In previous studies, dancing bees interpreted small light-patches as aligned along the sun's azimuth (sun-spot), 180° from the sun (anti-sun), or at a range of positions >90° from the sun (anti-solar sky). Green stimuli were always interpreted as a sun-spot, and UV stimuli were always interpreted as falling in the anti-solar half of the sky. **b.** In our experiments, we observe two new interpretation categories for UV stimuli. Our bright UV stimulus (4×10^{14} photons cm^{-2} s^{-1}) was interpreted as a sun-spot, and our dim UV stimulus (4×10^{12} photons cm^{-2} s^{-1}) was interpreted as falling at the boundary between the solar and anti-solar sky. Since both stimuli were brighter than those from previous studies, this suggests an additional effect of UV intensity, dimmer light-patches ($<4 \times 10^{12}$ photons cm^{-2} s^{-1}) being interpreted as anti-solar sky and brighter patches ($> 4 \times 10^{12}$ photons cm^{-2} s^{-1}) being interpreted as solar sky. **c.** While UV-sensitive photoreceptors are minimally sensitive to green light, green-sensitive photoreceptors have substantial sensitivity to UV light, due to beta-band absorbance. Hence both photoreceptor classes would respond to our UV LED. Photoreceptor spectral sensitivity curves generated using the Stavenga (2010) template, based on wavelengths of peak sensitivity from Menzel and colleagues (Menzel & Blakers, 1976; Menzel *et al.*, 1986). **d.** This fixed relationship between the sensitivities to UV light of the two photoreceptor classes would produce different apparent spectral contrast (green receptor / UV receptor response), depending on its absolute intensity. Assuming a similar intensity–response ($V\ log(I)$) for both classes, UV-sensitive photoreceptors should approach maximum response (saturation) at lower UV intensities than green-sensitive photoreceptors. Past the inflection point of the UV receptor response curve, the response ratio (spectral contrast) would rise, due to the simultaneous increase in response-curve slope for green receptors and decrease for UV receptors. Based on our results, we propose that a threshold in spectral contrast is reached around 4×10^{12} photons cm^{-2} s^{-1}, at which boundary orientation was observed in our experiments, and above which a transition from anti-sun to sun-spot orientation would occur. The photoreceptor response curve represents a main retina UV photoreceptor from Kolyfetis *et al.* (2025). Points along the x-axis, from left to right, indicate the intensities of the brightest UV stimulus used by Edrich and colleagues (1979), and our dim and bright UV stimuli (colour coded as in b.).

Antisolar Boundary Orientation to UV Light

While our dim green stimulus induced orientation in the same direction as both bright green and UV stimuli, our dim UV stimulus did not. Instead switching from dim UV to bright UV or between green and dim UV, resulted in changes of the mean dancing direction of approximately 90° (Fig. 2d). This finding differs from those of previous authors (Edrich *et al.*, 1979; Rossel & Wehner, 1984), who observed an average change in orientation of 180° between UV and green light spots. However it should be noted that in both of these publications, consistent with our data, the angular scatter across dances

(Fig. 3a) for dim UV light is considerably larger than for green light. For small patches of light, interpretation has been proposed to depend on a combination of angular size, UV content and degree of linear polarization; 10° being the largest visual angle at which a patch could be interpreted as the sun-spot (von Frisch, 1967; Brines & Gould, 1979). Our dim UV stimulus is both somewhat brighter (1.7 *versus* 4×10^{12} photons cm^{-2} s^{-1}) and considerably larger (2.3° *versus* 10°) than those that induced anti-sun orientation in previous studies. Its interpretation may therefore fall at the boundary between sun-spot (0° difference from green stimuli) and part of the anti-solar sky (>90° from green stimuli; Rossel & Wehner, 1984). A compromise between the two would then be a patch at the boundary between the solar and anti-solar sky (±90°; Fig. 5b), or even in the solar sky (<90°). Given that our dim UV stimulus was dimmer than typical saturating flashes for UV photoreceptors (Kolyfetis *et al*., 2025) but brighter than stimuli that previously induced anti-sun orientation (Edrich *et al*., 1979), partial saturation of the UV photoreceptors may suppress the green-UV response ratio enough to reject interpretation as the anti-sun, but not enough for interpretation as the sun (Fig. 5d).

