

Compass systems

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Abstract Three compass systems based on global cues known to exist in migrating birds are reviewed. Two of these systems are based on celestial cues, a time-dependent sun compass and time-independent, i.e. not involving the internal clock, star compass. The third system is the magnetic compass, based on a separate sensory modality, which currently attracts much attention from behavioural ecologists, physiologists and physicists. The complex pattern of hierarchy and interactions between these compass systems is briefly discussed. It is argued that rules of integration of information from different compass cues are likely dependent on ecological and geographic conditions the birds are facing during their journey, so it is likely that no single set of rules is shared by all migrating birds.

Keywords Orientation · Birds · Compass system · Celestial compass · Magnetic compass

Introduction

To select and maintain the direction of their movement on regional and continental scales, migrating birds need to use compass systems independent on landscape or other local

cues, based on the global sources of information. It has even been suggested that compass systems based on global cues are required for any animal moving across complex environments, not necessarily on a very large spatial scale (Finkelstein et al. 2016). Several possibilities have been tested, but three cues stand out. The use of solar compass (Schmidt-Koenig 1958), star compass (Emlen 1967a, b) and magnetic compass (Wiltschko and Wiltschko 1972) is supported by solid evidence, has been independently confirmed by many authors, and may be treated as established fact rather than hypotheses.

Of these three compass systems, most attention in the current years has been devoted to the magnetic compass. There are several reasons for this. First, magnetoreception is a sensory modality apparently not present in humans, and thus it fascinates human researchers. Second, the sensory basis of compass magnetoreception in birds is far from being fully understood, but is probably based on non-trivial physics (Ritz et al. 2000; Hore and Mouritsen 2016) and belongs in the emerging field of quantum biology (Hiscock et al. 2016). The avian magnetic compass currently attracts much attention and has been covered in several excellent recent reviews (Wiltschko and Wiltschko 2015; Mouritsen 2015; Hore and Mouritsen 2016); therefore, this contribution is more focused on the two other compass systems, the solar and the stellar ones, and on the intriguing topic of compass systems interaction and hierarchy.

Magnetic compass

A role for the geomagnetic field in guiding avian migration had been suggested as early as the nineteenth century (von Middendorff 1855), but it was not until the 1960s that the use of magnetic compass by migrating songbirds

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was experimentally shown (Merkel and Wiltschko 1965; Wiltschko 1968), and not until the 1970s that animal orientation community finally endorsed this idea and agreed with its early proponents (Wiltschko and Wiltschko 1972; Emlen et al. 1976). Behavioural experiments have shown that the avian magnetic compass has several important properties: it is based on the inclination angle of the magnetic field lines rather than on the polarity of the field (Wiltschko and Wiltschko 1972), it is light dependent (it should be kept in mind that the light intensity of a clear moonless night is sufficient for its work; Wiltschko et al. 1993, 2000, 2001a; Wiltschko and Wiltschko 2001) and it is disrupted by radio-frequency oscillating magnetic fields (Ritz et al. 2004; Thalau et al. 2005; Kavokin et al. 2014; Engels et al. 2014; but see Schwarze et al. 2016a). These features of the magnetic compass narrow down the spectre of possible biophysical mechanisms underlying its function. The leading concept is currently the radical pair model which suggests that the magnetic compass sense of migratory birds is based on reversible light-dependent chemical reactions. The yield of products of these reactions depends on the alignment of the photoreceptor molecule to the magnetic field. The idea was suggested in the 1970s (Schulten et al. 1978) and gained popularity when cryptochromes were proposed as possible magnetosensory molecules (Ritz et al. 2000), as they are the only known molecules in vertebrates that form radicals after photon absorption. The ability to absorb light is facilitated by the presence of flavin (in the form of flavin adenine dinucleotide cofactor) and pterin. Cryptochromes are known to play a key role in generating and maintaining circadian rhythms in plants and animals (Chaves et al. 2011). Furthermore, it has been shown that magnetic compass information is processed in the thalamofugal visual pathway (Heyers et al. 2007) at night (Zapka et al. 2010) and that the brain area known as Cluster N is required for magnetic compass orientation in a night-migratory songbird (Mouritsen et al. 2005; Zapka et al. 2009).

