



ELSEVIER



Sensory basis of lepidopteran migration: focus on the monarch butterfly

Patrick A Guerra and Steven M Reppert

In response to seasonal habitats, migratory lepidopterans, exemplified by the monarch butterfly, have evolved migration to deal with dynamic conditions. During migration, monarchs use orientation mechanisms, exploiting a time-compensated sun compass and a light-sensitive inclination magnetic compass to facilitate fall migration south. The sun compass is bidirectional with overwintering coldness triggering the change in orientation direction for remigration northward in the spring. The timing of the remigration and milkweed emergence in the southern US have co-evolved for propagation of the migration. Current research is uncovering the anatomical and molecular substrates that underlie migratory-relevant sensory mechanisms with the antennae being critical components. Orientation mechanisms may be detrimentally affected by environmental factors such as climate change and sensory interference from human-generated sources.

Addresses

Department of Neurobiology, University of Massachusetts Medical School, 364 Plantation Street, Worcester, MA 01605, USA

Corresponding author: Reppert, Steven M
(Steven.Reppert@umassmed.edu)

Current Opinion in Neurobiology 2015, 34:20–28

This review comes from a themed issue on **Molecular biology of sensation**

Edited by **David Julius** and **John Carlson**

<http://dx.doi.org/10.1016/j.conb.2015.01.009>

0959-4388/© 2015 Elsevier Ltd. All rights reserved.

Introduction

Many diverse animal taxa undergo long-distance migrations, in which individuals travel up to thousands of kilometers between different season-appropriate sites, in direct response to seasonally changing environments [1]. Recent research has elucidated critical aspects of migration, an evolved behavioral strategy used by several lepidopteran species, including both butterflies (e.g. the North American monarch butterfly, *Danaus plexippus* [2–4,5,6,7]; the painted lady butterfly, *Vanessa cardui* [8,9]) and moths (e.g. the silver Y moth, *Autographa gamma* [10–12]). To reach their destinations during the migratory journey, migrants likely use either compasses alone or a map and compasses, for navigation [1]. A map sense

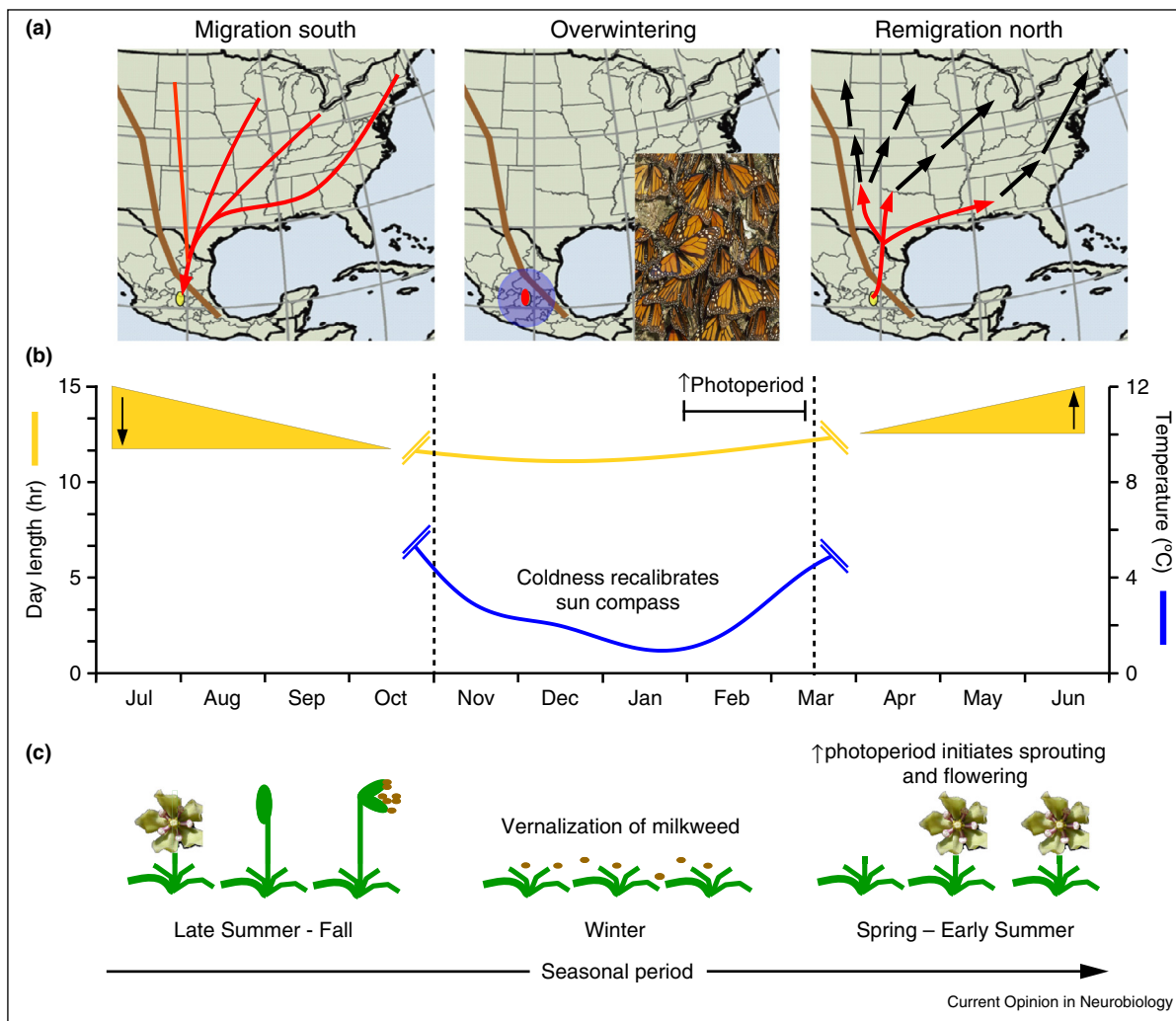
allows migrants to know their location relative to their destination, whereas compasses provide migrants with the ability to orient in the proper migratory direction during travel. Although there is debate as to whether or not migrant lepidopterans can possess a map sense (e.g. the monarch; see below), a body of work exists that demonstrates that these species have various and separate compass senses (e.g. [2–4,5,6,7]), in which they depend on reliable environmental cues to obtain directional information [13,14]. Having multiple modes for directionality may be advantageous for individuals, because they better inform and fine-tune navigational decision-making during migration.

