Magnetic orientation in night migrating passerines

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(Med et dansk resumé: Magnetisk orientering hos nattrækkende småfugle)

Abstract The magnetic compass of birds is considered to be of the inclination type and not based on the polarity of the magnetic field. The idea about the inclination compass can be traced back to Wiltschko & Wiltschko (1972) but outside of the Frankfurt-group, there have been very few attempts to verify and re-test the hypothesis. I have tried several times but could not confirm the hypothesis. New specially designed tests described here also failed, and in all probability both the inclination compass and in general the magnetic compass are poorly understood and much overrated phenomena. Wiltschko et al. (2008a, 2008b) still maintain their claim that the magnetic compass is superior to and calibrates other compasses such as the star compass and the sunset compass based on the polarized light pattern in the sunset sky. In contrast, Muheim et al. (2007, 2008) consider the sunset compass as the primary and calibrating compass in interplay with the magnetic and stellar compasses. Both hypotheses are weakly founded, and very probably the stellar compass may also be both superior and calibrating as revealed in my interpretation of Sjöberg & Muheim (2016).

Introduction

The present paper is about understanding how birds may set a course by means of the magnetic field of the Earth, i.e. set a course in the meaning of compass orientation. Furthermore, the paper seeks to understand the interplay between compass orientations in reference to the magnetic field, the sunset and the starry sky. To be more specific: is the magnetic compass of the inclination type and is the magnetic compass dominant compared with the stellar and sunset compasses?

Birds are supposed to use one or more compasses for establishing and maintaining the migratory direction. Some compasses are considered primary, while others are secondary and calibrated by a primary compass (Wiltschko *et al.* 2008a, 2008b, Sjöberg & Muheim 2016, Rabøl 2019).

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Juvenile migrants are supposed to carry out their first autumn migration by means of a program of vector orientation laid down in the genes (Wiltschko & Wiltschko 1995, 2003b). The designation vector signals two components, direction and distance. The direction may shift in the course of the season and is labelled as the standard direction. Presumably, distance is encoded as hours of flying while on migration, e.g. 100 hours which at an airspeed of 30 km/h corresponds to 3000 km (and here an example could be a European Robin *Erithacus rubecula* from Finland wintering in the Western Mediterranean region). The first question, with a focus on the magnetic compass, concerns how compass orientation is established in reference to the Earth's magnetic field, and two possibilities are envisioned: a compass based on the inclination of the magnetic field, or a compass based on the polarity of the magnetic field. The second question concerns the importance (position in the hierarchy) of the magnetic compass compared with other compasses rooted in the sun, sunrise, sunset and the starry sky. According to Wiltschko & Wiltschko (1972, 1995) the magnetic compass is an inclination compass. Furthermore, the magnetic compass is supposed to be the primary compass compared with other compasses. Concerning the first question, the common view is that birds use processes in the retinal rods as the sensory base for their migratory compass orientation (Holland 2014). Tissue in the nasal region innervated by the ophthalmic branch of the trigeminal nerve is also supposedly involved in the migratory progress though in the context of magnetic navigation (Holland 2014). If magnetic navigation exists, the compass used in the process is supposedly a magnetic one rooted in the nasal region.

Results and discussion

No influence of the magnetic compass

In autumn 2013 and 2014, juvenile Robins, captured during their first migration, were funnel-tested (see Appendix 1) during night under 'overcast' conditions, i.e. stars were not available for compass orientation nor for navigation. In 2013, the birds were tested in inverted magnetic fields (Appendix 2)[1] and in 2014 the magnetic North was deflected towards geographic West or East (Appendix 3)[2]. I was unable to demonstrate either a magnetic inclination compass or a magnetic polar compass: the Robins displayed significant close to standard orientation in reference to geographic N under both inverted magnetic inclinations and when magnetic N was deflected towards geographic E or W.

These findings should be considered together with the apparent lack of an active magnetic compass in the large-scale cue-conflict and calibration experiments of Rabøl (2019). In that work a magnetic compass was not used – or used only to a small extent – by birds tested in funnels within the first few days following the trapping of birds under active migration. The standard orientation displayed and lack of celestial information during testing suggested that some kind of inertial navigation (Barlow 1964) was possibly involved and responsible for the close to standard orientation in autumn 2013 and 2014. Possibly, a main reason for the discrepancies between my work and that of Wiltschko & Wiltschko is their use of long-term captive birds, whereas my normal practice is to use freshly caught migrants.

Compass dominances and calibrations

Sjöberg & Muheim (2016) is the latest contribution in an ongoing contest between R. Muheim and R. Wiltschko (e.g. Rabøl 2019, Wiltschko *et al*. 2008a, 2008b) about the primary role of the magnetic compass versus the sunset compass; which of these is the calibrating compass and which is the calibrated compass for the standard orientation?

