



The time-compensated celestial compass of insects

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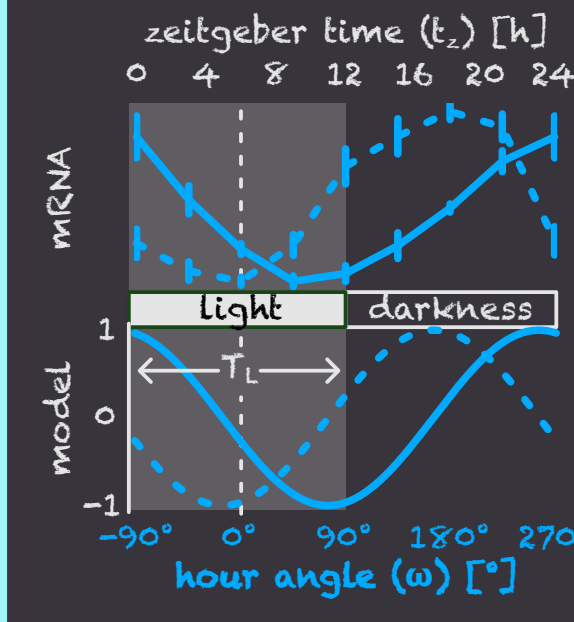
0. need more context?

Insects are excellent navigators. They can forage for hundreds of meters* and migrate for thousands of kilometers* in order to survive. They achieve that using their celestial compass. First, this compass needs to accurately detect the sun, even when this is covered by clouds or trees. To do that, it tries to match the sky's intensity and polarisation patterns with filters on the insect's eyes^{1,2}. Then, the compass needs to compensate for the movement of the sun during the day³. So it integrates light over the day to approximate the local time. Using the time, it transforms the sun's position into a geocentric compass and exploits geometrical constraints to save brain power. DN1pB neurons were proposed to inform the celestial compass about the time passed in *Drosophila melanogaster* fruit flies⁴. There are two of these neurons in each hemisphere of the brain⁵, expressing daily calcium oscillations⁶. However, how are these oscillations used by the compass and how they integrate into a geocentric compass is not yet understood.

1. summary

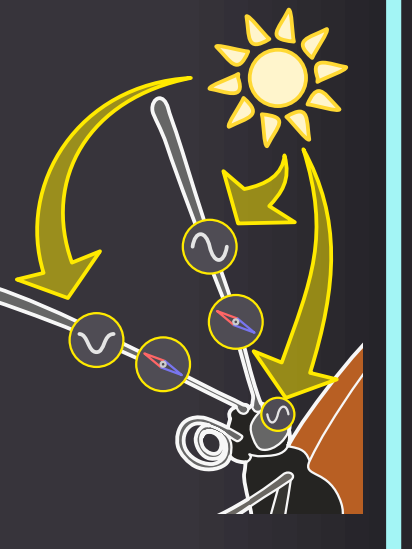
We propose a celestial compass sensor and model that imitates the one of insects. The design of our sensor is based on the fan-like arrangement of the polarisation filters in the insect's eyes^{1,2}. We propose a local processing pipeline of the light intensity and polarisation and how these integrate to create activity bumps in the ring attractors of central complex. We model the calcium oscillations based on light sensitive proteins and synchronise their phase to noon for stability³. We combine ring attractor bumps (spatial information) with activity oscillations (temporal information) to spatiotemporally integrate the sun's position and time into a geocentric compass⁷.

3. clock neurons



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In the insect brain, time is represented by proteins⁸, like the timeless (Tim) and cryptochrome type 2 (Cry2). These proteins are detected in the eyes and antennae of insects, and they translated into neural activity in the central brain through undiscovered mechanisms. In *D. melanogaster* the clock neurons that target the compass pathway are the DN1pB, which show in pairs per hemisphere⁹.