In this review, we discuss recent findings that further delineate the characteristics of several orientation tools used by migratory lepidopterans, as well as examine the potential relationships between them. Here, we highlight the eastern North American monarch butterfly, and its use of multiple compass mechanisms during migration. This iconic long-distance migratory insect migrates each fall to mountainous overwintering sites in central Mexico, as part of its annual migration cycle (depicted in Figure 1a). We also highlight the role of the antennae, multimodal sensory organs that are a key component in these different mechanisms. Finally, we consider how the threats of global climate change and human-generated sensory noise may interfere with orientation mechanisms.

Skylight cues

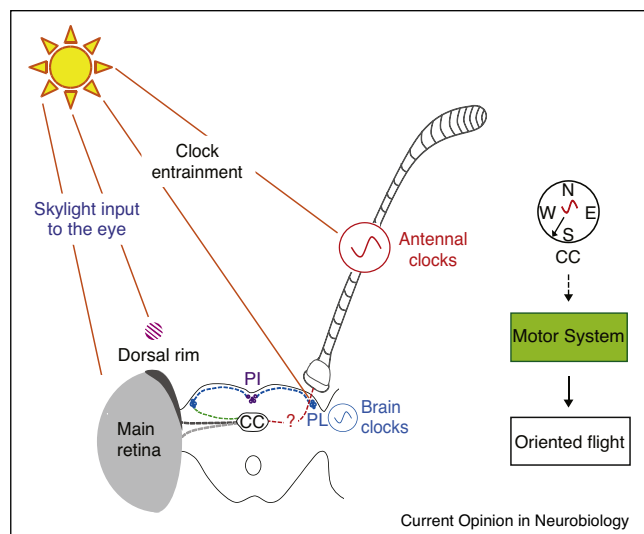
Among diurnal migratory lepidopterans, the sun compass is the most common orientation process involving the use of skylight cues. Here, individuals use daylight cues, such as the sun's azimuthal (horizontal) position in the sky and daylight polarization patterns [13,14], to obtain directional information to orient in the proper migratory heading [13,14,15]. In its simplest form, use of the sun compass consists of individuals using daylight cues to maintain their proper migratory heading, as seen in painted lady butterflies [8,15]. In contrast, some individuals use a more complex sun compass as it is time-compensated, in which information from daylight cues is adjusted for the time of day. Of special note are migrating monarch butterflies that use circadian clocks in their antennae as a timekeeping mechanism to adjust their directional flight throughout the day (Figure 2), as daylight cues appear to constantly shift in the sky as the day progresses [13,14,15]. Brain clocks, which reside in the par lateral regions appear to have no role in the monarch time-compensated sun compass, but they likely are important

Figure 1



The direction and recalibration of the time-compensated sun compass of migratory monarchs appears to have co-evolved with the seasonal development of milkweed plants, the obligate food source of monarch larvae. **(a)** Annual migration cycle of the eastern North American monarch butterfly. (Left) Migration south. As part of the migratory syndrome, monarchs possess a time-compensated sun compass that allows them to orient in the proper southerly direction during the fall migration (converging red lines with arrow on map) to their overwintering grounds in Mexico (yellow oval). (Middle) Overwintering period in Mexico with migrants congregated at the overwintering sites (red oval). Inset, photograph of monarchs clustered on a tree trunk at an overwintering site (courtesy of Getty Images). (Right) Remigration north. Overwintering monarchs use their recalibrated sun compass during the northwards remigration (red arrows). The offspring of these spring remigrants continue the migratory cycle by repopulating the northern ranges of the monarch habitat throughout the spring and summer (black arrows). It is unclear if these generations of monarchs also migrate northwards or whether they are simply dispersing. Brown line on the maps, Rocky Mountains. **(b)** North American environmental conditions during migration. (Left) Decreasing day length during migration south. (Center) Overwintering site conditions. Coldness experienced by migrants while at the overwintering sites (blue line and blue circle on Overwintering map above) is the environmental cue, independent of photoperiod that recalibrates the orientation of the sun compass. The cue that initiates the actual remigration north is likely the sensing of increasing photoperiod (yellow line, bracketed section) at the overwintering sites. The temperature data and day length data are modified from Ref. [5**], and the black vertical dashed lines indicate the beginning and end of the time spent by migratory monarchs at the overwintering sites. (Right) Increasing day length during movement north. **(c)** Annual milkweed cycle. (Left) Milkweed growth, pollination, and seeding. (Middle) The vernalization of milkweed plants and seeds via coldness coincides with the recalibration of the sun compass. (Right) Vernalization conveys to milkweed plants the ability to sprout and flower in the spring by conferring them the competence to respond to appropriate spring inductive cues. Similarly, vernalization facilitates the germination of milkweed seeds. As with remigration, the sensing of increasing photoperiod is a reliable cue that is correlated with warmer spring temperatures, the emergence of milkweed, and subsequent spring flowering. Photograph of milkweed flower courtesy of Monarch Watch (www.monarchwatch.org).

