Appendix 2 to J. Rabøl 2022: Magnetic orientation in night migrating passerines. – Dansk Orn. Foren. Tidsskr. 116: 61-66.

Migrating European Robins did not make use of a magnetic inclination compass in funnel-tests during sunset or night in inverted magnetic fields without sight of the stars, Christiansø, Denmark, autumn 2013

(Med et dansk resumé: Rødhalse testet i inverterede magnetfelter ved solnedgang eller om natten uden synlige stjerner på himlen: Intet spor af et magnetisk inklinations-kompas i aktion)

Abstract This study aims to test the idea that migrating birds make use of a magnetic inclination compass as first proposed by Wiltschko & Wiltschko (1972). Outside the group of Wiltschko & Wiltschko very few tests of the hypothesis have been carried out, and I found only a single confirmation myself. When I tested the hypothesis under carefully controlled conditions, where celestial cues were absent, the birds showed standard orientation under both normal and inverted magnetic inclinations. The simple conclusion is that the birds used a polar magnetic compass. Another ‘problem’ is that it is difficult or impossible to distinguish between standard orientation based in a magnetic inclination compass system and motivationally induced reverse orientation rooted in a polar compass system. Perhaps the inclination compass is mostly a phantom?

Introduction

Back in 1968, W. Wiltschko demonstrated that European Robins *Erithacus rubecula* (Robin from here on) were endowed with a magnetic compass steering the migratory orientation. Up to then, hardly anybody believed in the significance of magnetic orientation in birds or other animals. In their 1995 book, Wiltschko & Wiltschko presented a range of examples of magnetic compass orientation in various animals. However, indications of (gradient/coordinate) navigation rooted in magnetism were few and weakly founded.

Presently, almost all scientists believe in the paramount influence of magnetism on compass orientation as well as gradient navigation. In fact, magnetism is considered the most powerful source behind both compass orientation and navigation. Magnetism is supposed to be influential (e.g. Holland 2014) through processes in the retina (the compass) and in the nasal region innervated by the ophthalmic branch of the trigeminal nerve (the navigational process).

Considering the magnetic compass, Wiltschko & Wiltschko (1972) published a very influential paper based on Frankfurt cage orientation experiments with Robins showing inversion of the magnetic inclination vector leading to reverse orientation. Furthermore, the (sample) orientation seemingly broke down in a horizontal magnetic field. Wiltschko & Wiltschko proposed that birds were endowed with what was designated an inclination compass, i.e. the polarity of the magnetic vector was not used as in case of the technical compass needle but (considering birds on the northern hemisphere) magnetic N was considered to be in the direction of the smallest intersection angle of the magnetic inclination vector. Such a scenario also explained the disorientation[1] claimed under condition of a horizontal magnetic inclination.

Over the years, Wiltschko & Wiltschko and co-workers published many papers presenting results compatible with the inclination compass hypothesis, which nowadays rank as a law-of-nature: birds are endowed with an inclination compass based in sensory processes in the retina. However, some other organisms are endowed with a polarity compass (e.g. Wiltschko & Wiltschko 1995).

Anyway, the question is – and always was – whether the interpretation of the results of Wiltschko & Wiltschko (1972) was right/appropriate, or – perhaps more correctly expressed – could be more restricted and less general than supposed: is the reverse orientation following the shift to an inverted magnetic field rooted in 1) the sensory system or 2) motivationally steered and dependent on the experimental circumstances. The attention of Wiltschko & Wiltschko is solely on 1).

Rabøl *et al*. (2002) – in four independent investigations – were unable to demonstrate reverse orientation following inversion of the magnetic inclination. Not surprisingly, this inconvenient paper in a not top-rated journal with few exceptions is largely ignored in the literature on magnetic orientation. Other people (such as the Swedish orientation scientists) also had problems demonstrating reverse orientation following inversion of the magnetic field. Therefore, the third possibility 3) that the inclination compass based in sensory processes is a phantom has to be considered seriously; sometimes scientific phantoms exist persistently if promoted by strong leaders.

