The time-compensated celestial compass of insects

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ϕ. need more context?

Insects are excellent navigators. They can forage for hundreds of meters[4] and migrate for thousands of kilometers[5] 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[1,6,7]. Then, the compass needs to compensate for the movement of the sun during the day[8]. 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 flies[9]. There are two of these neurons in each hemisphere of the brain[9], expressing daily calsium oscillations[10]. 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 immitates 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 stability[3]. We combine ring attractor bumps (spatial information) with activity oscillations (temporal information) to spatiotemporally integrate the sun's position and time into a geocentric compass[3].

2. sun's position

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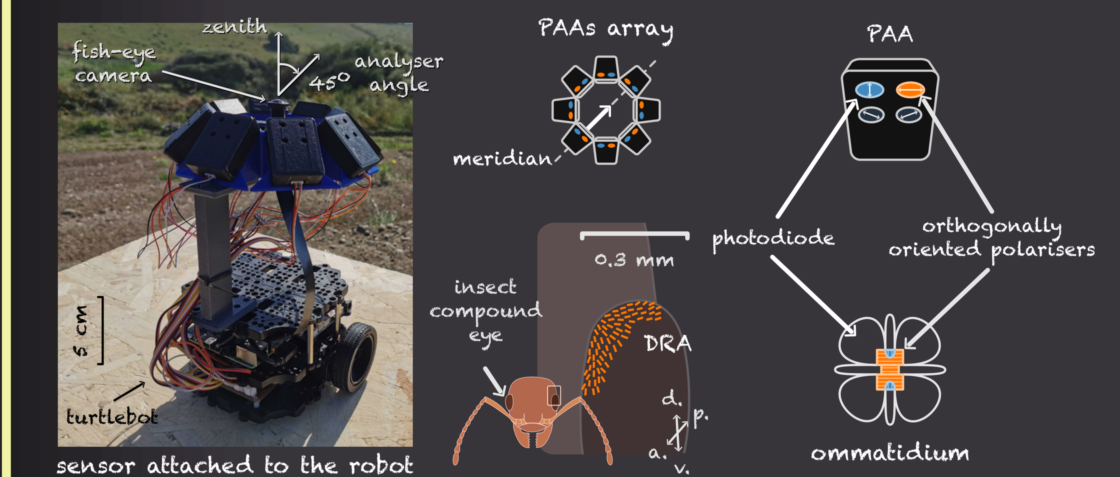
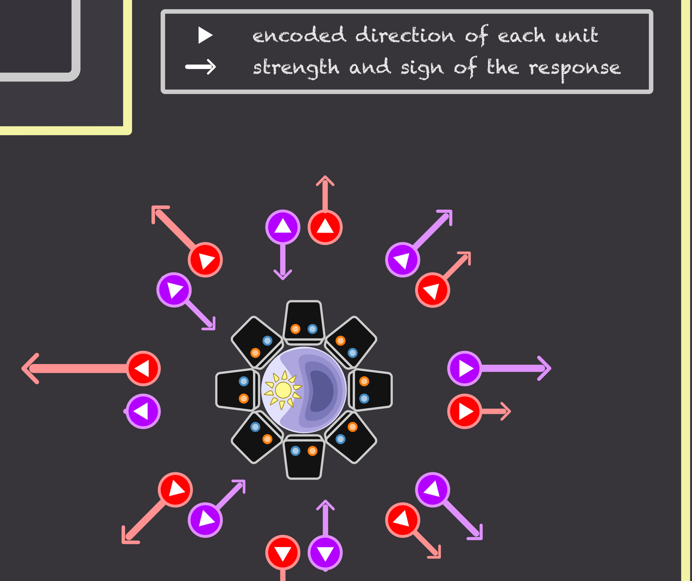
We built a sensor prototype that uses 8 polarisation axis analysers (PAAs). Each PAA uses 2 UV photodiodes with orthogonal polarisation filters, immitating the properties of the ommatidia on the dorsal rim area (DRA) of the insect's eye.