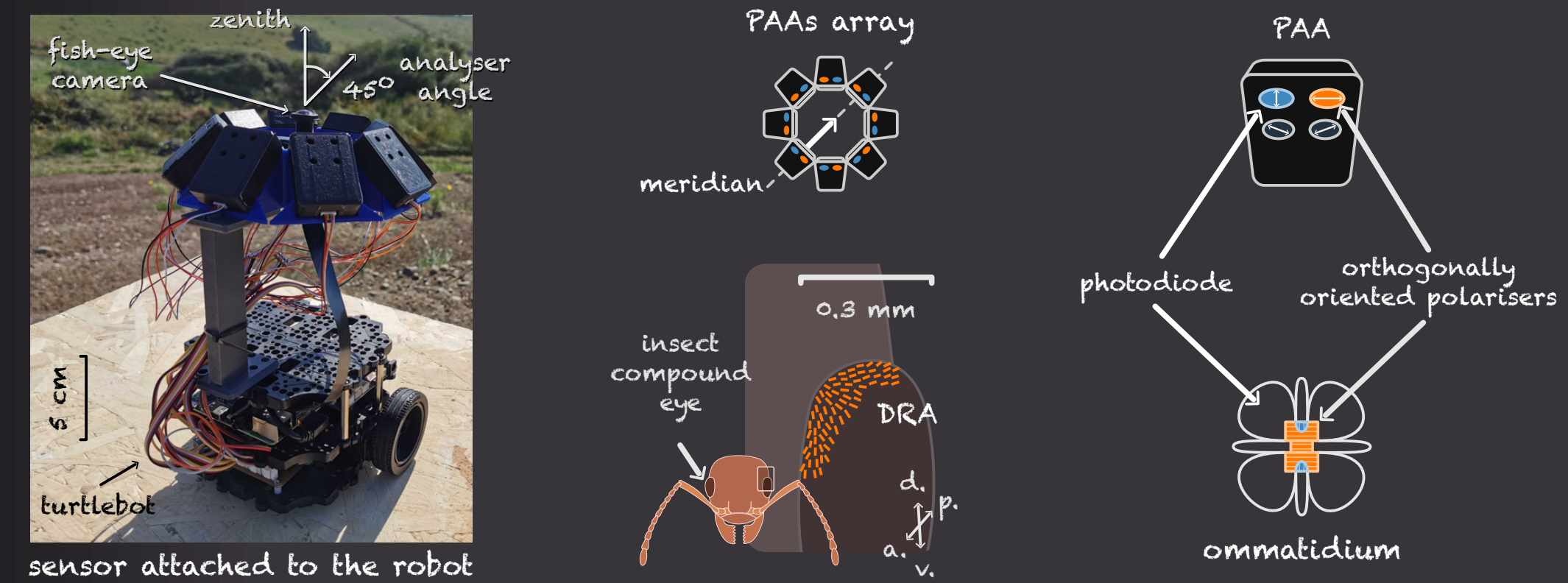


2. sun's position



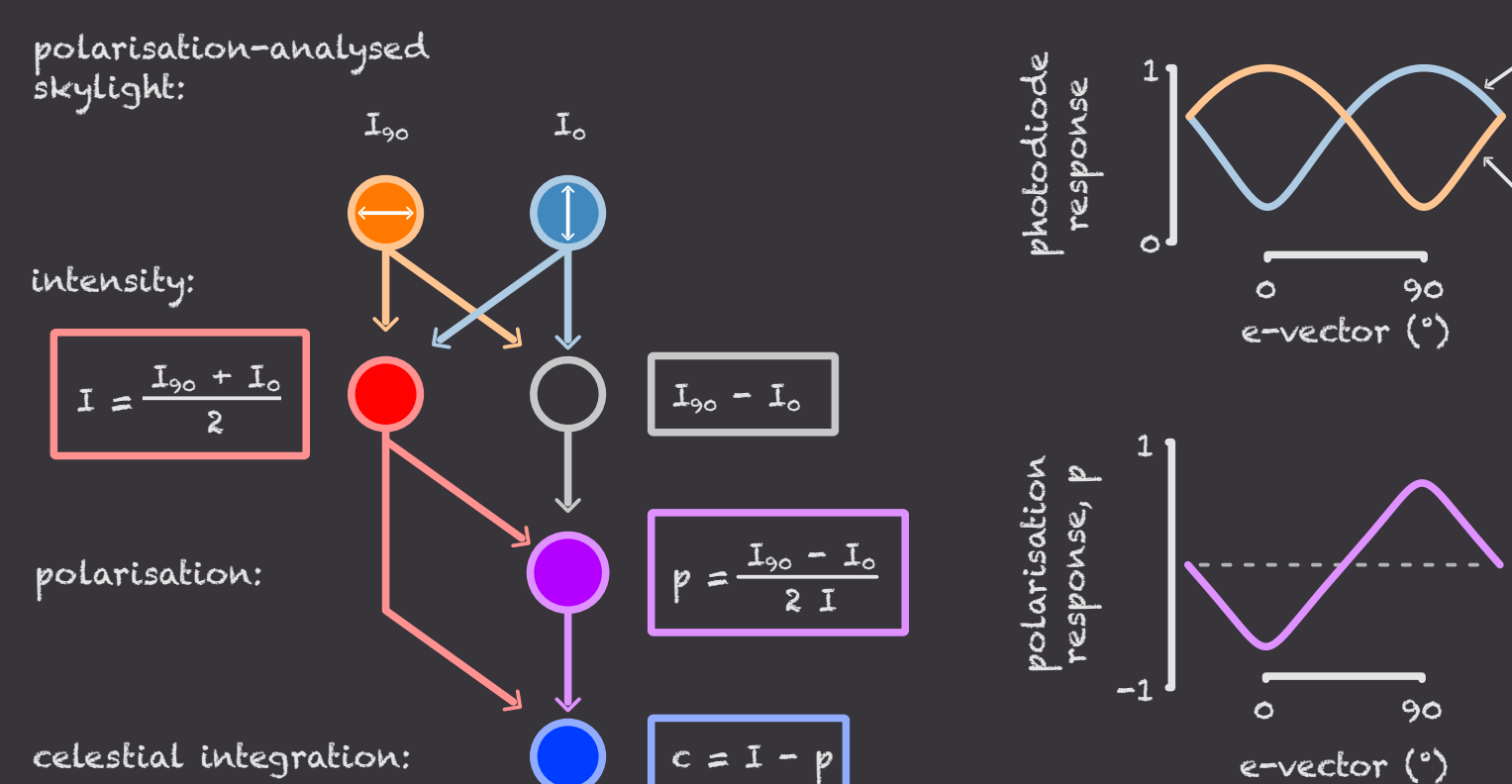
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We built a sensor prototype that uses 8 polarisation axis analysers (PAAs). Each PAA uses 2 UV photodiodes with orthogonal polarisation filters, imitating the properties of the ommatidia on the dorsal rim area (DRA) of the insect's eye.