Advantages and Drawbacks of Observing Spontaneous Dances

In this study we chose to focus on spontaneous dances as a means of maximising data collection. As a result, we recorded dances advertising a range of locations at different bearings (Fig. S2) as would be the case under natural conditions. Although we did not explicitly focus on recording different individuals, the short intervals between dances for distinct directions (Fig. S1), and balanced spread of observations across three months, minimise the possibility of any one individual being overrepresented in our dataset. We attempted to control for effects of food source and individual identity by focussing on continuous dances as a grouping factor, within which the same individual advertised the same food source, but the stimulus properties could be changed. This approach is somewhat conservative, since dances corresponding to the same individual and food source undoubtedly shared similar properties that, if accounted for, would exclude sources of variation in our estimates of stimulus effects. In the absence of this information dances must be assumed to be uncorrelated. The GLMM approaches used here allowed us to estimate population-level effects while accounting for differences between dances, but would gain further explanatory power if applied to dataset in which food source and individual identity were known.

Future work could benefit from both large sample size and explanatory power by incorporating methods that allow post-identification of individual identity and food source location. Collection and marking of individuals directly following a recorded dance, or large-scale marking of bees in an observation hive (Wild *et al*., 2021) would make it possible to account for individual differences in dance consistency or accuracy. These individual differences may also potentially interact with our observed effects. By training marked individuals to visit feeders at known distances, it would be possible to determine a distance-calibration curve (Srinivasan *et al*., 2000) for the hive under study, which could then be used to identify the distance from the length of each dance (von Frisch, 1967, pp.64–75), and hence even the approximate location (Wario *et al*., 2017), of the advertised food source. This in turn would make it possible to predict effects of distance on consistency (Weidenmüller & Seeley, 1999) and measure how these interact with the effects of light stimuli.

Conclusions

We observe a previously unreported switch in dancing honeybees from sky to sun-spot orientation for high intensity UV light. While it remains unclear under what circumstances this may occur in nature, a potential function could be that originally proposed by von Frisch (1967, pp. 373–377) to distinguish bright UV sunlight transmitted through thin cloud from dimmer UV scattered in the anti-solar sky. We propose the suppression of spectral contrast by beta-band sensitivity of green photoreceptors as a potential driver of this switch in interpretation, although we cannot rule out a corresponding neural

mechanism. Future work may focus on integrating the effects of intensities into existing models of the honeybee's sky compass.

Acknowledgements

We thank Niklas Kühn and Florian Dersch their assistance in developing the system and collecting data for this study. We thank Jutta Seyfarth for maintaining the bee hive and the mechanics workshop of the University of Marburg for building the holder and the rail system for the observation hive. We are also grateful to Anna Stöckl, Giovanni Galizia, Frida Hildebrandt and Georgios Kolyfetis for their feedback on this work. J.J.F. was supported by a DFG research grant (project number 451057640) and funding from the DFG Centre of Excellence 'Centre for the Advanced Study of Collective Behaviour' (EXC 2117-422037984). J.M.G. acknowledges support from the NVIDIA Corporation's Academic Hardware Grant program. K.P. was supported by a DFG research grant (project number 436624328).

