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Unraveling the neural basis of insect navigation

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One of the defining features of animals is their ability to navigate their environment. Using behavioral experiments this topic has been under intense investigation for nearly a century. In insects, this work has largely focused on the remarkable homing abilities of ants and bees. More recently, the neural basis of navigation shifted into the focus of attention. Starting with revealing the neurons that process the sensory signals used for navigation, in particular polarized skylight, migratory locusts became the key species for delineating navigation-relevant regions of the insect brain. Over the last years, this work was used as a basis for research in the fruit fly *Drosophila* and extraordinary progress has been made in illuminating the neural underpinnings of navigational processes. With increasingly detailed understanding of navigation circuits, we can begin to ask whether there is a fundamentally shared concept underlying all navigation behavior across insects. This review highlights recent advances and puts them into the context of the behavioral work on ants and bees, as well as the circuits involved in polarized-light processing. A region of the insect brain called the central complex emerges as the common substrate for guiding navigation and its highly organized neuroarchitecture provides a framework for future investigations potentially suited to explain all insect navigation behavior at the level of identified neurons.

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Introduction

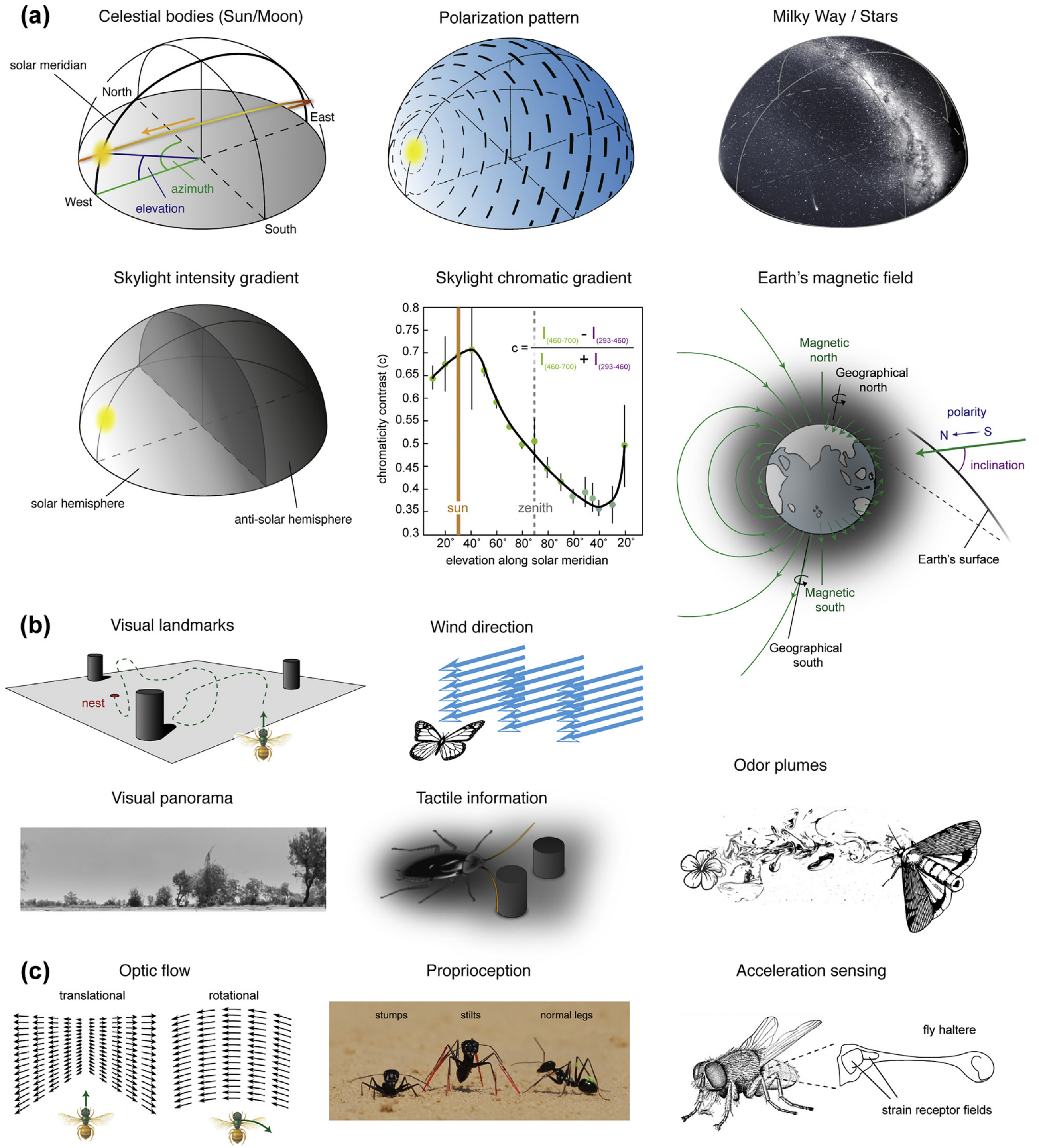
Animals navigate their surroundings to find food, to avoid being eaten, to find reproductive partners, and to escape unfavorable environmental conditions. In order to do this, all animals, including insects, have to select a goal and establish where they currently are in relation to that goal by using appropriate sensory information (Figure 1). Navigational goals can either be physical locations or goal directions and are continued to be actively pursued after disturbance, a feature not present in directional escape reflexes. Independent of which strategy an animal uses to pursue a navigational goal, it has to continuously compare its current heading (body orientation) with its desired heading (goal-direction) and translate any mismatch into compensatory steering commands (Figure 2). The brain has to extract relevant information from the continuous stream of diverse, navigation relevant sensory signals and eventually use it to initiate steering. This task is not trivial even in seemingly simple animals, as in each moment in time the animal's intended heading will be additionally defined by behavioral and motivational state and by previous experience, which together provide the context for adequate behavioral decisions that amount to a coherent navigational strategy [1–3].