2.1 optical processing

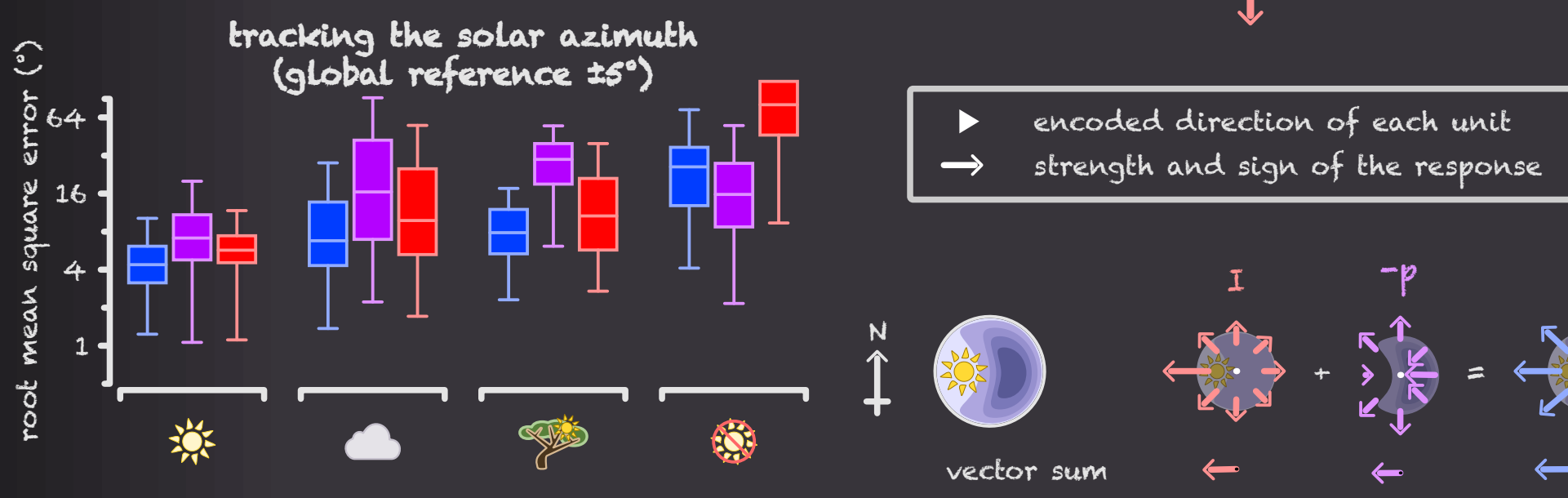
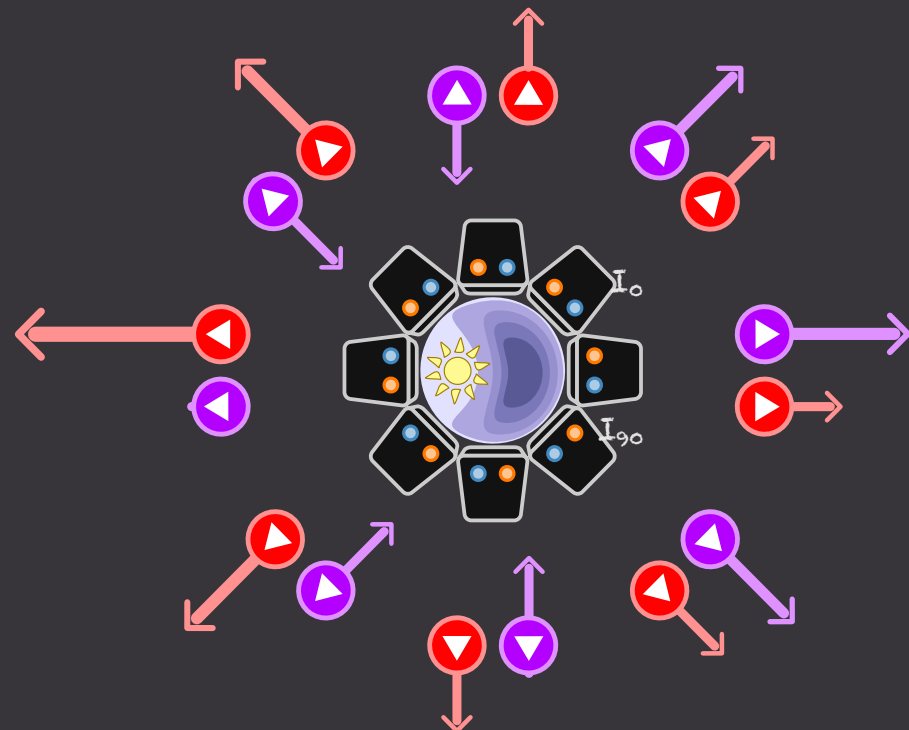
We process the outputs of the photodiodes in each PAA locally, imitating the per-column processing in the optic lobes of insects¹¹. For each PAA, we compute the light intensity, polarisation contrast, and their celestial integration.



2.2 resolving the solar azimuth

A vector is assigned to every optical processing neuron. The direction of the vector correlates with the viewing direction of the PAA. Its length depends on the response of the neuron.