Figure 2



Model delineating the components used for time-compensated sun compass orientation. The compass mechanism involves the monarch eye sensing of skylight cues, including the horizontal position of the sun itself and the polarization daylight pattern, and the brain integration of skylight-cue stimulated neural response in the central complex (CC; grey dashed lines). Time-compensation is provided by circadian clocks located in the antenna. The integrated time-compensated sun compass information is relayed to the motor system to induce oriented flight. The brain circadian clocks are located in the pars lateralis (PL) and communicate with the pars intercerebralis (PI). The PL likely play a role in the initiation of the migration syndrome. Redrawn from Ref. [30].

for sensing decreasing daylength to trigger the migratory generation. Daylight cues used for sun compass orientation are sensed by the compound eyes, in which different regions have been specialized for the detection of specific cues; sun position is sensed by the main retina, while ultraviolet plane polarized skylight is detected by the dorsal rim area [13,14]. Directional information from these cues are relayed from the eye downstream through complex circuitry to the brain, in particular the central complex region which is the proposed site for the sun compass and in which daylight cues are thought to be processed and integrated (Figure 2) [13,14]. The neuro-anatomical structures and putative neural pathways for sun compass integration have been described in several insect species [16], including migratory monarchs [17–19]. Time-compensated directional information from the central complex ultimately communicates with the motor system to direct flight orientation (Figure 2).

It has been recently shown that the time-compensated sun compass can be bidirectional, in which it is used by migrants on both legs of the migratory journey, with sun compass directionality adjusted towards the appropriate seasonal heading. Migrant monarchs use their time-compensated

sun compass throughout their migratory journey — the sun compass is initially tuned southwards during the fall migration and is then recalibrated to have a northwards bearing during the spring remigration [5**]. Coldness, temperature conditions consistent with those found at the overwintering high altitude coniferous forests during the overwintering period, is the environmental trigger that underlies the switch in orientation direction in monarchs [5**]. It still remains to be determined, however, what minimum degree and duration of coldness are needed to recalibrate the time-compensated sun compass of monarchs.

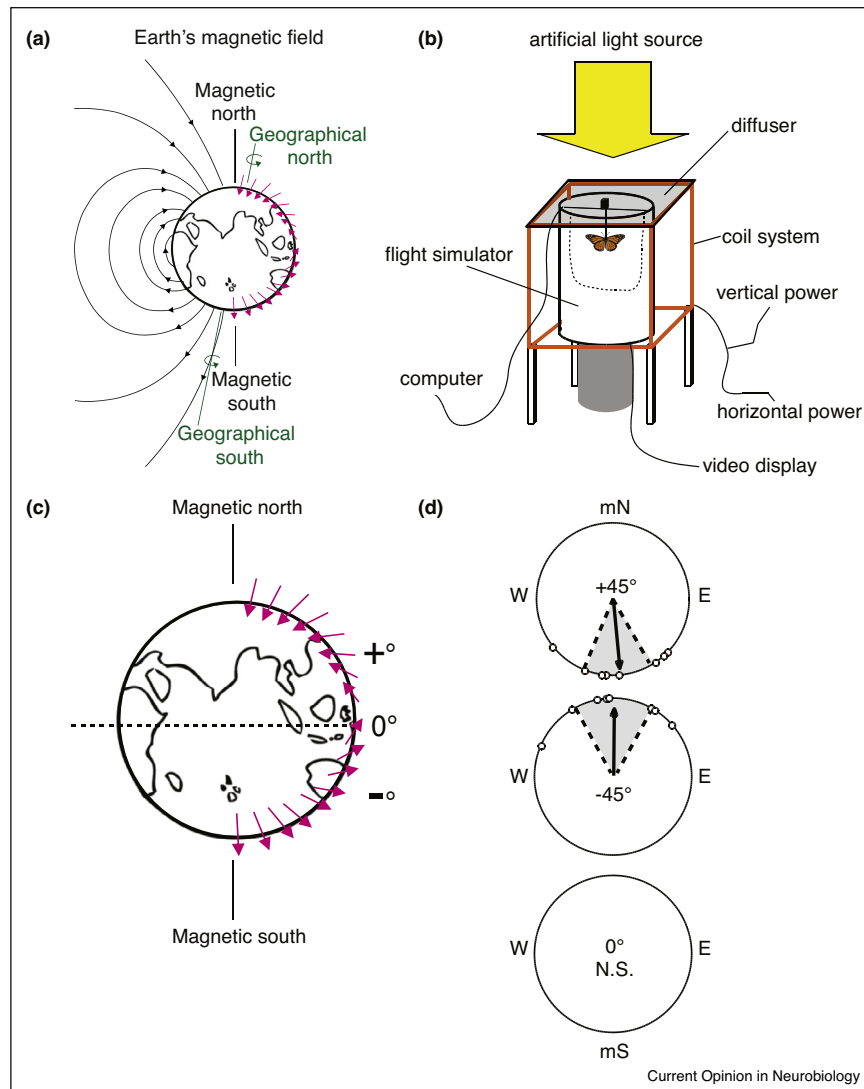
Once having a re-tuned sun compass after appropriate cold exposure, we propose that increasing daylength initiates the actual departure of remigrants northward from their overwintering sites (Figure 1). Interestingly, the effect of coldness on the time-compensated sun compass of monarchs occurs in parallel with the vernalization of milkweed (genus *Asclepias*) [20,21], the obligate food source of monarch larvae. Here, a period of cold temperatures in the late fall and winter serves to effectuate appropriate responses by milkweed towards conditions in the following spring. This necessary effect of coldness on both monarchs and milkweed suggests that the recalibration of the monarch sun compass, and the initiation of the return northwards by increasing photoperiod, have likely co-evolved with the timing and onset of newly emerged milkweed in the spring (Figure 1). In this way, remigrant females can oviposit on freshly emerged milkweed at the appropriate time and place. This monarch-milkweed synchrony is critical for the subsequent northward perpetuation of spring and summer generations to repopulate monarchs throughout their range and complete the migration cycle (Figure 1a, right).