Sjöberg & Muheim (2016) – presented in Appendix 4 – is an atypical contribution in the contest room because the authors fail to confirm their favored hypothesis. However, good reasons for this failure are given. After exposure under the sunset sky (no stars present) in a deflected magnetic field, Garden Warblers *Sylvia borin* were released under the more or less starry sky where the directions chosen by the vanishing birds indicated no calibration of the magnetic compass. As regards the reason for the absence of calibration of the magnetic compass, the authors state that "we cannot exclude the possibility that the birds recalibrated their magnetic compass but relied on their previously calibrated star compass to determine their departure direction." One may wonder about the authors' formulation "previously calibrated star compass" instead of considering the possibility that the orientation could be the result of a 'here and now' dominant magnetic or stellar compass.

According to Muheim *et al.* and W. and R. Wiltschko, the third compass in action, the stellar compass, is always calibrated. However, their arguments are not convincing. Rather, it appears that the stellar compass is

1 The sample mean vector of the controls and experimentals was 175^{0} – 0.407 (N = 38, P < 0.01) and 192^{0} – 0.626 (N = 23, P < 0.001), respectively.

2 The sample mean vector of the controls was 199^{0} – 0.401 (N = 51, P < 0.001). The W-experimentals appeared bimodal 222^{0}/(42^{0}) – 0.524 (N = 25, P < 0.001). The E-experimentals showed 201^{0} – 0.490 (N = 20, P < 0.01).

The author on the Queen's Bastion on Christiansø operating the magnetic field deflection tests. Photo: Peter Lyngs.
Forfatteren i gang med forsøgene på Christiansø med at teste nattrækkende småfugles reaktioner på manipulerede magnetiske felter.

very often the dominant compass and is not calibrated either by the magnetic compass or the sunset compass. The problem with the compass conflict experiments of Muheim and Wiltschko is that the three different compasses are normally not present together in the calibration-phase prior to testing. At best, the stars first appear late in that phase. Therefore no one should be surprised about the apparent low position of the stellar compass in the hierarchy considerations of Muheim and Wiltschko.

Rabøl (2010, 2019) presented the formal conditions for demonstrating compass dominance and calibration and introduced the use of symmetrical E/W compass deflections instead of the unilateral deflection used by others, which make interpretation of the results much more uncertain. Rabøl (2019) also reviewed the literature on compass calibrations. Apart from the indications of Wiltschko & Wiltschko and Muheim *et al.*, the phenomenon of compass calibration seems to be largely non-existent and there are very few claims that could not be explained in other more convincing ways.

In perspective

The designation orientation covers both navigation and compass orientation.

Navigation

The question is whether migrant birds navigate in reference to the magnetic field of the Earth. For several years, I have considered magnetic navigation to be a grossly overrated phenomenon (Rabøl 2014, Appendix 2). It is indeed difficult to believe that the magnetic field means nothing, because it is there all the time, during the day and at night, and whether the sky is overcast or clear. However, contrary to intuition, there seems to be very little or nothing like an extended navigational grid with magnetic intensity and inclination as gradients. Nevertheless, perhaps 'stretches of gradients' of intensity or inclination sometimes operate together with gradients from other sensory systems? The literature is burdened with examples of something – not understood – that is happening when the magnetic field is changed. But this 'something' is mostly some or other accessory detail brought into play to demonstrate the influence of the magnetic field (e.g. Wiltschko & Wiltschko 2003a in the case of Gernheim, as well as Bianco *et al.* 2019, Fransson *et al.* 2001, Boström *et al.* 2010, 2012, and many more).

Two recent cases should be considered in more detail. Bianco *et al.* (2022) found (1) close to E/W-body-alignment in caged, migrant Reed Warblers *Acrocephalus scirpaceus* around sunset (autumn), which was supposed to be (2) the prime time for calibrations between different compasses in a vector orientation system. Later in the night, the alignment was close to SW/NØ and was supposed to reflect migratory orientation (standard direction around SW). The bimodal distributions were rather indistinct but mostly significant at the 0.05 level. For Bianco *et al.* there is a connection and not just a correlation between the processes behind (1) and (2). The birds were tested indoors in the local magnetic field (but not controlled for use of a magnetic compass). Celestial cues were not available. In my optic the E/W-response is better perceived as the simple start of the nightly SW/NE (standard/reverse) orientation, and why it should be a precursor of compass calibrations is unfounded. Compass calibrations are sometimes demonstrated in deflected magnetic fields, under the very unnatural '16-star-sky', or when the polarized pattern of the sunset sky is deflected in a crude way. Whether compass-calibrations occur in the natural world is not known, but in the larger parts of Europe and Africa there is no urgent need of calibrations because the compass references of geographic N and magnetic N are very close.