How exactly cryptochromes participate in magnetoreception is not currently known; different models have been suggested (Solov'yov and Schulten 2009; Qin et al. 2015; Hore and Mouritsen 2016; Hiscock et al. 2016). It is not the aim of this review to go into much detail in this topic; for our ends and purposes, it is sufficient to accept that the avian magnetic compass exists, is vision-based, light-dependent, and based on inclination rather than polarity of the geomagnetic field. The inclination nature of the avian magnetic compass means that it is based on the axes of the magnetic lines and their inclination with respect to the surface of the Earth, or to the gravity vector (Wiltschko and Wiltschko 1972). The birds do not distinguish between magnetic north and magnetic south, but rather between the directions towards a magnetic pole and towards the magnetic equator; directions towards the north in the Northern

Hemisphere and towards the south in the Southern Hemisphere are equivalent for them. This feature of the magnetic compass also means that it cannot be used on and around the magnetic equator, because at the equator magnetic field lines are parallel to the surface of the Earth and do not provide compass information to avian migrants. Birds using a magnetic compass were shown to be randomly oriented in a magnetic field with 0° inclination (Wiltschko and Wiltschko 1972; Wiltschko 1974). The breadth of the dead zone around the magnetic equator, where migrants must rely on alternative compass systems, is probably ca. 500 km and certainly narrower than 1100 km (Schwarze et al. 2016b). When movement towards the magnetic equator and across it into the Southern Hemisphere was simulated in bobolinks *Dolichonyx oryzivorus* in a planetarium, they were able to maintain their southerly course, probably by relying on celestial cues or by reversing their magnetic migratory direction from equatorwards to polewards after experiencing zero inclination (Beason 1992). Reversing magnetic migratory direction after staying in a horizontal magnetic field without stellar cues has been shown by Wiltschko and Wiltschko (1992) in garden warblers *Sylvia borin*.

Another important feature of avian magnetic compass is that it works only within a certain functional window, i.e. in magnetic fields not much weaker or stronger than the ambient field. Increasing or decreasing the field intensity by more than 25–30% resulted in disorientation (Wiltschko 1978; Wiltschko et al. 2007). This functional window is not fixed, however, but can adjust to other intensities within hours. This ability is important for migrants, because the geomagnetic field intensity varies between ca. 60,000 nT at the magnetic poles and ca. 30,000 nT (locally down to 24,000 nT) near the magnetic equator, and long-distance migrants must thus be able to use their magnetic compass within this range of intensities.

The angular resolution of the magnetic compass is not known; it was hypothesized to be ca. 15° (Wiltschko and Nehmzow 2005). This is difficult to imagine; to be useful for long-distance migrating birds, especially those crossing ecological barriers and pinpointing rather small islands, like, e.g. Pacific golden plovers *Pluvialis fulva* migrating from Alaska to Hawaii, a compass system must have an angular resolution of at least 1° and probably better. Åkesson et al. (2001) showed that Savannah sparrows *Passerculus sandwichensis* could orient in a magnetic field with 88.6° inclination, which is only possible if they could detect the axis of the field lines with a precision better than 1.4°. Lefeldt et al. (2015) showed that migratory blackcaps *Sylvia atricapilla* can orient in a field with 85° inclination. Birds tested under these steep dip angles did not only detect that the inclination was different from 90°, but were also able to orient in an appropriate migratory direction in the

horizontal plane. This requires a much more precise determination of the magnetic field line axis (see Fig. 2 and the associated text in Lefeldt et al. 2015). Hiscock et al. (2016) recently demonstrated that a radical pair-based magnetoreception mechanism theoretically can provide a very precise magnetic compass.