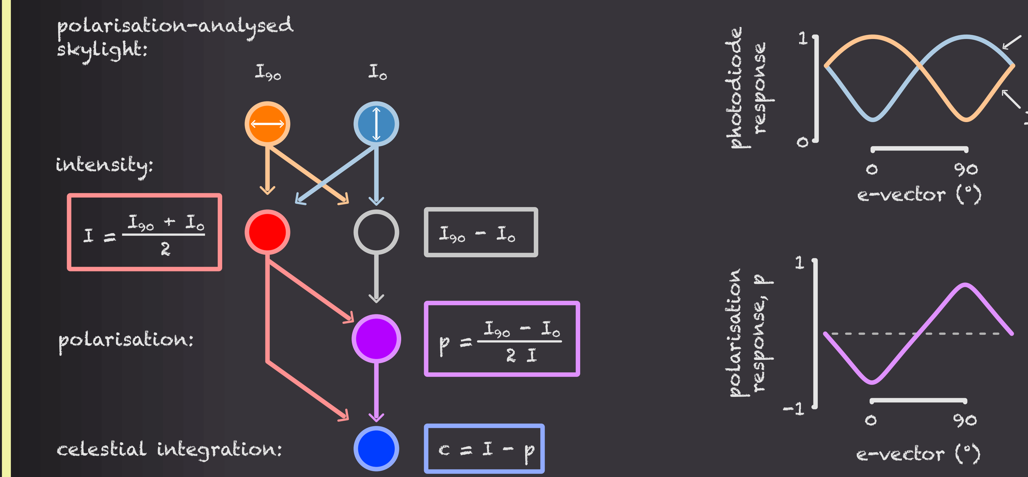


sensor attached to the robot



2.1 optical processing

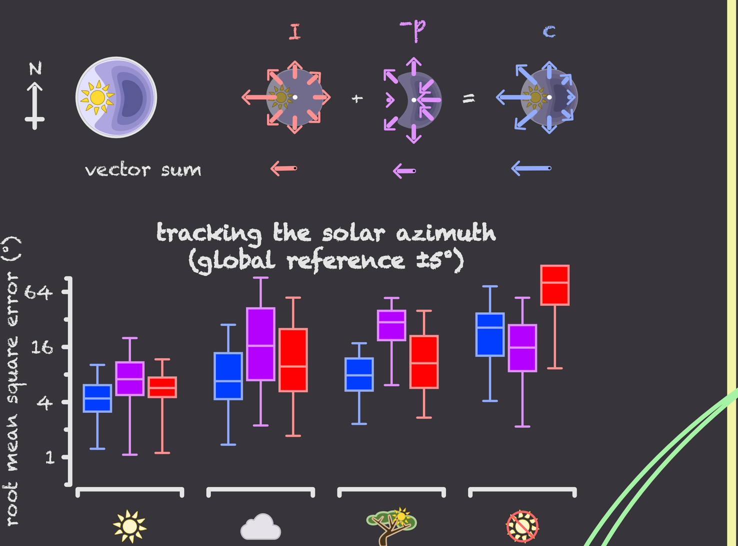
We process the outputs of the photodiodes in each PAA localy, immitating the per-column processing in the optic lobes of insects[11]. For each PAA, we compute the light intensity, polarisation contrast, and their celestial integration.