As direct sun cues are unavailable to nocturnal lepidopteran migrants, individuals may rely on lunar or stellar compasses for orientation information [14]. The use of lunar or stellar cues by nocturnal migrants is possible, since nocturnal insects, including lepidopterans (moths), have been shown to have surprisingly acute visual capabilities [22*]. Thus one way insects can detect nighttime cues, such as moonlight, is via their compound eyes, in which photoreceptor cells mediate moonlight perception [23]. Moreover, nocturnal insects have been shown to use night sky cues, such as the faint light provided by the Milky Way, for orientation [24*]. Further work is needed to elucidate the likely celestial compass mechanisms utilized by nocturnal migratory lepidopterans.

Magnetic compass

Similar to other migratory taxa [25,26], a magnetic compass is another orientation tool that is used by migratory lepidopterans, in which individuals use aspects of the Earth's magnetic field (polarity, inclination angle, intensity) as sources of directional information (Figure 3a).

Figure 3



Fall migrant monarch butterflies possess an inclination-based magnetic compass [7**]. **(a)** Geomagnetic components used for directionality. The magnetic field of the Earth can be viewed as a large magnet with the north and south polar components. (Left side) Earth's magnetic field originates from the Southern hemisphere, encircles the planet, and then re-enters in the Northern hemisphere. (Right side) The intersection of magnetic field lines with the horizontal surface of the earth provides the inclination angle of magnetic dip; there is a gradual change in the inclination angle and intensity of the Earth's magnetic field from each pole to the equator (represented by the angle and length of the magenta arrowed lines). Modified from Ref. [14]. **(b)** A magnetic compass sense by monarchs was examined in flight simulator orientation trials, in which the orientation direction of tethered flying monarchs (monarch in cut-away view of flight simulator) was monitored by computer. Individual monarchs were tested under diffuse light conditions within a magnetic coil system that allowed for the presentation of a generated magnetic field in which the relevant magnetic field parameters (polarity, inclination, and intensity) could be manipulated during the flight trials. Modified from Ref. [7**]. **(c)** Expanded view of the latitudinally positioned inclination angles. The angle ranges from 0° at the equator (dashed line) to 90° at the magnetic poles. Inclination angles in the Northern hemisphere are designated as positive, with a +90° at the North magnetic pole, while inclination angles in the Southern hemisphere are designated negative, with a -90° at the South magnetic pole. As inclination angles vary with latitude, an inclination-based magnetic compass provides monarchs the ability to approximate their latitudinal position on Earth. **(d)** Orientation behavior of monarchs is consistent with an inclination-based magnetic compass [7**]. Orientation of monarchs to different artificially generated inclination angles with the polar components (north-south magnetic axis) unchanged. (Top) Monarchs orient equatorward away from the North magnetic pole when tested under positive inclination angle conditions, consistent with a bearing that will bring them towards their overwintering sites in Mexico. (Middle) Monarchs flew northward when the inclination angle of the generated magnetic field was reversed. Reversing the inclination angle alters the directional information provided by the inclination angle (180° shift) and is a true test for the existence of an inclination compass [7**]. (Lower) Monarchs tested under 0° inclination angle conditions, as though they were flying at the equator, flew in a non-directional manner, suggesting that the detection of an inclination angle is necessary for proper directionality. Despite being exposed to consistent polarity components during these conditions, monarchs flew in a disoriented manner, supporting the notion that the inclination magnetic compass is the dominant magnetic sense in monarchs. For each circlegram, a single dot represents the orientation of an individual monarch that flew continuously for 5 min (assessed by video monitoring); arrows indicate mean group orientation; shaded area is 95% confidence interval; mN is magnetic north. Modified from Ref. [7**].

Although earlier work provided conflicting evidence for and against the use of a magnetic compass in fall monarchs [13], current work has demonstrated that individuals can use an Earth-strength, light-dependent inclination magnetic compass, to maintain the proper southwards fall migratory bearing in the absence of directional daylight cues (Figure 3) [7**]. An inclination magnetic compass uses the inclination angle of the Earth's magnetic field to guide latitudinal movement (see Figure 3). The exposure of monarchs to ultraviolet-A/blue light between 380 and 420 nm is necessary for a functioning inclination compass, a light requirement that was not considered in past studies [7**,13]. This light requirement supports a light-sensitive, chemical-based mechanism for magnetoreception in monarchs [7**]. Here, the magnetic compass sense is likely activated via photochemical reactions involving cryptochrome (CRY) proteins, in which the occurrence of these reactions requires specific wavelengths of light (see below) [27].

The idea that migrant insects, such as the monarch, possess a map sense along with having different compass senses is unclear [13], especially given preliminary results from longitudinal displacement studies [6]. Future experiments testing the use of the magnetic compass as part of a geomagnetic map sense in monarchs, as seen in other animals that use an inclination magnetic compass [28,29], can help resolve this issue. If monarchs do possess a geomagnetic map sense, it may help answer the long-standing question of how migrants find their overwintering sites, a handful of oyamel fir groves in a small mountainous area of central Mexico, year after year. Similar to the geomagnetic map sense of other animals that can be imprinted at juvenile stages [29], the map sense of migrant monarchs that is involved in finding the overwintering sites is likely encoded genetically as part of their migratory syndrome [30,31**], as individuals migrating to Mexico in the fall are on their maiden voyage.

Wind-based movement

Certain migratory lepidopteran species, including monarchs, have been observed to facilitate their migration via a windborne movement strategy [9,12,13]. For example, these migrants will fly at high-altitudes and select to ride high-speed winds moving in the appropriate seasonal migratory heading [9,12,13,32,33]. Moreover, if winds become unfavorable during flight and are no longer consistent with preferred orientation directions, individuals have been shown to actively compensate their flight behavior, for example, adopt flight headings to compensate for crosswind drift, to stay on course [10,34].