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Supplement

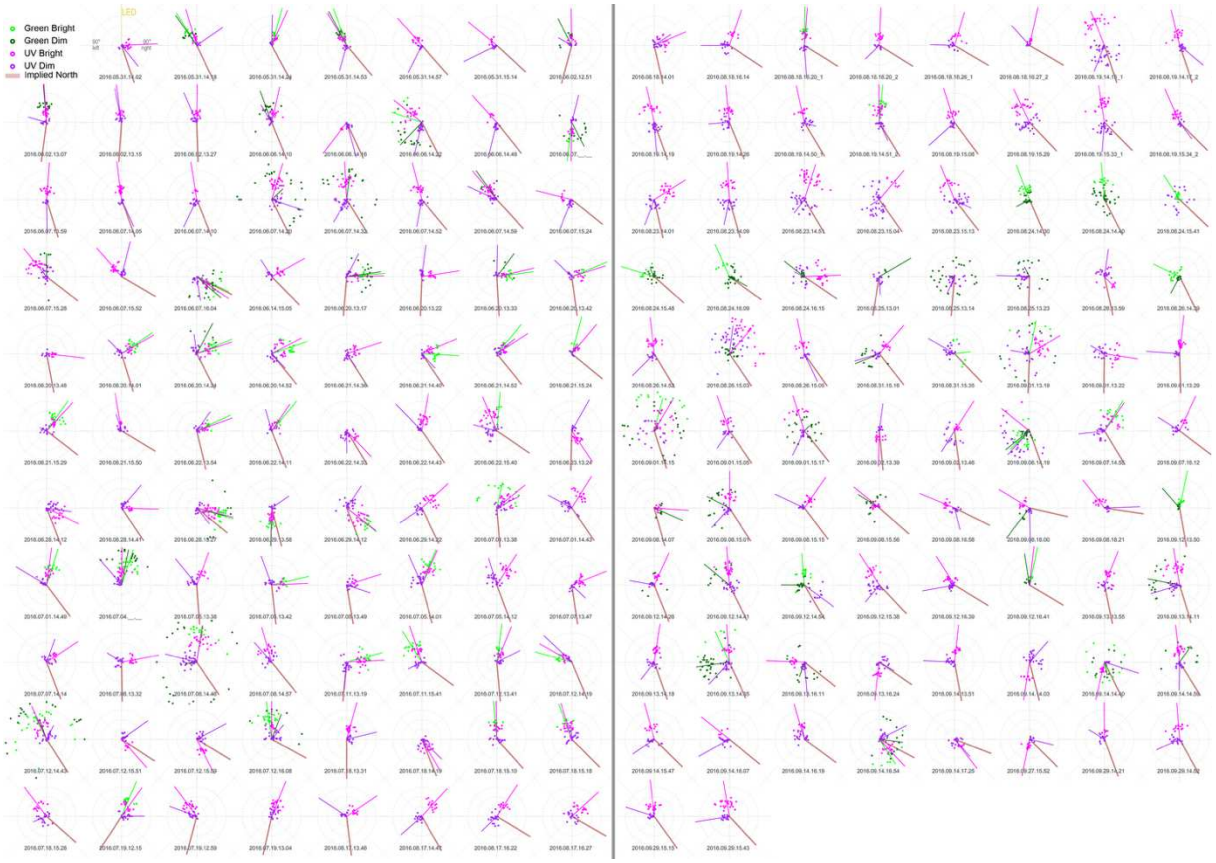


Figure S1. Raw data for all dances.

As in Fig. 2b, angles for each waggle run are shown on radial plots, with angles relative to the light source (up) as viewed from above. Points closer to the centre indicate earlier runs and points towards the edge of the circle indicate later runs within the same dance; dashed circles show the 20th, 40th and 60th run. Mean angles for each stimulus are shown as thin coloured lines, and North (substituting the light source's position for the sun) is shown as a thick red line.

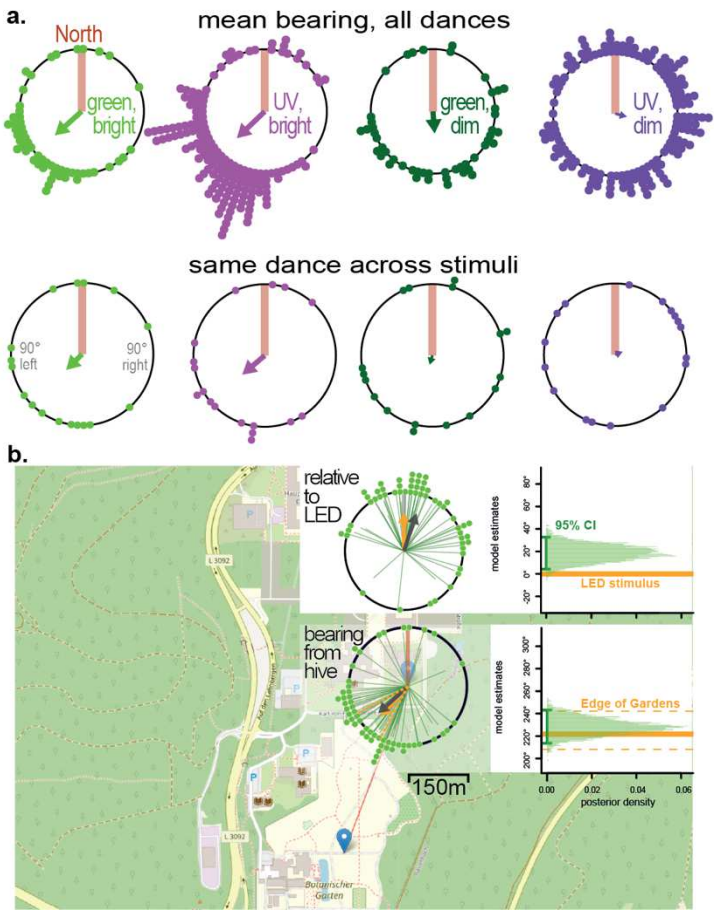


Figure S2. Assessing sun-spot orientation.

a. The mean advertised bearing for each dance was obtained by adding the sun's azimuth to the mean dance angle, to estimate the advertised direction. A wide range of individual bearings were observed, with a preponderance to the South-West for the two bright stimuli. This pattern was also present for the subset of dances during which all stimuli were presented. **b.** Since many dances were oriented close to the LED light source, we compared the hypotheses that phototaxis or menotaxis were the main drivers of dance direction across the population, by fitting circular GLMMs to the data for the bright green stimulus (expected to elicit sun-spot orientation) in each frame of reference. The inset circular plots show the mean angles and model estimates for both reference frames. Orange arrows show the population mean vector component in the expected direction, black arrows show the estimated mean vector, and green lines show individual mean vectors. For phototaxis, 99% of posterior estimates (inset histogram) indicated a population mean to the right of the LED. For menotaxis, the population mean bearing was aligned with the nearest edge of the Botanic Gardens (centre 228°, 95%CI 214°–243°). Nonetheless, individual dances covered a wide range of bearings (estimated SD = 50°) suggesting numerous distinct foraging locations. Map provided by Openstreetmap (openstreetmap.org) via the 'leaflet' package in R (Cheng *et al*., 2025).

