Dispatches

Animal Behaviour: Monarchs Catch a Cold

The spectacular migration of the Monarch from northeastern America to its overwintering grounds in Mexico requires the butterfly to set its time-compensated compass south in the autumn, then north in the spring for its return home. The stimulus responsible for compass resetting has been identified as a reduction in temperature.

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One of the most impressive sights in the natural world is the autumn migration of the Monarch butterflies, *Danaus plexippus*, in their tens of millions, from their summer homes in the eastern USA and southern Canada to their overwintering grounds in the Michoacá mountains of central Mexico. Some of these Monarchs travel up to 4,000 km, and for each individual this is the one and only time that they will perform this heroic feat. Once they arrive in Mexico, they remain there until early spring, they mate and start their long trek home, laying eggs on the newly growing milkweed plant in the southern USA. Indeed, it takes two further generations, moving progressively northwards and tracking the emerging milkweed, before they reach their home ranges [1].

Not surprisingly, the clocklike annual regularity of this phenomenon and the navigational skill of these insects have attracted the attention of biologists who wish to study how they perform this remarkable adventure. Effort has focused on how the butterflies get to Mexico — they use a variety of skills, including a sun compass located in the brain [2,3], which is time compensated by circadian clocks located in the antennae and is used for orientation in 'restless' animals in the fall [4]. On cloudy days the butterflies can use a polarised light detector mediated by specialised UV-sensitive cells in the dorsal rim of the retina to help them orient [5]. There is also some indirect evidence that they have a magnetic sense which may provide a fall-back orientation mechanism on very densely cloudy days, probably mediated by Cryptochrome, which also doubles up as a clock molecule [6]. Needless to say, given the relevance of the clock to the butterfly's migration, the molecular clockworks have been identified and provide an interesting comparative model to flies and vertebrates [7]. In addition, the Monarch genome has recently been assembled and provides a wealth of information about the butterfly's biology and adaptations [8].

The one feature of this epic migration that has not received as much attention is the trip back home. We know that in the fall their sun compass GPS directs them southwards, but in the spring, what switches them to move northwards? Steven Reppert and Patrick Guerra at UMass Medical School report in a recent issue of *Current Biology* [9] that temperature change is the key variable that switches the sun compass direction from south to north. In spring, they collected 're-migrant' butterflies that have survived both the migration and the overwintering in Mexico and have managed to get as far as Texas on the first leg of the return trip. Needless to say these older individuals look pretty scruffy and battered (Figure 1) but in orientation tests, their compass robustly tells them to 'go north'. When the circadian clock of re-migrants is phase shifted by 6 hours using delayed light–dark (LD) cycles, the predictable change in direction is obtained, revealing the role of the circadian mechanism in directionality. These types of experiments have been done before in the fall migrants in Massachusetts, with similar results, in that the normal southwards orientation can be altered by phase shifting the LD cycle. In other words, whether you are a fall migrant, or a Texan spring re-migrant, your time-compensated sun compass works in the same way, a conclusion buttressed by the finding that removal of the antennae in both groups disrupts orientation.

To try and discover how this bidirectional compass switches direction, Guerra and Reppert took fall migrants in New England during autumn, and subjected them for 24 days to the type of overwintering conditions that they would find in Mexico, which meant gentle changes in photoperiod but rather colder daily temperature cycles. Photoperiodic changes are well known in the insect world to trigger overwintering responses [10]. When the fall migrants were examined for their orientation, they now pointed north in the same direction as the Texan re-migrants. However, when this experiment was repeated but photoperiod was held constant, the butterflies still migrated north, showing that photoperiodic changes were not causing the compass switch. The orientation of these cold-treated fall migrants was also susceptible to a delayed LD cycle revealing that the time-compensated compass had also shifted its direction.

These results suggest that an annual timer is not responsible for the switch in direction northwards, which was probably the first hypothesis on the authors' minds. This was further reinforced by taking fall butterflies from roosts in the southern USA in October and maintaining them until the following spring in 'warm', fall-like conditions. These aged individuals that had not been subjected to any cold burst maintained their normal southwards orientation.

These experiments reveal that a reduction in temperature is responsible for the directional switch in the Monarch's sun compass. Consequently, to avoid the severe cold of northern winters, the Monarchs escape to warmer Mexico, yet it is the gentler cold of early spring in Mexico that provides the signal for returning home. How this is effected at the molecular level is unknown. An educated guess might focus on clock molecules because changes in direction can be mediated by simply phase-shifting the LD cycle which entrains the clock. In flies, seasonal changes in circadian phenotypes can be mediated by temperature-dependent splicing of *period* mRNA [11] or alternative translational starts in *timeless* mRNA

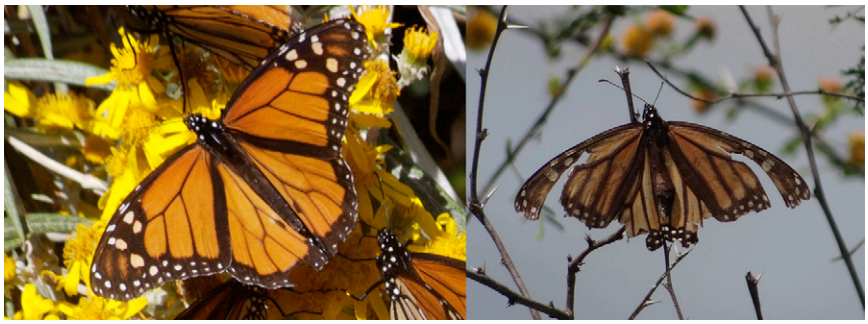

Figure 1. Migrant and re-migrant Monarchs.

Left, fall migrant Monarch. Right, re-migrant from Texas; note the damaged wings and generally poor condition of this older butterfly. (Photos courtesy of Monarch Watch and the Aschens.)