Integration of compass systems

Despite our current understanding of these separate orientation mechanisms used by migratory lepidopterans, there still remains a paucity of work that examines

the potentially important relationships between these different orientation processes. It has been proposed that the magnetic compass serves as an important backup orientation mechanism to the primary time-compensated sun compass, when directional daylight cues are unavailable to monarchs, such as on overcast days when the sun and blue sky are obscured from view [7**]. Clock-shift experiments testing aspects of the sun compass used by monarchs supports the dominant position of the sun compass and the secondary nature of the magnetic compass in the hierarchy of orientation tools used by monarchs. Clock-shifted migrants will fly in the predicted, adjusted orientation direction during clear, sunny skies, even when the Earth's magnetic field is perceivable and remains unmanipulated [2–4,5**]. During overcast evenings, the magnetic compass may also serve as a backup mechanism for nocturnal lepidopteran migrants that use night sky cues for orientation.

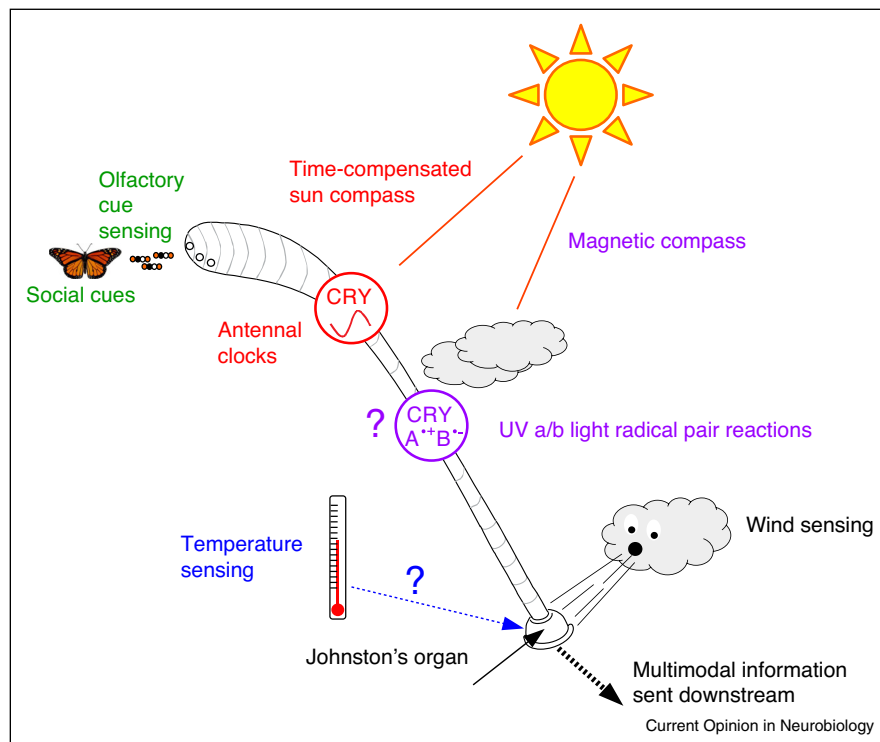
In addition to serving as a backup mechanism, the magnetic compass may also serve as a key calibrator of the sun compass in monarchs, where it can augment time-compensated sun compass usage. The magnetic compass may calibrate for increased accuracy in the time-compensated sun compass of monarchs at specific times of the day in relation to the individual's current location along the migratory route, such as before the current day's (i.e. at sunrise) or the next day's (i.e. at sunset) bout of migratory flight. A similar mediating effect of the magnetic compass may occur in nocturnal migrants that use lunar or stellar compasses for orientation as a major mechanism for directionality.

Critical role of the antennae in orientation

The antennae, multimodal sensory organs that perceive various cues, are common to all aspects of the orientation and sensory mechanisms described previously (Figure 4). As already mentioned, the antennae are necessary for a functioning time-compensated sun compass (Figure 2) [3,4,5**]. The antennae are paired organs that contain the light-entrained circadian clocks that comprise the relevant timing mechanism for the time compensation of integrated skylight cues in the sun compass [3,4,5**]. As part of a distinct circadian clock mechanism, monarchs possess two types of CRY proteins, a *Drosophila*-like type 1 CRY (dpCRY1) and a vertebrate-like type 2 CRY (dpCRY2) [13,14]. These are two important circadian clock molecules, because dpCRY1 functions as a circadian photoreceptor for light entrainment, and dpCRY2 functions as the major transcriptional repressor of the clockwork feedback loop of the monarch circadian clock [13,14].

Recent results support the idea that the monarch antennae contain magnetosensors, with antennal dpCRYs the likely molecular candidates involved in light-dependent magnetoreception (Figure 4) [7**]. This is consistent with

Figure 4



The monarch antennae are multimodal sensors of orientation information during long-distance migration. The antennae are involved in sensing potential migration-relevant olfactory cues derived from social interactions with conspecific migrants (orange). Cryptochrome (CRY) proteins in the antennae have a dual role as they are involved in time-compensated sun compass use (red) and likely in magnetic compass use (purple). The antennae are potentially the sensors of coldness, the environmental cue that recalibrates the time-compensated sun compass in migrant monarchs (blue). The antennae also contain Johnston's organ, the organ in the pedicel that senses various forms of migration-relevant mechanosensory stimuli such as wind (black). The placement of the cue symbols on the antenna are arbitrary and do not denote regionalization of the antenna in which these cues are sensed.

the light-dependent activity of antennal dpCRY1 as part of the monarch circadian clock that crucially underlies time-compensated sun compass use, a phenomenon also observed using orientation trials in which the antennae were painted either black (to block clock light entrainment) or clear (as a control) [3,4,5^{**}]. Moreover, corroborating the role of monarch CRYs in magnetosensation is the finding that dpCRY1 and dpCRY2 can each rescue magnetosensitivity in a light-dependent manner when expressed as transgenes in CRY-deficient *Drosophila* [13,14]. With a sequenced genome [30], along with viable genetic approaches for targeting specific genes [35^{*}], the stage is set in monarchs for exciting and timely experiments that can genetically evaluate and verify the role of the dpCRYs and the mechanism of action in the magnetic compass.