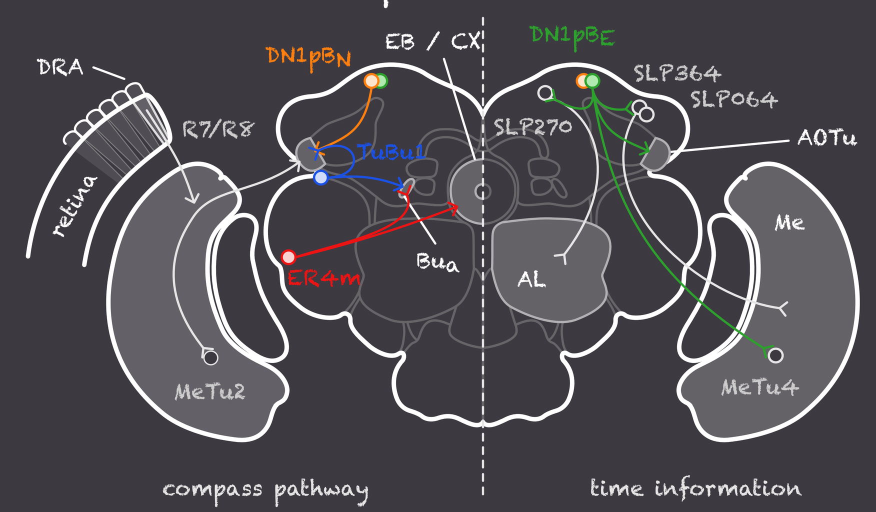
2.2 resolving the solar azimuth

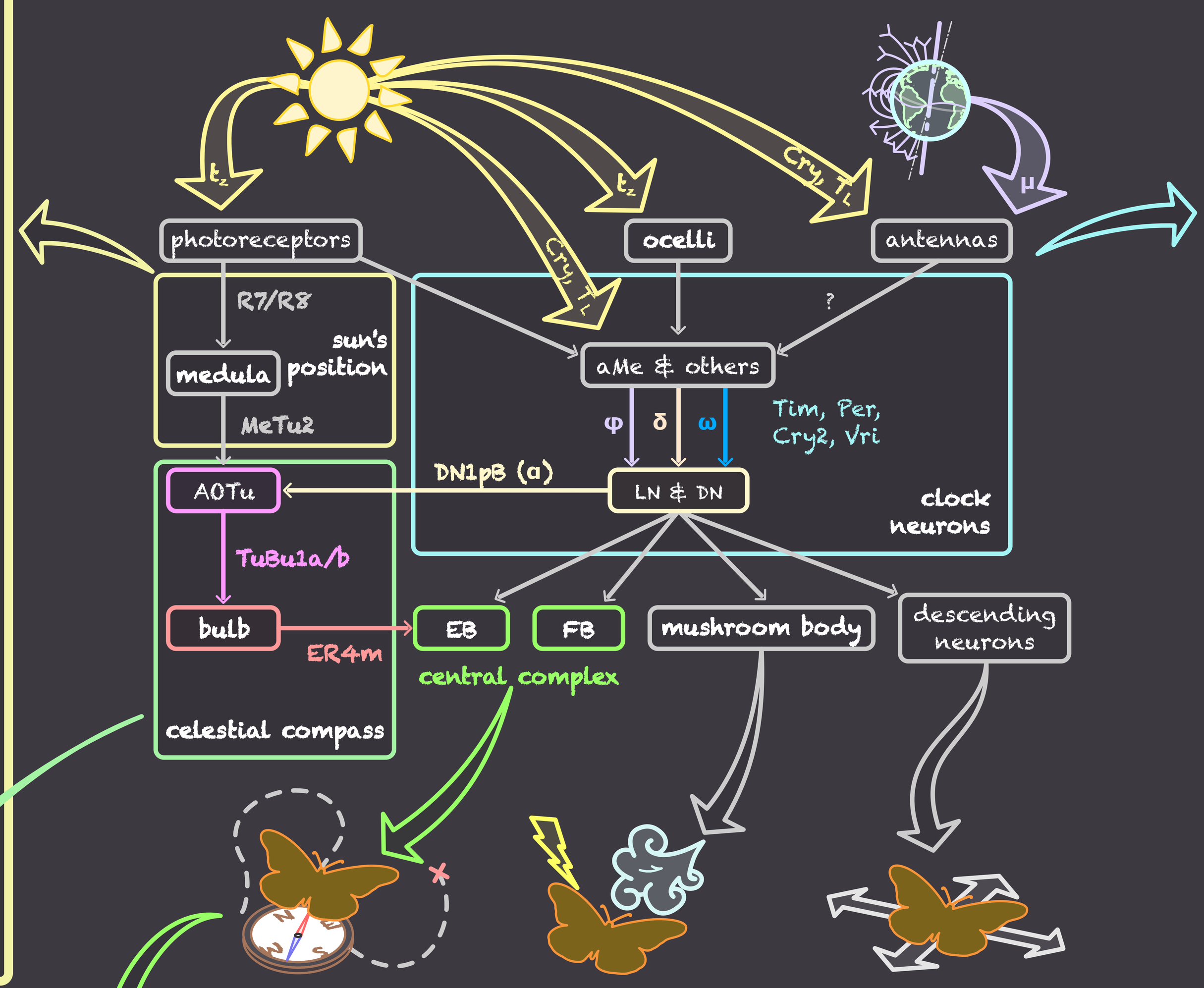
A vector is assigned to every optical processing neuron. The direction of the vector correlates with the viewing direction of the PAA. Its length depends on the response of the neuron.