It should also be mentioned that a magnetic compass has also been demonstrated in day migrants (Munro and Wiltschko 1993b; Åkesson et al. 2006) and in non-migrants like domestic chickens and zebra finches (Wiltschko et al. 2007; Voss et al. 2007), i.e. it is a general ability of many, if not all, birds.

Sun compass

The sun compass was historically one of the first mechanisms proposed (Kramer 1950). It is based on the regular apparent movement of the sun across the sky from the east to the west via south (in the Northern Hemisphere) or via north (in the Southern Hemisphere). It should be emphasized that using the sun's apparent regular movement across the sky for detecting compass direction is only possible when taking the time of the day into account, i.e. the solar compass is time dependent (Kramer and von Saint Paul 1950). In the Northern Hemisphere at solar noon the sun is in the south—but to use this information, one should know when the solar noon is. This means that the solar compass can only be used together with a well-synchronized internal clock.

Furthermore, for the efficient use of the solar compass, it is necessary to account for the non-uniform rate of solar azimuth change: just after sunrise, the sun climbs rapidly, and just before sunrise, it descends quickly, with low horizontal movement rate (azimuth change). Conversely, around solar noon, the elevation of the sun changes slowly, and the azimuth changes more rapidly than in the morning and in the evening. The form of the solar arch varies with geographic latitude and with season.

As it is not possible to experimentally manipulate the position of the sun, and a realistic imitation in a planetarium is challenging, most studies of the solar compass have been performed by clock shifting the birds, i.e. desynchronizing their internal clock. The birds are for a sufficient period of time kept in an artificial photoperiod which is shifted by several hours as compared to the natural one. When the internal clock of the birds is synchronized with this artificial photoperiod, the birds are tested outdoors in sunny weather. However, when interpreting the results of such tests, one must take the non-uniform movement of the sun into account. Earlier authors assumed that shifting the clock by 1 h results in the solar compass being offset by 15°. However, in reality in summer at 50° N, a 6-h clock

shift may offset the solar compass by as much as 130° (Wiltschko and Wiltschko 2015). Homing pigeons account for that (Wiltschko et al. 2000). When using the solar compass, pigeons consider only the azimuth of the sun and ignore its elevation above the horizon (Schmidt-Koenig 1958; Keeton 1979).

Most studies of solar compass of birds were performed with homing pigeons (Schmidt-Koenig 1958; Keeton 1979; Wiltschko et al. 1976, 1984). To clock shift a wild bird, one has to take it into captivity for several days, which may significantly impact its motivation to return to its nest. Because of that, many studies of solar compass in passerines have been done in a non-migratory behavioural context, in caching birds that were retrieving their caches with the help of the sun compass (Wiltschko and Balda 1989; Duff et al. 1998; Wiltschko et al. 1999a). It has been even suggested that the solar compass is not used for migratory orientation by day-migrating birds (Wiltschko and Wiltschko 2015), because daytime migrants in several experiments did not seem to rely on the sun compass (Munro and Wiltschko 1993a; Åkesson et al. 2006). However, these results may partially be due to difficulties of testing migratory birds in orientation cages in the daytime, with phototaxis and shade effects playing a role. At least some nocturnally migrating birds, e.g. grey-cheeked thrushes *Catharus minimus* and Swainson's thrushes *C. ustulatus*, select the direction of migratory flights on the basis of the information derived from sunset cues (i.e. from the sun), but maintain the direction by the magnetic compass (Cochran et al. 2004). The use of such a mechanism has been also suggested for American sparrows (Muheim et al. 2006a, 2009).