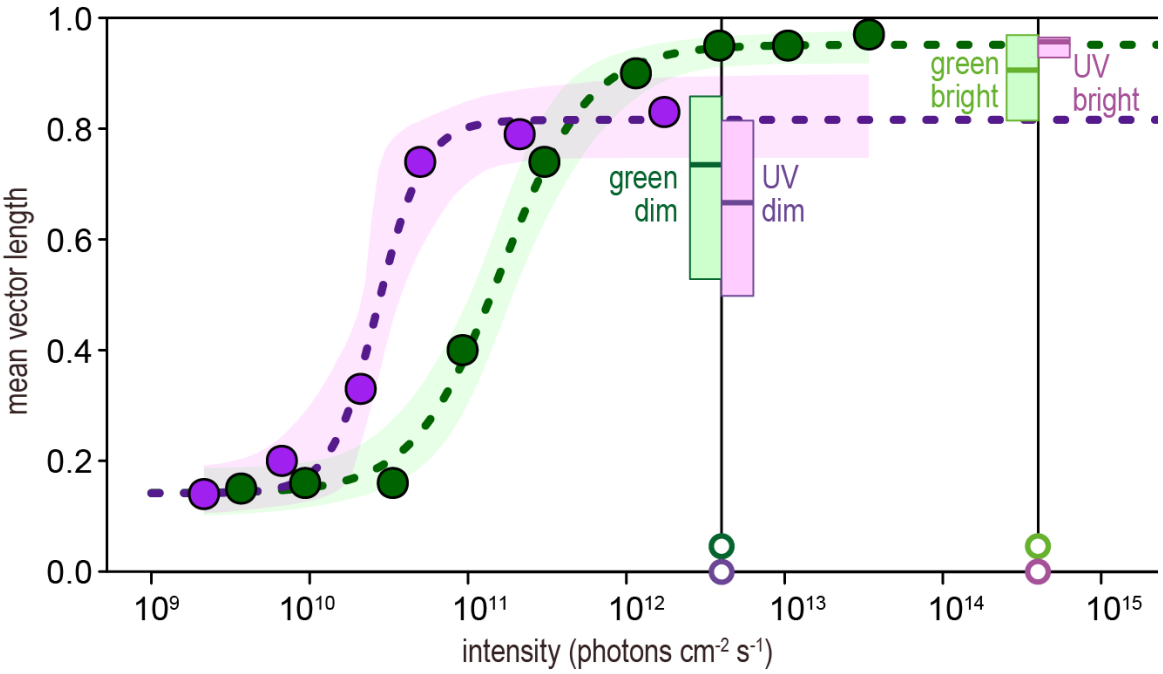


Figure S3. Comparison with example dance consistency curve from Edrich *et al*., 1979.
Example data from Edrich and colleagues (1979) for dancing bees viewing a projected light spot from a Xenon arc lamp filtered to present mainly UV or green light, compared with the quartiles of data from all dances in our experiments with an LED light source. Dashed lines show the median estimates of non-linear psychometric curves fitted using a beta distribution, and the shaded regions show their 95% credible intervals. The curves suggest that the UV stimulus induces high consistency at lower intensities than the green stimulus, resulting in a horizontal offset between the two curves of nearly one log-unit. This may result from a difference in absolute photoreceptor sensitivity between the respective photoreceptor classes, or a difference between the requirements for sun and anti-sun orientation behaviour. Since the upper asymptote for the green stimulus is higher than for the UV stimulus, it is possible that the sun-spot orientation it induced was also more consistent than the anti-sun orientation induced by the UV stimulus. For our dim stimuli consistency is generally lower than for the green stimulus of the same intensity in the example data, possibly because of the larger angular size (10°*versus* 2.7°). Both of our bright stimuli induce consistency close to the maximum found in the example data. For the bright UV stimulus, this may correspond to a switch to sun-spot orientation behaviour, which appears to enable higher maximum consistency than the anti-sun orientation curve for the example UV data.

Supplementary Files

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- FigS1RawDances20260213.png
- FigS2SunSpot20260213.png
- FigS3Consistency.png