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



celestial compass and clock connection





3. clock neurons

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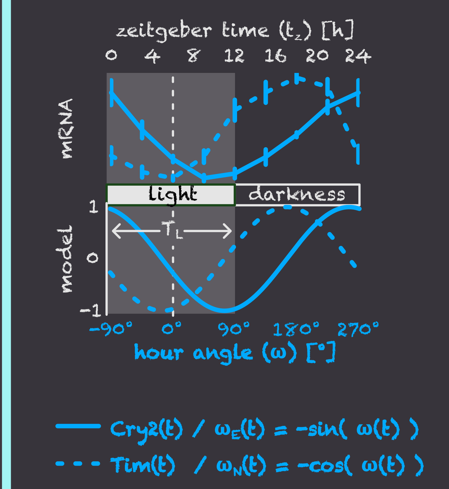
In the insect brain, time is represented by proteins[5], like the timeless (Tim) and cryptochrome type 2 (Cry2). These proteins are detected in the eyes and antennas of insects, and they translated into neural activity in the central brain through undiscoverred mechanisms. In D. melanogaster the clock neurons that target the compass pathway are the DN1pB, which show in pairs per hemisphere[9].



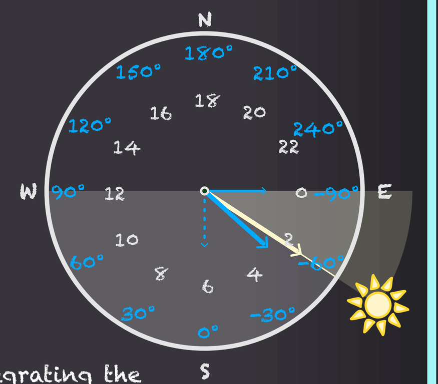
3.1 the hour angle model (ω)

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, increading 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.

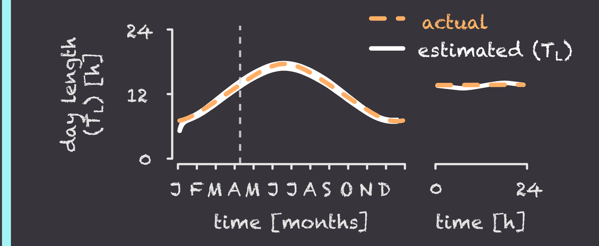
$$\omega(t) = \left(t_z - \frac{T_L}{2}\right) 15°$$

$$T_L \frac{dT_L}{dt} = \mathrm{Cry1}(t) + b - T_L$$

$$\mathrm{Cry1}(t) = a\, I_{sky}(t)$$



However, the phase of the hour angle oscillation should not be bount to sunrise (and as a result the zeitgeber time). To unbind 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.

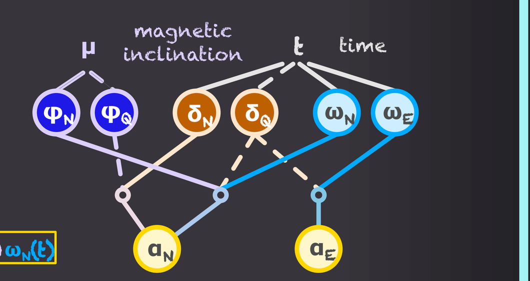


3.2 the complete solar azimuth model (α)

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. Insects can compute these values locally by utilising the solar declination and geomagnetic inclination respectively.

$$\alpha_E = -\sin(\alpha) = \delta_Q(t)\ \boxed{\omega_E(t)}$$

$$\alpha_N = -\cos(\alpha) = \varphi_Q(\mu)\ \boxed{\delta_N(t)} + \delta_Q(t)\ \boxed{\varphi_N(\mu)\,\omega_N(t)}$$

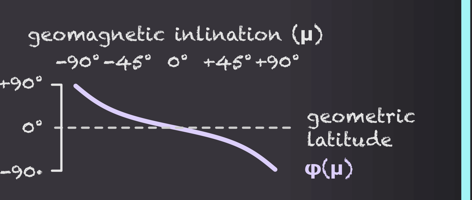


solar declination (δ)

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 ±23.45°. The insect brain could encode the solar declination with two clock neurons with annual period.

geomentric latitude (φ)

Some insects can detect the geomagnetic inclination[12] (μ), which is a monotonic function of their geometric latitude.