Apart from the time-dependent solar compass, another method of determining cardinal directions from the movement of the sun has been proposed (Muheim et al. 2006a). This hypothetical method is based on the idea that if birds detect (directly or from the band of the maximum polarization on the sky) the sunset point and remember its position, and then, without changing their position, detect the sunrise point, they would be able to find the bisector of the angle between the sunset and sunrise directions. This bisector is always, in any season and everywhere on Earth (except of the regions very close to geographic poles), the N–S axis. This assumed method of sunset/sunrise orientation would be very simple and elegant, but the claim that this hypothesis is supported by the experimental data (Muheim et al. 2006a) is erroneous (Liu and Chernetsov 2012). The existence of this time-independent form of the solar compass is still pending confirmation. The time-dependent solar compass undoubtedly exists and is probably used for migratory orientation by diurnal migrants. It is, however, notoriously difficult to study in a laboratory setting, and most laboratory experiments in round arenas are thus performed with nocturnal migrants. Nocturnal migratory restlessness

(*Zugunruhe*) is clearly distinct from the diurnal locomotory activity and therefore its directedness is relatively easy to quantify. In diurnal migrants, *Zugunruhe* also exists but is very difficult to separate from the diurnal activity, which undoubtedly contributed to the scarceness of studies of orientation of diurnal migrants in round arenas (but see Munro and Wiltschko 1993a, b). However, recent developments in video surveillance of activity in diurnal migrants in round arenas (Babushkina and Bojarinova 2011; Bojarinova and Babushkina 2015) and in methods of analysing these data (Muheim et al. 2014) make it possible to tackle this problem and open the road to the much-needed research into compass mechanisms of diurnal avian migrants.

Star compass

Even though the star compass of migrating songbirds was scientifically described at the dawn of modern avian orientation research (Sauer 1956), it has been the subject of relatively few studies (Emlen 1967a, b, 1970; Bingman 1984, 1987; Wiltschko et al. 1987; Mouritsen and Larsen 2001; Michalik et al. 2014), i.e. much fewer than, for example, the magnetic compass. The star compass has been shown to undergo complex ontogenetic development (Emlen 1967b). During the pre-migratory period, juvenile indigo buntings *Passerina cyanea* learn to find the centre of rotation of the starry sky, located near the Polaris, which in the Northern Hemisphere shows the direction towards the geographic north. When starting autumn migration, indigo buntings had learned to use the pattern of the constellations to determine the geographic north and no longer need to observe the rotation (Emlen 1967b). Birds raised in the planetarium under the stellar pattern rotated around Betelgeuse, under the natural autumnal sky considered the north to be the direction towards Betelgeuse and laid off their inherited population-specific autumn migratory direction from this false 'North' (Emlen 1967b, 1970). Indigo buntings seemed to ignore the fact that the sky was no longer rotating, i.e. positional information was now derived from the pattern of constellations and not from the stellar rotation. These observations have later been confirmed in garden warblers (Wiltschko et al. 1987), pied flycatchers *Ficedula hypoleuca* (Weindler et al. 1995) and European robins (Michalik et al. 2014). If young night-migratory songbirds do not get a chance to observe proper celestial rotation prior to their first migration, they seem to be able to learn the location of the centre of rotation at a later stage in life: a potentially important observation if one would want to release captive-bred migratory birds after their first autumn migration (Alert et al. 2015).

Ontogenetic development of the stellar compass in indigo buntings is astonishingly complex. Its use demands

very advanced cognitive abilities, much more sophisticated than the use of the magnetic compass, which usually amazes humans most (Chernetsov 2015): the birds need to detect a very slow rotational motion of the sky (0.0042°/s) and to identify the centre of rotation, which may be hardly possible for them to directly perceive. It is more likely that when learning how to use stellar compass, juvenile birds detect the centre of celestial rotation by the snapshot strategy, i.e. by comparing the current star pattern with a memorized snapshot of the pattern relative to fixed local landmarks from some prior time (Alert et al. 2015). The neurobiological mechanism of learning the stellar compass clearly deserves further study.

Sun and stellar compasses share many important features. They both require clear skies to be used. The information underlying both these compass systems is perceived through the eyes. It is probably transmitted via the tectofugal pathway, because European robins *Erithacus rubecula* with lesioned Cluster N, an important part of the alternative thalamofugal pathway, remained capable of star orientation (Zapka et al. 2009). Furthermore, both star and solar compass have to be learned (Emlen 1970, 1975; Wiltschko and Wiltschko 1980, 1990a), i.e. they are not innate, unlike the magnetic compass. Both compasses are based on the apparent rotation of the celestial objects, and it has been suggested that they may be parts of a single celestial compass systems (Alert et al. 2015; Mouritsen et al. 2016). However, a very important feature is not shared by these two systems: the stellar compass is time independent, whereas the solar compass is crucially dependent on the synchronized internal clock. This is a fundamental difference between these two systems.