The antennae are also likely involved in wind-assisted lepidopteran migration (Figure 4), as the antennae can serve as mechanoreceptors for wind detection as seen in several insect species [36,37]. In this case, Johnston's organ, a chordotonal organ found in the pedicel of the

antenna (second antennal segment) of insects, is responsible for detecting mechanical stimuli [38,39].

Although the mechanisms involved in sensing coldness for sun compass recalibration remain unknown in monarchs, one possibility is that coldness, and temperature in general, is also sensed by the antennae (Figure 4). In *Drosophila*, the antennae are important temperature-sensing organs that form part of the neural circuits responsible for thermosensation, as they contain temperature-sensitive transient receptor potential channels (thermoTRP) channels. ThermoTRP channels are found in thermosensory antennal neurons that detect a wide range of temperature conditions and are involved in mediating behavior [40,41].

Given their role in detecting chemosensory cues, such as volatile species-specific pheromones, migration-relevant olfactory cues would also be sensed by the antennae during social interactions such as those that might occur during migratory flight or within roosts (Figure 4). Although much of the work on olfaction in lepidopterans

has been done with moths, butterflies, despite being diurnal and thought of to not rely on olfactory cues, have been recently shown to have an olfactory system that is similar in many respects to that of moths, albeit with a reduced number of olfactory sensilla and olfactory receptor neurons [30,42].

The central complex region, the already highlighted site of the sun compass that integrates eye-sensed skylight cues and is time-compensated by antennal clocks (Figure 2), is also the potential location for the integration of different orientation stimuli [16]. The pathways that connect the antennae to the central complex have yet to be completely determined; directional information from the various compass senses is likely transmitted in yet to be defined neural pathways or neuronal-independent pathways involving diffusible molecules [4,13].

Environmental pollution

Although not fully understood, environmental conditions may have a significant effect on the usage of the orientation mechanisms in migrant lepidopterans, thereby making it possible that current threats to the environment can adversely affect migration in these species. For example, as coldness is necessary for sun compass recalibration in monarchs, global warming and overall climate change may disrupt the migratory cycle in this species [5**]. Changes in global wind patterns due to climate change [43], for example, stronger winds that may carry migrants too far or weaker winds that may not carry individuals far enough, can hamper windborne migratory strategies.

Similarly, human-induced noise and pollution in relevant sensory modalities are other vulnerabilities. For example, electromagnetic noise, which can disrupt normal movement [44] or geomagnetic orientation [45*] in other species, may similarly hinder magnetic compass usage by migrant lepidopterans [7**]. Similarly, nocturnal migrants that may rely on night sky cues for orientation potentially face disruptive influences from nighttime artificial light pollution. Artificial light can significantly alter natural nighttime light regimes and patterns, on spatial and temporal scales, and across wavelengths, as well as potentially obscure celestial cues used for orientation [46,47].

The future

Recent work with migratory lepidopterans, especially with monarch butterflies, has greatly increased our knowledge of the different orientation mechanisms used by migratory species. To push the field forward, experimental approaches that examine the use of these different mechanisms together are now necessary to better understand how different directional information is used by migrants. Furthermore, recent advances such as population genetic studies [31**] have increased our

understanding of the evolutionary history of the migration and of the mechanistic aspects of the migration. The breadth of orientation mechanisms at the disposal of migrant monarchs, along with the availability of powerful nuclease-mediated genetic approaches for studying and manipulating these mechanisms [35*], make migratory monarchs an exemplary model system. Taken together, the migratory monarch rivals even the most complex of vertebrate systems, for studying orientation, long-distance migration, and environmental spatial awareness in animals.

Conflict of interest statement

Nothing declared.

Acknowledgements

We appreciate the logistical support and expertise of members of the Reppert lab during the course of some of the work mentioned here. The work described here was supported by National Institutes of Health grant GM086794 and United States Air Force Office of Scientific Research (AFOSR) grant FA9550-10-1-0480.

References and recommended reading

Papers of particular interest, published within the period of review, have been highlighted as:

- of special interest
 - of outstanding interest
1. Dingle H: *Migration: The Biology of Life on the Move*. edn 2. Oxford University Press; 2014.
This reference is an authoritative and up-to-date resource on animal migration and animal movement. It takes an integrative and taxonomically comprehensive approach on the study of migration, with an emphasis on the ecological and evolutionary consequences of this behavioral phenomenon.
 2. Zhu H, Gegear RJ, Casselman A, Kanginakudru S, Reppert SM: **Defining behavioral and molecular differences between summer and migratory monarch butterflies**. *BMC Biol* 2009, **7**:14.
 3. Merlin C, Gegear RJ, Reppert SM: **Antennal circadian clocks coordinate sun compass orientation in migratory monarch butterflies**. *Science* 2009, **325**:1700-1704.
 4. Guerra PA, Merlin C, Gegear RJ, Reppert SM: **Discordant timing between antennae disrupts sun compass orientation in migratory monarch butterflies**. *Nat Commun* 2012, **3**:958.
 5. Guerra PA, Reppert SM: **Coldness triggers northward flight in remigrant monarch butterflies**. *Curr Biol* 2013, **23**:419-423.
The finding that coldness is the environmental cue that switches the orientation of the time-compensated sun compass of monarchs solves one of the longstanding mysteries of the monarch migration. It also is one of the few studies that show how a navigational mechanism can be recalibrated by the environment. Given the current threats of global warming and climate change, the discovery from this study underscores how vulnerable migratory phenomena in animals may be as a result of changing climatic conditions.
 6. Mouritsen H, Derbyshire R, Stalleicken J, Mouritsen OØ, Frost BJ, Norris DR: **An experimental displacement and over 50 years of tag-recoveries show that monarch butterflies are not true navigators**. *Proc Natl Acad Sci U S A* 2013, **110**:7348-7353.
 7. Guerra PA, Gegear RJ, Reppert SM: **A magnetic compass aids monarch butterfly migration**. *Nat Commun* 2014, **5**:4164.
This study is the first work that demonstrates the use of an Earth-strength, inclination magnetic compass in a long-distance migratory insect. The discovery that the monarch magnetic compass is a light-dependent mechanism helps explain previous discrepancies in the literature, as well as supports the notion that the magnetic compass sense in animals involves a light-dependent, chemical mechanism. Moreover, this work sets the stage for future work where the role of multiple compass senses, as well as a geomagnetic map sense, can be studied in long-distance migratory animals.