Overall, three neural processes are required for navigation and will be covered by this review: First, representation of the animal's current heading; second, representation of the animal's desired heading; and third, comparing both to generate steering commands.

Neural correlates of an insect's current heading

The first insights into brain circuits underlying navigation resulted from illuminating neural responses to polarized light. Polarized skylight is a visual compass cue that allows animals to infer the sun's azimuth when viewing a small patch of blue sky (Figure 1a). Thus, neurons tuned to specific polarized-light angles (POL-neurons) likely mediate navigation-relevant signals about body orientation with respect to a global, sky-based reference frame. After POL-neurons had been identified in the optic lobes of crickets and locusts [4–7], a pathway to the central complex (CX), a group of neuropils in the center of the insect brain [8–10], was characterized (reviewed in [11,12]). Along this pathway, polarized-light information is integrated with other skylight derived directional cues (Figure 1a) into a coherent compass signal [6,13–16]. The CX then contains a multitude of POL-neurons, described in locusts [12], butterflies [16], beetles [17••], and bees [18••] (Figure 3a). They define a neural network proposed to transform purely sensory compass signals into premotor commands suited to guide navigation [11,19]. Importantly, in the protocerebral bridge (PB) (one CX-compartment) each POL-neuron's tuning correlates with its anatomical position within this structure [20]. As the polarization angle of skylight directly relates to the sun's azimuth, this arrangement is essentially equivalent to an array of head-direction cells tethered to a sky-based reference frame (Figure 3b).

Figure 1



Sensory information used for insect navigation. **(a)** Global external cues. Polarization pattern, intensity-gradient and chromatic gradient result from scattering of direct sunlight (or moon-light) in the upper atmosphere. They are most prominent during the day, but their much dimmer nocturnal versions can also be used for navigation by night-active insects. The chromatic gradient in the sky results from a higher proportion of green light in the solar hemisphere (curve from [14]). The Earth's magnetic field offers three main cues for navigation, the inclination of the field lines, their polarity, as well as the intensity of the field (not shown). The Milky Way is used for straight-line navigation by dung beetles [66,67]. **(b)** Local external cues. Visual panorama from [68]. Wind has been shown to play a role in moths [69] and ants [70]. Tactile cues perceived through the antenna provide major information to nocturnal cockroaches and are encoded by neurons in the central complex [71]. Odor plumes are key for pheromone following behavior in moths [64] but are also important for, for example, ant navigation [72]. **(c)** Internal cues (idiothetic cues). Translational and rotational optic flow in response to self-motion provides information about forward velocity and angular velocity of an animal.