Compass hierarchy and interaction

As can be seen from this overview, compass systems of long-distance migratory birds are redundant. When more than one system is present for the same purpose in the same organism, the question of information integration and hierarchy naturally arises. Integration of compass cues in avian migrants has been the subject of a number of studies and several reviews (Wiltschko and Wiltschko 1990b, 1999; Muheim et al. 2006a, b; Liu and Chernetsov 2012; Sjöberg and Muheim 2016). It is generally agreed that before the onset of first migration, the magnetic compass is calibrated by celestial rotation (Wiltschko 2017). During migration, the patterns of cue calibration are variable: some studies suggested calibration of celestial cues by the magnetic compass (Wiltschko et al. 1998, 1999a, b, 2001a, b; Sandberg et al. 1991, 2000), whereas others showed a reverse pattern (Moore 1985; Cochran et al. 2004; Muheim et al. 2006a, b, 2009). A not uncommon outcome in cue

conflict studies is simple domination of one compass, when incorrect readings of the experimentally manipulated compass are ignored (Katz and Mihelson 1978; Wiltschko et al. 2008; Chernetsov et al. 2011; Schmaljohann et al. 2013; Åkesson et al. 2015).

Muheim et al. (2006a) reviewed a large body of evidence and suggested that response to cue conflict, either before the onset of migration or during migration, was correlated with access to celestial cues. Birds exposed to cue conflict during sunset used sunset information as the primary cue if they had an unobstructed view of the whole sky including its part near the horizon. Conversely, if cue conflict experiments were conducted at times of day that did not include sunset or the birds could not see the sky near the horizon, they used geomagnetic field as the primary compass cue. However, not all data fit this pattern, and the results obtained under similar conditions may differ (Cochran et al. 2004 vs. Chernetsov et al. 2011 and Schmaljohann et al. 2013; Muheim et al. 2006a vs. Wiltschko et al. 2008; etc.). In a recent review, a rather complicated ‘extended unified theory’ of compass cue calibration by migrating birds has been suggested: birds recalibrate their magnetic compass by polarized light cues at sunset/sunrise, provided they have access to the polarization pattern near the horizon and a view of landmarks. Otherwise, the birds are assumed to temporarily transfer the previously calibrated magnetic compass information to the available celestial compasses; and once the stars become visible, the birds recalibrate the star compass with respect of the previously recalibrated magnetic compass (Sjöberg and Muheim 2016).

Probably, a more parsimonious explanation of the variable results obtained by different authors in different avian species is that compass system hierarchy differs between the species of migrants, or maybe even between the population within one species. Some birds, for instance those that perform long-distance migrations and cross the areas with very different magnetic declination values, have to regularly calibrate their magnetic compass from the celestial one. Other species that migrate shorter distances or even during rather long flights remain within similar declination values and can survive relying on the magnetic (or stellar) compass alone. Furthermore, mortality risk of an orientation error is much different for a bird that migrates for short or medium distance over land, without crossing major ecological barriers, and for a bird that crosses deserts or ocean and winters in relatively small islands, e.g. for a bar-tailed godwit *Limosa lapponica baueri* flying from Alaska to New Zealand (Gill et al. 2009). In the former case, a directional error of 5° or even 10° may have no negative consequences, whereas in the latter case an error of 0.5° is fatal. If different species and populations of migrants are forced by natural selection to solve navigational and orientation tasks of varying complexity, it is

only natural that their orientation systems will differ, even if the sensory basis of orientation is similar or identical. To settle this dispute, carefully designed and performed experiments on compass cue calibration in many different migrant species are necessary.

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Compliance with ethical standards

Conflict of interest The author declares that he has no conflict of interests.

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