8. Nesbit RL, Hill JK, Woivod IP, Sivell D, Bensusan KJ, Chapman JW: **Seasonally adaptive migratory headings mediated by a sun compass in the painted lady, *Vanessa cardui***. *Anim Behav* 2009, **78**:1119-1125.
9. Stefanescu C, Páramo F, Akesson S, Alarcón M, Ávila A, Brereton T, Carnicer J, Cassar LF, Fox R, Heliölä *et al.*: **Multi-generational long-distance migration of insects: studying the painted lady butterfly in the Western Palaearctic**. *Ecography* 2013, **36**:474-486.
10. Chapman JW, Reynolds DR, Mouritsen H, Hill JK, Riley JR, Sivell D, Smith AD, Woivod IP: **Wind selection and drift compensation optimize migratory pathways in a high-flying moth**. *Curr Biol* 2008, **18**:514-518.
11. Alerstam T, Chapman JW, Bäckman J, Smith AD, Karlsson H, Nilsson C, Reynolds DR, Klaassen RHG, Hill JK: **Convergent patterns of long-distance nocturnal migration in noctuid moths and passerine birds**. *Proc R Soc B* 2011, **278**:3074-3081.
12. Chapman JW, Lim KS, Reynolds DR: **The significance of midsummer movements of *Autographa gamma*: implications for a mechanistic understanding of orientation behavior in a migrant moth**. *Curr Zool* 2013, **59**:360-370.
13. Reppert SM, Gegear RJ, Merlin C: **Navigational mechanisms of migrating monarch butterflies**. *Trends Neurosci* 2010, **33**:399-406.
14. Merlin C, Heinze S, Reppert SM: **Unraveling navigational mechanisms in migratory insects**. *Curr Opin Neurobiol* 2012, **22**:353-361.
15. Guilford T, Taylor GK: **The sun compass revisited**. *Anim Behav* 2014, **97**:135-143.
 This paper serves as a useful summary and framework of how the sun compass can be used by animals for orientation, and highlights that sun compass usage need not always be time-compensated. In addition, it highlights other uses for solar information that can be extremely relevant to migrating individuals, such as the sun's time-dependent effect on the visual appearance and recognition of landmarks used for orientation.
16. el Jundi B, Pfeiffer K, Heinze S, Homberg U: **Integration of polarization and chromatic cues in the insect sky compass**. *J Comp Physiol A* 2014, **200**:575-589.
17. Heinze S, Reppert SM: **Sun compass integration of skylight cues in migratory monarch butterflies**. *Neuron* 2011, **69**:345-358.
18. Heinze S, Reppert SM: **Anatomical basis of sun compass navigation. I: The general layout of the monarch butterfly brain**. *J Comp Neurol* 2012, **520**:1599-1628.
19. Heinze S, Florman J, Asokaraj S, el Jundi B, Reppert SM: **Anatomical basis of sun compass navigation. II: The neuronal composition of the central complex of the monarch butterfly**. *J Comp Neurol* 2013, **521**:267-298.
20. Amasino R: **Vernalization, competence, and the epigenetic memory of winter**. *Plant Cell* 2004, **16**:2553-2559.
21. Song J, Angel A, Howard M, Dean C: **Vernalization – a cold-induced epigenetic switch**. *J Cell Sci* 2012, **125**:3723-3731.
22. Warrant E, Oskarsson M, Malm H: **The remarkable visual abilities of nocturnal insects: neural principles and bioinspired night-vision algorithms**. *Proc IEEE* 2014, **102**:1411-1426.
 This paper describes the visual capabilities of nocturnal insects, a sensory capacity that is typically thought to be less functional in these animals, in comparison to that of their diurnal counterparts. By highlighting potential mechanisms that underlie night-vision in insects, in conjunction with experimental results from work based on the capacities of these nocturnal insects, the authors show how visual sensing can operate to a high-degree, even under suboptimal sensory conditions.
23. Schlichting M, Grebler R, Peschel N, Yoshii T, Helfrich-Förster C: **Moonlight detection by *Drosophila*'s endogenous clock depends on multiple photopigments in the compound eyes**. *J Biol Rhythms* 2014, **29**:75-86.
24. Dacke M, Baird E, Byrne M, Scholtz CH, Warrant WJ: **Dung beetles use the Milky Way for orientation**. *Curr Biol* 2013, **23**:298-300.
 This paper is the first to demonstrate that insects can use stellar sky cues for orientation. Using natural (open, outdoor field) and artificial (planetarium domed ceiling) night sky conditions, the authors elegantly show that dung beetles use the Milky Way as a means for orientation, during dung ball-rolling behavior.
25. Lohmann KJ: **Q&A: animal behavior: magnetic-field perception**. *Nature* 2010, **464**:1140-1142.
26. Lohmann KJ, Putman NF, Lohmann CMF: **The magnetic map of hatchling loggerhead sea turtles**. *Curr Opin Neurobiol* 2012, **22**:336-342.
27. Ritz T, Ahmad M, Mouritsen H, Wiltschko R, Wiltschko W: **Photoreceptor-based magnetoreception: optimal design of receptor molecules, cells, and neuronal processing**. *J R Soc Interface* 2010, **7**:S135-S146.
28. Putman NF, Endres CS, Lohmann CMF, Lohmann KJ: **Longitude perception and bicoordinate magnetic maps in sea turtles**. *Curr Biol* 2011, **21**:463-466.
29. Putman NF, Scanian MM, Billman EJ, O'Neill JP, Couture RB, Quinn TP, Lohmann KJ, Noakes DLG: **An inherited magnetic map guides ocean navigation in juvenile Pacific salmon**. *Curr Biol* 2014, **24**:446-450.
30. Zhan S, Merlin C, Boore JL, Reppert SM: **The monarch butterfly genome yields insights into long-distance migration**. *Cell* 2011, **147**:1171-1185.
31. Zhan S, Zhang W, Niitepöld K, Hsu J, Haeger F, Zalucki MP, Altizer S, de Roode JC, Reppert SM, Kronforst MR: **The genetics of monarch butterfly migration and warning coloration**. *Nature* 2014, **514**:317-321.
 This exceptional paper traces the evolutionary history of the monarch, as well as identifies important signatures of selection for migration at the genetic level. The results show that the migratory North American monarch is the ancestral state, and monarchs later dispersed from North America to other parts of the world. Surprisingly, the strongest signatures of migration were genes associated with flight muscle function.
32. Feng H, Wu X, Wu B, Wu K: **Seasonal migration of *Helicoverpa armigera* (Lepidoptera: Noctuidae) over the Bohai sea**. *J Econ Entomol* 2009, **102**:95-104.
33. Tojo S, Ryuda M, Fukuda T, Matsunaga T, Choi D, Otuka A: **Overseas migration of the common cutworm, *Spodoptera litura* (Lepidoptera: Noctuidae), from May to mid-July in East Asia**. *Appl Entomol Zool* 2013, **48**:131-140.
34. Srygley RB, Oliveira EG: **Sun compass and wind drift compensation in migrating butterflies**. *J Navig* 2001, **54**:405-417.
35. Merlin C, Beaver LE, Taylor OR, Wolfe SA, Reppert SM: **Efficient targeted mutagenesis in the monarch butterfly using zinc finger nucleases**. *Genome Res* 2013, **23**:169-180.
 This paper describes the development of a highly efficient gene-targeting technique, based on nuclease technology, for studying the genetic basis of migratory behavior. The described approach can be applied to a multitude of different insect systems, which can facilitate a greater understanding of the genetic basis of a large variety of biological phenomenon.
36. Reynolds AM, Reynolds DR, Smith AD, Chapman JW: **Orientation cues for high-flying nocturnal insect migrants: do turbulence-induced temperature and velocity fluctuations indicate the mean wind flow?** *PLoS ONE* 2010, **5**:e15758.
37. Fuller SB, Straw AD, Peek MY, Murray RM, Dickinson MH: **Flying *Drosophila* stabilize their vision-based velocity controller by sensing wind with their antennae**. *Proc Natl Acad Sci U S A* 2014, **111**:E1182-E1191.
38. Matsuo E, Kamikouchi A: **Neuronal encoding of sound, gravity, and wind in the fruit fly**. *J Comp Physiol A* 2013, **199**:253-262.
39. Dieudonné A, Daniel TL, Sane SP: **Encoding properties of the mechanosensory neurons in the Johnston's organ of the hawk moth, *Manduca sexta***. *J Exp Biol* 2014, **217**:3045-3056.
40. Gallio M, Ofstad TA, Macpherson LJ, Wang JW, Zuker CS: **The coding of temperature in the *Drosophila* brain**. *Cell* 2011, **144**:614-624.