[12], and cold can change RNA editing patterns in ion channel genes [13]. One could imagine a situation where a temperature-dependent post-transcriptional event might alter a clock isoform and/or a downstream effector that interacts with the time-compensated compass in the brain. Another obvious avenue of investigation would be to identify the temperature sensors, and trp channels might be a first place to look [14], but so might the orthologous sensors that convey temperature to the fly brain clock, such as nocte [15]. No doubt the molecular answer to how the compass switches direction will provide a further fascinating glimpse into the mechanisms that drive migration.

Finally, these findings expose the vulnerability of the Monarch's life cycle to temperature change. While the authors have not investigated how brief a period of cold, nor the maximum and minimum temperatures that might be required to effect a south-to-north directional switch, it could be that any prolonged unseasonal cold episodes during the autumn in New England could have quite serious ramifications for those migrants beginning their journey from there. Furthermore, warmer temperatures at the overwintering sites could prevent or significantly modify the return trip north with equally severe costs. Finally, in January 2002, 250 million Monarchs, ~80% of the population in the El Rosario forest sanctuary, were killed because of cold weather, the effects of which were amplified by illegal logging, which allowed the cold air to penetrate more deeply into the forest [16]. Consequently, the work of Guerra and Reppert also highlights the delicate nature of this most spectacular of natural phenomena and its sensitivity not only to human encroachment but also to climate change [17].

References

1. Brower, L.P. (1995). Understanding and misunderstanding the migration of the monarch butterfly (Nymphalidae) in North America, 1857–1995. J. Lepidopt. Soc. *49*, 304–385.
2. Heinze, S., Florman, J., Asokaraj, S., El Jundi, B., and Reppert, S.M. (2013). Anatomical basis of sun compass navigation II: the neuronal composition of the central complex of the monarch butterfly. J. Comp. Neurol. *521*, 267–298.
3. Heinze, S., and Reppert, S.M. (2011). Sun compass integration of skylight cues in migratory monarch butterflies. Neuron *69*, 345–358.
4. Merlin, C., Gegear, R.J., and Reppert, S.M. (2009). Antennal circadian clocks coordinate sun compass orientation in migratory monarch butterflies. Science *325*, 1700–1704.
5. Reppert, S.M., Zhu, H., and White, R.H. (2004). Polarized light helps monarch butterflies navigate. Curr. Biol. *14*, 155–158.
6. Gegear, R.J., Foley, L.E., Casselman, A., and Reppert, S.M. (2010). Animal cryptochromes mediate magnetoreception by an unconventional photochemical mechanism. Nature *463*, 804–807.
7. Zhu, H., Sauman, I., Yuan, Q., Casselman, A., Emery-Le, M., Emery, P., and Reppert, S.M. (2008). Cryptochromes define a novel circadian clock mechanism in monarch butterflies that may underlie sun compass navigation. PLoS Biol. *6*, e4.
8. Zhan, S., Merlin, C., Boore, J.L., and Reppert, S.M. (2011). The monarch butterfly genome yields insights into long-distance migration. Cell *147*, 1171–1185.
9. Guerra, P., and Reppert, S.M. (2013). Coldness triggers northward flight in remigrant monarch butterflies. Curr. Biol. *23*, 419–423.
10. Schiesari, L., Kyriacou, C.P., and Costa, R. (2011). The hormonal and circadian basis for insect photoperiodic timing. FEBS Lett. *585*, 1450–1460.
11. Low, K.H., Lim, C., Ko, H.W., and Edery, I. (2008). Natural variation in the splice site strength of a clock gene and species-specific thermal adaptation. Neuron *60*, 1054–1067.
12. Sandrelli, F., Tauber, E., Pegoraro, M., Mazzotta, G., Cisotto, P., Landskron, J., Stanewsky, R., Piccin, A., Rosato, E., Zordan, M., *et al*. (2007). A molecular basis for natural selection at the timeless locus in Drosophila melanogaster. Science *316*, 1898–1900.
13. Garrett, S., and Rosenthal, J.J. (2012). RNA editing underlies temperature adaptation in K+ channels from polar octopuses. Science *335*, 848–851.
14. Kwon, Y., Shim, H.S., Wang, X., and Montell, C. (2008). Control of thermotactic behavior via coupling of a TRP channel to a phospholipase C signaling cascade. Nat Neurosci. *11*, 871–873.
15. Sehadova, H., Glaser, F.T., Gentile, C., Simoni, A., Giesecke, A., Albert, J.T., and Stanewsky, R. (2009). Temperature entrainment of Drosophila's circadian clock involves the gene nocte and signaling from peripheral sensory tissues to the brain. Neuron *64*, 251–266.
16. http://windstar.org/uncategorized/as-butterflies-die-so-goes-a-way-of-life/, http://monarchwatch.org/blog/2010/01/monarch-population-status-6/.
17. Brower, L.P., Taylor, O.R., Williams, E.H., Slayback, D.A., Zubieta, R.R., and Ramirez, M.I. (2012). Decline of monarch butterflies overwintering in Mexico: is the migratory phenomenon at risk? Insect Cons. Diver. *5*, 95–100.

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Chromosome Segregation: Disarming the Protector

One of the key features of meiosis is that shugoshin in complex with protein phosphatase 2A (PP2A) protects centromeric cohesin during meiosis I, but not during meiosis II. A new model suggests that a PP2A inhibitor mediates deprotection of centromeric cohesin during meiosis II.

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The cohesin complex mediates cohesion between sister chromatids during both mitosis and meiosis. According to the 'ring model', cohesin mediates sister chromatid cohesion by topologically entrapping sister chromatids. At the onset of anaphase, cohesin is cleaved by a protease called