A vector sum gives us the solar azimuth based on the light intensity (I), polarisation contrast (p) or their integration (c).



4. celestial compass

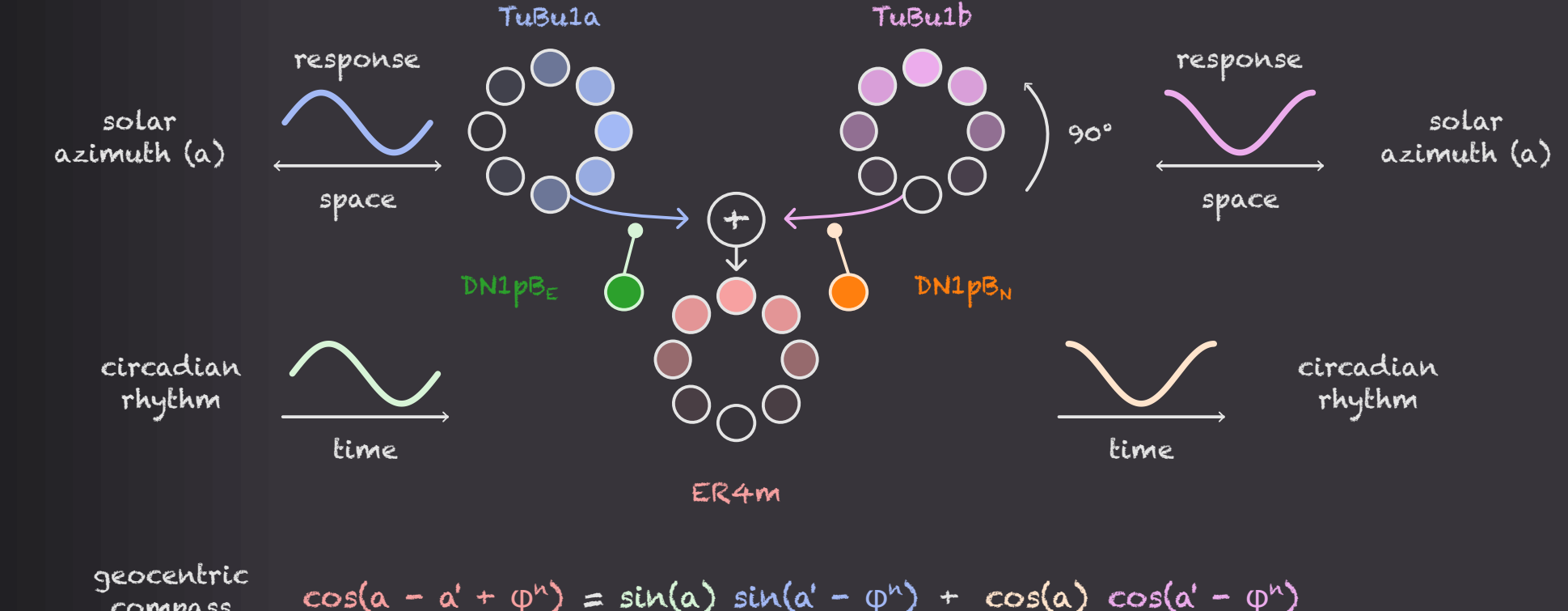


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Cartesian vectors can be represented by ring attractors that form bumps of activities¹². These bumps describe sinusoidal signals: their phase is the angle and their amplitude is the length of a vector.