41. Tang X, Platt MD, Lagnese CM, Leslie JR, Hamada FN: **Temperature integration at the AC thermosensory neurons in *Drosophila***. *J Neurosci* 2013, **33**:894-901.
42. Carlsson MA, Schäpers A, Nässel DR, Janz N: **Organization of the olfactory system of nymphalidae butterflies**. *Chem Senses* 2013, **38**:355-367.
43. Sydeman WJ, Garcia-Reyes M, Schoeman DS, Rykaczewski RR, Thompson SA, Black BA, Bograd SJ: **Climate change and wind intensification in coastal upwelling ecosystems**. *Science* 2014, **345**:77-80.
44. Fedele G, Green EW, Rosato E, Kyriacou CP: **An electromagnetic field disrupts negative geotaxis in *Drosophila* via a CRY-dependent pathway**. *Nat Commun* 2014, **5**:4391.
45. Engels S, Schneider NL, Lefeldt N, Hein CM, Zapka M, Michalik A, Elbers D, Kittel A, Hore PJ, Mouritsen H: **Anthropogenic**

electromagnetic noise disrupts magnetic compass orientation in a migratory bird. *Nature* 2014, **509**:353-356.

This paper demonstrates how weak electromagnetic fields produced by daily human activity can be detrimental and disruptive to the use of orientation mechanisms by migratory animals. Not only do the authors provide further evidence describing the mechanism of magnetic compass use by migrants, it underscores the vulnerability of animal migratory phenomenon at a sensory level.

46. Gaston KJ, Bennie J, Davies TW, Hopkins J: **The ecological impacts of nighttime light pollution: a mechanistic appraisal**. *Biol Rev* 2013, **88**:912-927.
47. Gaston KJ, Duffy JP, Gaston S, Bennie J, Davies TW: **Human alteration of natural light cycles: causes and ecological consequences**. *Oecologia* 2014, **176**:917-931.