4. celestial compass

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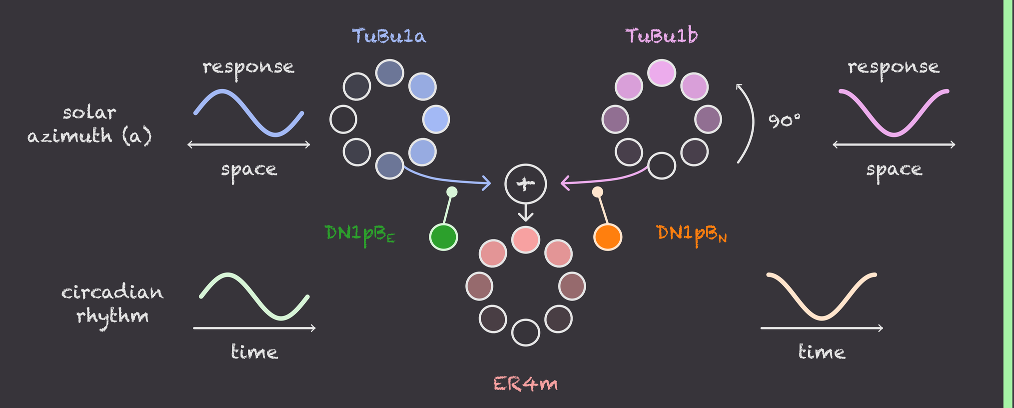
Cartesian vectors can be represented by ring attractors that form bumps of activities[1,2]. These bumps describe sinusoidal signals: their phase is the angle and their amplitude is the length of a vector.

We assume a 90° phase shift between two neuron types in the insect brain (TuBu1a and TuBu1b). This represents the sine and cosine of the solar azimuth.

We then predict that one DN1pB$_E$ neuron (e.g., activated by the Tim protein) targets one TuBu1 type and another DN1pB$_N$ 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 claculated using the clock neurons. The result is a compass that points North!



$$\cos(a - a' + \varphi'') = \sin(a)\ \sin(a' - \varphi'') + \cos(a)\ \cos(a' - \varphi'')$$

5. central place foraging

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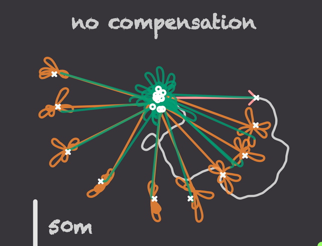
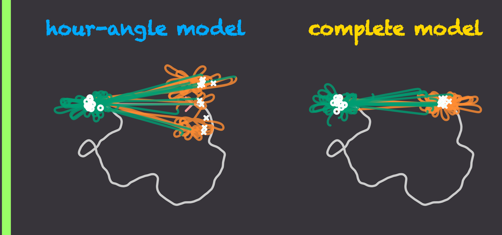
We tested the performance of our compass in a foraging scenario, where an insect searches for food and finds it 100m away from the nest. It stores the location in its memory and returns to its nest. The insect attempts to forage at the stored location repeatedly every hour.

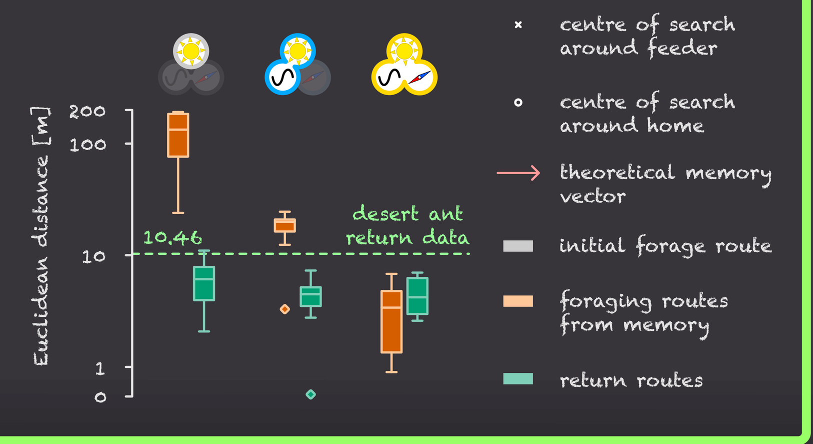




Based on the travelling speed of desert ants (0.5 m sec^{-1}), the foraging duration in this experiment was around 6.5 min. At the end of foraging the sun's position did not change much, which made the return routes suggessful even when time compensation was not used.