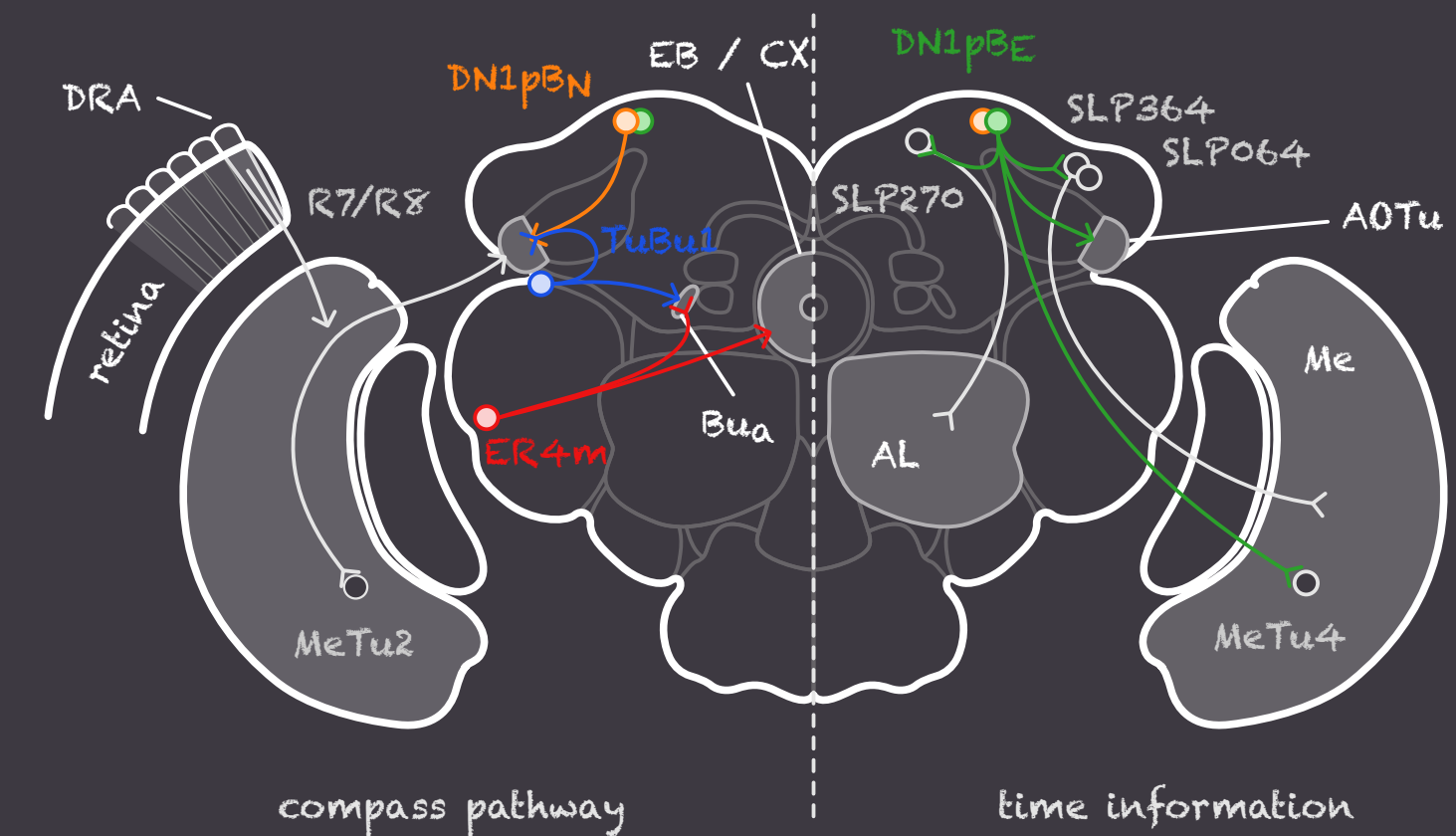
We assume a 90° phase shift between two neuron types in the insect brain (TuBua and TuBub). This represents the sine and cosine of the solar azimuth.

We then predict that one DN1pB neuron (e.g., activated by the Tim protein) targets one TuBua type and another DN1pB neuron (activated by the Cry2 protein, respectively) targets the other one.



This implements a crucial trigonometric identity that shifts the detected sun's position by the expected solar azimuth as calculated using the clock neurons. The result is a compass that points North!

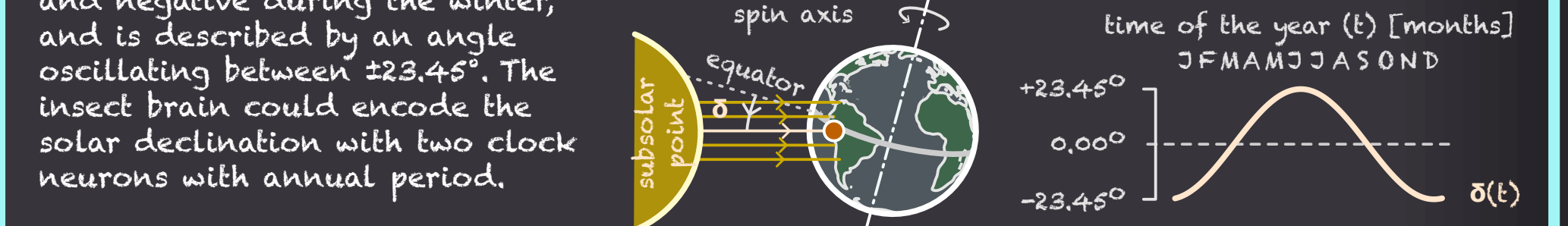
celestial compass and clock connection



3.1 the hour angle model (ω)

We model the protein levels of the Tim and Cry2 proteins as the sine and cosine of the hour angle. The hour angle is zero at noon and completes a circle by next noon, increasing by 15° per hour. The sine and cosine can then be used to create a Cartesian representation of the hour hand of a clock, that roughly tracks the sun's position.

However, the phase of the hour angle oscillation should not be bound to sunrise (and as a result to the zeitgeber time). To unwind the phase from the zeitgeber time, we must add half the day length. This amount can be computed by integrating the blue-light sensitive Cry1 protein level over a year. To understand how insects might calculate the day length, we optimised a differential equation that uses the overall blue light intensity in the sky. Our result suggests that a continuous update of the day length estimation needs less than 5 days to synchronise to the local time.

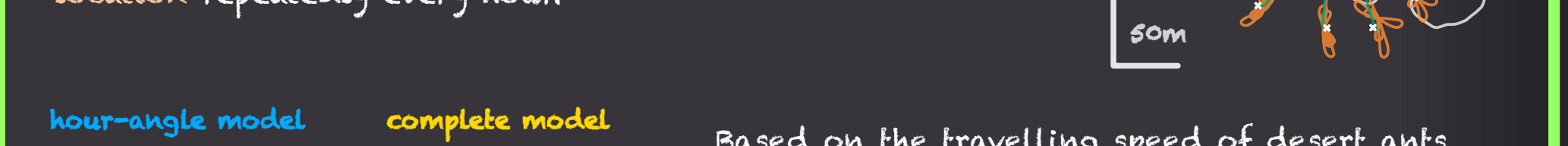


The hour angle model can accurately predict the local solar time but it does not predict the solar azimuth. To do that, we need the time of the year (season) and geographic latitude of the observer. We suggest that insects can compute these values locally by utilising the solar declination and geomagnetic inclination respectively.