In contrast to these cases, Wynn *et al.* (2022) have convincingly shown that year to year fluctuations in magnetic inclination were connected to the position of where Reed Warblers finished their spring migration or settled to breed. This observation is compatible with a system of learned mono-gradient navigation plus inherited fixed vector orientation. However, as a practical biologist I find it hard to believe that tiny fractions of a degree of magnetic inclination can be registered and remembered until the following year by the warblers and used in the way perceived. But you never know.

Compass orientation

As far as magnetic compass orientation is concerned, the evidence from Appendix 2 and 3 together with Rabøl (2019) suggests that its influence on bird migration has been overrated. However, the magnetic compass is there – somewhere or sometimes – but probably under natural conditions mostly in a 'sleeping' state.

Wiltschko & Wiltschko have produced a lot of papers and have had an enormous influence on what was published as well as on the paradigms recognised. They were always convinced that the magnetic compass dominates the celestial compasses or at least always has a significant influence on the migratory direction selected. According to them goal-area navigation in juvenile birds is not possible, stellar navigation is non-existent and olfactory navigation in pigeons is a phantom (Wiltschko 1996). Conviction is fine but very often the approach of the Wiltschkos was too biased, and they were too quick to reach their interpretations and generalizations. As an example, the concept of "setting" was seemingly invented to ensure the influence of the magnetic compass: the stellar compass was reduced to delivering only N/S-orientation, whereas the magnetic compass then took over and delivered the necessary E/W-orientation (e.g. Weindler *et al*. 1996). To prove this scenario, it was claimed that the grand mean vector did not deviate significantly from due S (autumn) when birds were tested under a (stationary) '16-star-sky' in the absence of a proper magnetic field. However, and apart from the doubtful appropriateness of the '16-star-sky' as substitute for the natural starry sky, a grand mean vector (direction) that does not deviate from due S (confidence interval test) cannot (normally) be used as proof that the directional system works on a more basic individual level. Anyway, when the two experimental groups for early and late autumn (Weindler *et al*. 1996, Table 1) are summed, five out of eleven individual sample mean vectors deviated significantly from due S at least at the 0.05 level. Rabøl & Thorup (2006) tested juvenile Common Whitethroats *Curruca communis* raised under the natural starry sky in a destroyed magnetic field. The grand mean vectors of the experimentals and controls were 153^0 – 0.788 (N = 12, $P < 0.001$) and 154^0 – 0.872 (N = 10, $P < 0.001$), respectively. Several of the individual sample mean vectors and both grand mean vectors deviated significantly from due S, thus making the "setting" scenario invalid. Wiltschko & Wiltschko never refer to Rabøl & Thorup (2006).

In the cue conflicts of mine – as presented in Rabøl (2010, 2019) – a very different picture emerges than that of Wiltschko & Wiltschko. The magnetic compass seems not to have much influence at least in the short run (as is also apparent in Appendix 2 and 3). And probably the unnatural '16-star-sky' (rotating or not) of Wiltschko & Wiltschko produces results not necessarily related to what is going on in the natural world. Much hard work remains to be done before a balanced understanding of migratory orientation is re-established. It is likely that magnetic orientation is an ancient system going all the way back to fish and amphibians. But now, in birds this system is rudimentary and is reactivated only when birds are kept under circumstances where they are deprived of other sensory cues for a long time, such as was the case for the Garden Warblers and Pied Flycatchers *Ficedula hypoleuca* used by Gwinner & Wiltschko (1978) and Beck & Wiltschko (1988), respectively.

Recently, Johnsen *et al.* (2020) more or less concurred with this point of view considering the magnetic compass as "noisy" and "unable instantaneously to acquire magnetic information that is highly precise and accurate". This means that other compasses take over. K. Lohmann was one of the co-authors of Johnsen *et al.* (2020). In a series of papers, Lohmann & Lohmann (1994, 1996, 1998) reported that hatchling turtles initially orientate towards the sea without any guidance from a magnetic compass that only becomes directionally calibrated by the horizontal glow in the direction of the sea when the hatchlings are on their way down the beach towards the sea. Furthermore, even while on the beach, the hatchling is apparently able to perform meaningful magnetic navigation when collected and placed in a water-filled arena and presented with navigational stimuli corresponding to current and future locations far out in the Atlantic gyre (Rabøl 2014). Obviously, these remarkable skills do not fit well with the present day perceptions of K. Lohmann (in Johnson *et al.* 2020) nor in the critical mind of most other scientists, including myself.

Postscript: our skilled students

Scientists are much concerned to break new ground, and their PhD-students are much involved in such projects. However, scientists also educate students at a lower level than the PhD and have – I think – a responsibility to their field that is not recognized, which is that their best students should be involved in re-testing some of the basic hypotheses, such as the inclination compass hypothesis, or the hypothesis of whether the magnetic compass dominates and calibrates the sunset and stellar compasses. Such kinds of studies will not be rewarding for scientists and their PhD-students in the short term, but they may be rewarding for science. It is apparent that several hypotheses are based on weak foundations or may simply be misleading.