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 ants[4].



6. migration

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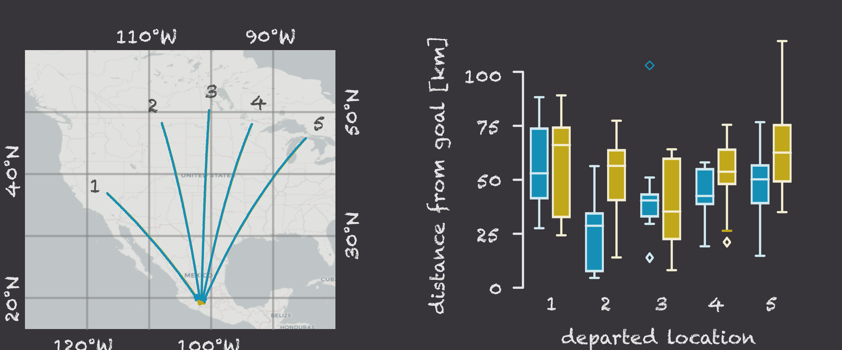
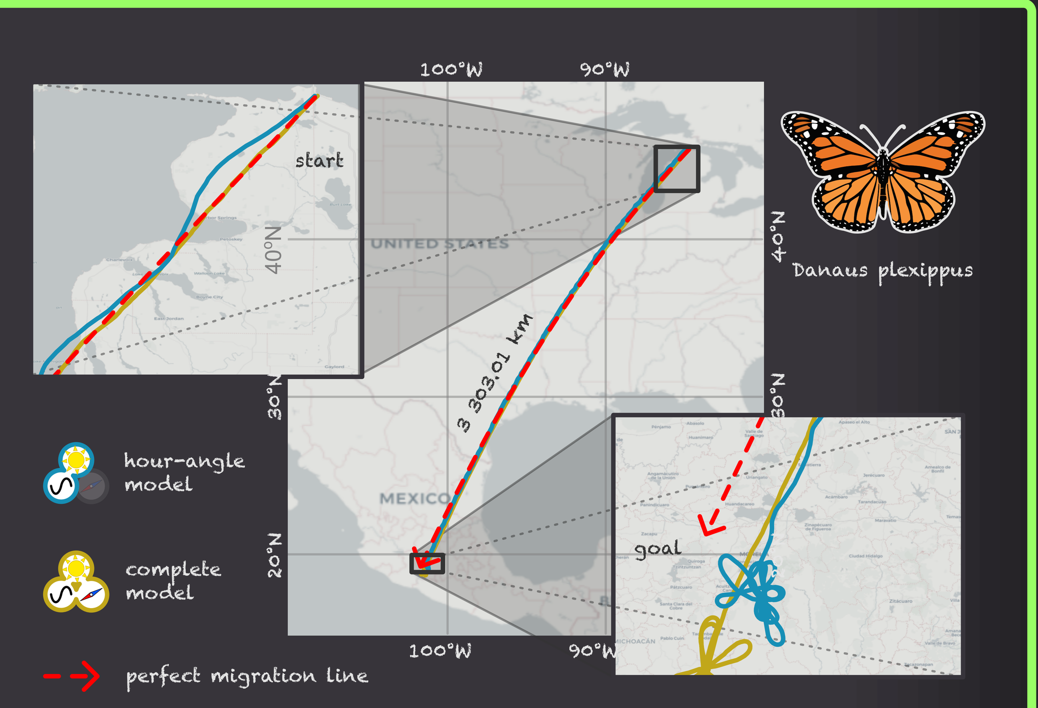
We challenged our compass model in migration scenarios, imitating the autumn migration of monarch butterflies (Danaus plexippus).

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





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 long distance migrations. A more complete model might be necessary for smaller scale navigation.

We are currently working on improving the sun's detection to boost the perfrormance 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.

Acknowledgments: Engineering and Physical Sciences Research Council · Insect Neuro Nano · European Innovation Council

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