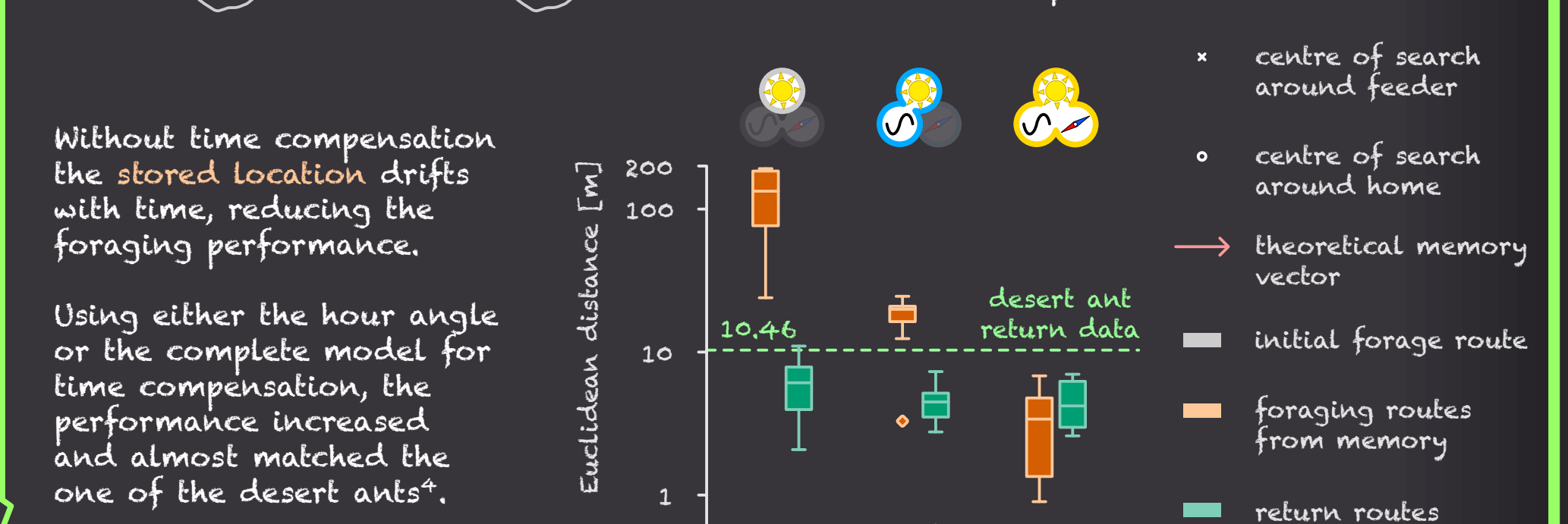
This is the angle of the subsolar point (point on Earth that the sun is at the zenith) from the equator. In the northern hemisphere, this is positive during the summer and negative during the winter, and is described by an angle oscillating between ±23.4°. The insect brain could encode the solar declination with two clock neurons with annual period.

3.2 the complete solar azimuth model (α)

Some insects can detect the geomagnetic inclination¹³, which is a monotonic function of their geometric latitude.



Without time compensation the stored location drifts with time, reducing the foraging performance. Using either the hour angle or the complete model for time compensation, the performance increased and almost matched the one of the desert ants⁴.