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Resumé

Magnetisk orientering hos nattrækkende småfugle
Dette er en kompilation af tre artikler, der bringes vedhæftet på nettet (Appendiks 2-4). Det gennemgående tema er magnetisk orientering. Formålet med de to første artikler er at efterkontrollere, om fuglenes magnetkompas er af inklinationstypen, dvs. baseret på kraftlinjernes hældningsvinkel og ikke på polariteten, dvs. fortegnet på kraftlinjerne. Inklinationskompas hypotesen har været god latin siden 1972, men er måske mere eller mindre gal. Formålet med den tredje artikel er at rokke ved det etablerede paradigme, at fuglenes stjernekompas er underordnet det magnetiske kompas og solnedgangskompasset. Tværtom, synes det at være det dominerende og primære kompas. Trækruten kan tænkes at være genetisk programmeret som enten a) vektororientering, også kaldet kalender & kompasorientering (Rabøl 1988), eller b) koordinat/gradientnavigation. Vi skal ikke her komme nærmere ind på b). I a) holder trækfuglen sin normalkurs i forhold til en retningsgiver (et kompas), der kan være baseret i Jordens magnetfelt, stjernehimlen eller solnedgangs-/solopgangshimlen. Spørgsmålet er, hvilke kompasser, der er medfødte og kommer først til syne. Dertil hvilke kompasser, der dominerer og kalibrerer de andre. For at finde ud af det laver man konfliktforsøg, hvor man gennem manipulation undersøger, hvad der fx sker, når magnetisk N drejes om i geografisk V, medens stjernehimlen stadig signalerer, at stjerne N ligger i retningen geografisk N. Der er efterhånden lavet mange sådanne konfliktforsøg, men resultaterne og især fortolkningerne af dem er ret så modstridende. Dette i samspil med fuglenes måde at sanse retningsreferencen magnetisk N på fik mig til i efterårene 2013 og 2014 grundlæggende at undersøge, om fuglenes magnetkompas virkelig var af inklinationstypen, som gennem mange år hævdet af det paradigmesættende par R. og W. Wiltschko.

Ligesom tidligere (Rabøl *et al.* 2002) kunne jeg ikke påvise tilstedeværelsen af et magnetisk inklinationskompas (Appendix 2). Den fremkomne, omtrentlige normalorientering kunne heller ikke tilskrives indflydelse fra stjernerne, der var dækket af med uigennemsigtigt plastik. Der kunne heller ikke være tale om et polært magnetisk kompas (Appendix 3), for der var ingen reaktion på, om magnetisk N blev drejet om i geografisk Ø eller V. Kort sagt, fuglene brugte slet ikke magnetkompasset til bestemmelse af deres trækorientering. Nu var mine fugle i disse forsøg fanget samme eller foregående dag, så måske ligger magnetorienteringen dybere i trækfuglene og tages først frem ved særligt indskrænkede lejligheder. Under alle omstændigheder: Dette er en bombe under de etablerede paradigmeholdere, som nu enten må (bort)forklare sig eller indgå aktivt i et paradigmeskift.

Hvis jeg ikke kan påvise et tilstedeværende magnetkompas i ovennævnte forsøg, hvordan kan Wiltschko & Wiltschko så opfatte det som det vigtigste og kalibrerende kompas i sammenhæng med solnedgangs- og stjernekompasset? Ja – det er en gåde, og ikke så nemt at (bort)forklare, men en vigtig del af forklaringen er nok, at tyskerne bruger 'burfugle', medens jeg bruger fugle, der lige er fanget ud af trækket (jeg tester normalt mine fugle samme eller næste dag efter fangsten). Tyskernes fugle er som regel langtidsfangenskabsfugle, der derfor – måske – falder tilbage på noget urgammelt dybt inde i den pri-

mitive del af hjernen. Rabøl *et al.* (2002) – hvor forsøgsfuglene var op til flere uger i fangenskab – kunne dog heller ikke vise tilstedeværelse og indflydelse af et magnetisk inklinationskompas, så helt enkelt er det ikke. Bortset fra de lange burophold favoriseres magnetkompasset formentlig også af tyskernes forsøgsprocedure før og under testet.

Jeg slutter af med en observation; Wiltschko & Wiltschko har haft meget stor indflydelse på udviklingen indenfor forskningsfeltet trækfuglenes orienteringssystem. De har bidraget voldsomt, men deres fokusering på magnetorientering har sandsynligvis skævvredet udviklingen, så der bliver noget at rette op på for de kommende generationer af orienteringsforskere.

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Appendix 3: https://pub.dof.dk/link/2022/2.appendiks3
Appendix 4: https://pub.dof.dk/link/2022/2.appendiks4

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