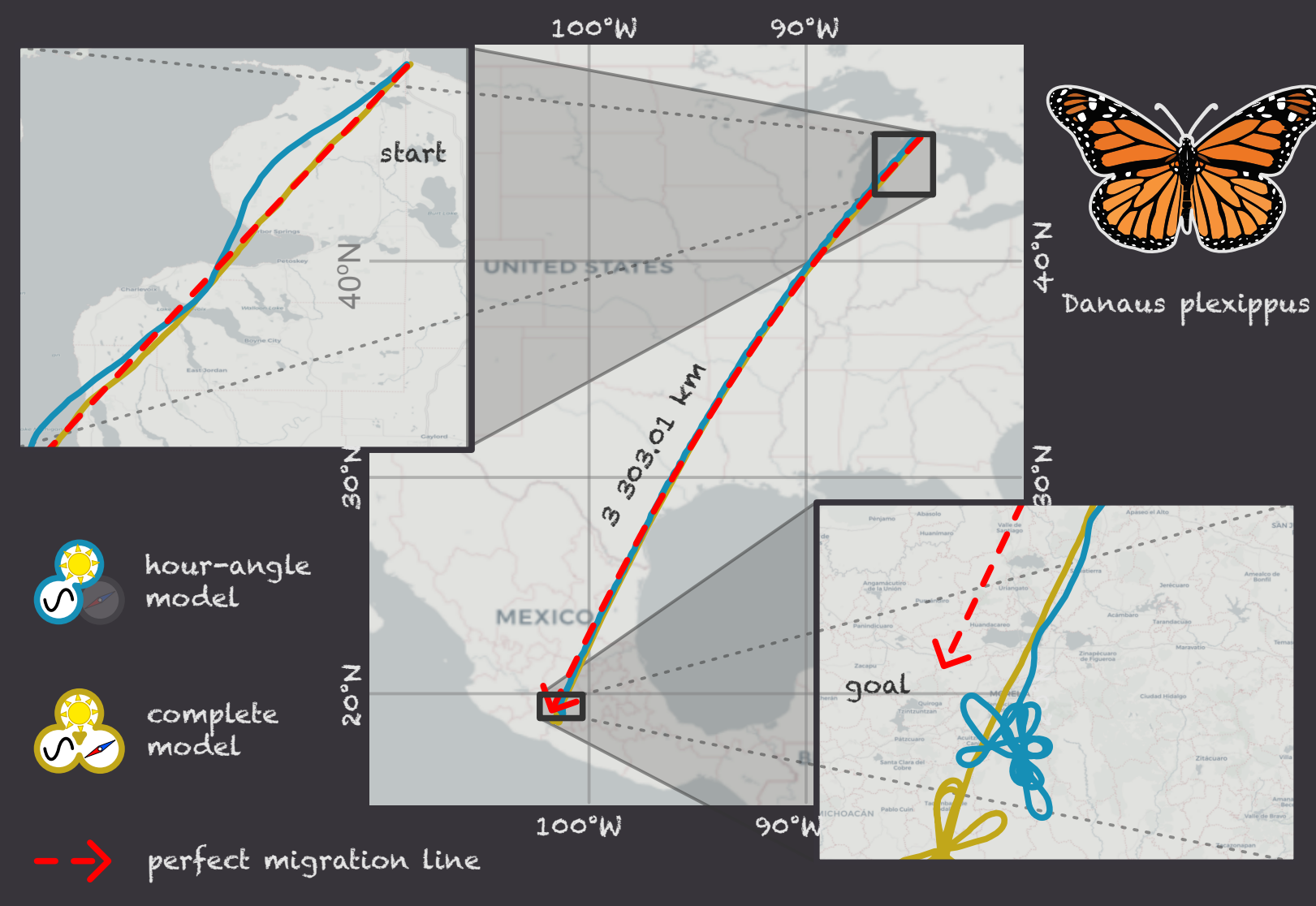
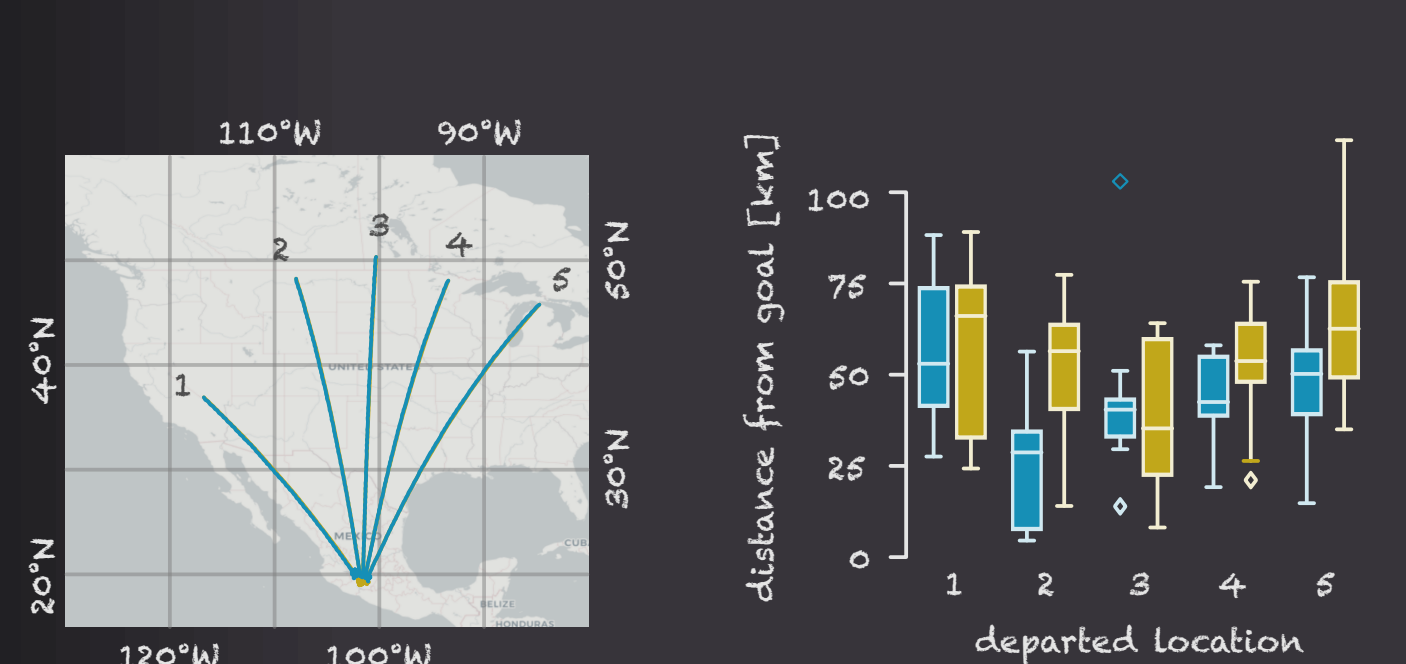
6. migration



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We challenged our compass model in migration scenarios, imitating the autumn migration of monarch butterflies (*Danaus plexippus*).

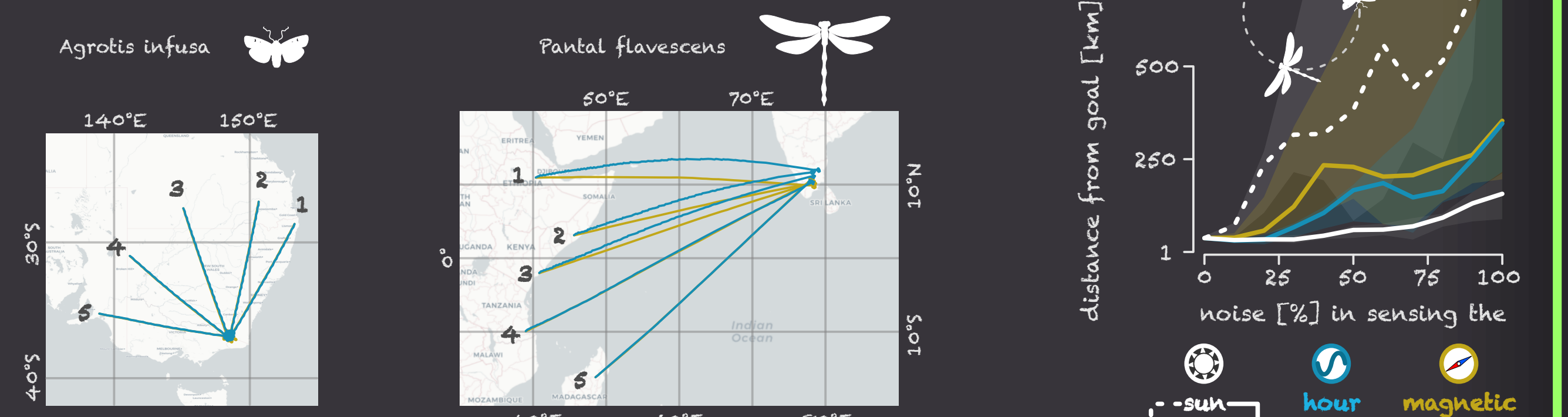
Both the hour-angle and complete time compensation models successfully drove the butterflies from the Canadian borders to Mexico.



We further challenged the two models in the south hemisphere (Bongong moths) and close to the equator (globe skimmer dragonfly), where the sun moves counterclockwise and biannually switches moving direction respectively.

When we hardwired a switch in its moving direction, the hour-angle model did well in the south hemisphere. However, even when we hardwired a switch from east to west in the afternoon, the model drifted close to the equator as its latitude diverged from the subsolar latitude.

On the other hand, the performance of the complete model was unaffected. Our sensitivity analysis revealed that the multidimensional representation of the sun made the model more resilient to noise, while temporal and magnetic noise disturb the model in a similar rate.



references

1. Gkaniats et al. (2019). From skylight input to behavioural output: a computational model of the insect polarised light compass. *PLoS Comput Biol* 15, e1007123.
2. Gkaniats et al. (2023). Celestial compass sensor mimics the insect eye for navigation under cloudy and occluded skies. *Commun Eng* 2, 72.
3. Gkaniats and Webb (2025). Spatiotemporal computations in the insect celestial compass. *Nat Commun* 16, 2832.
4. Huber and Knaden (2015). Geocentric and geocentric navigation during extremely long foraging paths of desert ants. *J Compar Physiol A* 201, 609-616.
5. Merlin et al. (2009). Antennal circadian clocks coordinate sun compass orientation in migratory monarch butterflies. *Science* 325, 1700-1704.
6. Beck et al. (2014). Receptive fields of locust brain neurons are matched to polarization patterns in the sky. *Curr Biol* 24, 2124-2129.
7. Wehner (1987). 'Matched filters'-neuronal models of the external world. *J Compar Physiol A* 161, 511-531.
8. Wehner and Lanfranconi (1981). What do the ants know about the rotation of the sky? *Nature* 293, 731-733.
9. Hulst et al. (2021). A connectome of the *Drosophila* central complex reveals network motifs suitable for flexible navigation and context-dependent action selection. *eLife* 10, e66039.
10. Guo et al. (2018). A circadian output circuit controls sleep-wake arousal in *Drosophila*. *Neuron* 100, 624-635.e4.
11. Hardcastle et al. (2021). A visual pathway for skylight polarization processing in *Drosophila*. *eLife* 10, e63225.
12. Guerra et al. (2014). A magnetic compass aids monarch butterfly migration. *Nat Commun* 5, 4164.

7. conclusions and future directions

Our sensor prototype accurately detects the sun under natural skies with occlusions.

Our time compensation mechanism can correct for the sun's movement during the day, transforming the sensor into a geocentric compass.

Our results suggest that a simpler hour angle model is sufficient for most of the long distance migrations. A more complete model might be necessary for smaller scale navigation, where the geometric latitude can be hardwired in the brain.

We are currently working on improving the sun's detection to boost the performance in scenarios with extremely occluded skies.

We are also working on miniaturising the compass sensor and moving the processing on board with analogue electronics.

Another future direction would be to implement the light-based dynamic clock on board and test the time-compensated celestial compass sensor in long experiments.

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