Since 2000 I carried out many orientation experiments with funnels where the focus was on compass dominance and compass calibration (e.g. Rabøl 2010). I was not considering the sensory mechanism of the magnetic compass but just supposed that such a compass was somewhere more or less dominating and/or calibrating. However, evidence for any kind of magnetic influence was weak or absent (Rabøl 2010, 2019). Therefore, the autumn of 2013 on Christiansø in the central Baltic was devoted to a thorough investigation of the very type of magnetic compass. The procedure was

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[1] As the sample concentration in these experiments with normal or inverted inclination was rather low (though statistically significant) it is not possible to distinguish between a) disorientation, b) bimodal standard/reverse orientation, or c) bimodal right-angle orientation in the sample tested in the horizontal magnetic field, so the interpretation of disorientation under this condition may be wrong.

testing in funnels under condition of ‘overcast’[2], i.e. no other (appreciated) migratory compass cues than magnetic were available: a control group tested in the normal magnetic field of Christiansø (inclination +70º, magnetic N (mN) = geographic N (gN), and an experimental group tested in an inverted magnetic field (inclination -70º, mN (polar) = gN) should be compared. The question was whether reverse orientation could be demonstrated in the experimental group as the first and necessary step for an indication of a magnetic inclination compass in charge. Such an experiment could be considered as distrusting/provocative by the established magnetic society, but the meaning was not provocation but basic understanding. All too often basic experiments are not repeated for testing their claim of generality.

Material and methods

Rabøl *et al*. (2002) and Rabøl (2010) described the magnetic coil fields used. In short, eight coil fields each consisting of two frames 80 × 80 cm with 45 cm in between, were employed. The magnetic field produced could be set in the neighbourhood to 1) two times the strength of the vertical component of the inclination vector in Denmark, or 2) √2 the strength of the horizontal component of the inclination vector in Denmark. 1) is intended for inverting the inclination vector of the combined field to 70º upwards (named -70º), whereas 2) is intended for shifting the direction of magnetic N in the combined magnetic field into geographic E or W maintaining the same intensity and numeric inclination (+70º) of the combined field and the local magnetic field. As seen below there were some irregularities from these intentions. The main reason was that I first after the initial sunset experiments realized that the intensity of my artificial magnetic fields could be turned significantly up or down.

The (predominantly) juvenile birds were caged two by two in conical plastic baskets (diameter 30 cm in the bottom, 40 cm in the top and a height of 40 cm). There was a free view almost down to the horizon in most directions (towards W in fact down to the horizon) through the lattice structure at the sides of the basket. The top was covered with a cloth net, and two wooden sticks were set across horizontally through the basket, one close to the ceiling in order to offer the bird a good view of the sky through the cloth net. The birds were tested singly in plastic funnels with a side slope of 45° and measuring 30 cm in upper diameter. The funnels were placed horizontally on wooden boards, and in the experimentals each funnel was placed in the central part of the coil system. The inner slope of the funnel was painted with a thin layer of chalk, where the hopping and fluttering bird left its feet marks (Fig. 1 in Rabøl 2022 Appendix 1). It is no longer possible to buy typewriter correction paper, but the modified method works just as well.

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[2] The designation ‘overcast’ means that the funnels were covered with translucent but not transparent plastic leaving no sight of the stars nor the surroundings including the frames of the artificial magnetic field and in all probability the polarized evening sunset sky.

The orientation and amount of activity of the individual birds were estimated as previously described by e.g. Rabøl (1979, 1993, 2010, 2022 Appendix 1).

During six sunset-experiments carried out 14 through 27 September 2013 the upward directed magnetic vector of the seven coil-fields was not always twice the length/strength of the downward directed vector of the local magnetic field, i.e. the inclination of the combined/resulting field was not always -70º but varied between -70º and -30º.

During the six night-experiments 25 September through 2 October 2013 we succeeded to calibrate the magnetic intensity in six out of seven coil fields in such a way that the inclination of the combined field turned into -70º. In the last field the combined inclination was -60º.

Several series of experiments were carried out, all with Robins only (95% 1Y birds), and all tested under ‘overcast’ conditions. The trapped birds were first caged in the garden of the Miller’s House. They were trapped on the same or the preceding day as the experiment was carried out at sunset or night. The birds were caged in pairs in plastic baskets with an open lattice structure. The top of the baskets was covered with a wired cloth-net and during daytime also by a plywood plate for protection of sun, rain and Eurasian Sparrowhawks *Accipiter nisus*. The birds were transported to the funnels on the Bastion of the Queen just before the start of the experiment and immediately transferred into the funnels. However, the approximate direction towards the setting sun or the brighter sunset sky in all probability was apparent for the birds in the sunset experiments 14 through 21 September when tested in the funnels under condition of ‘overcast’.

Results

Fig. 1 shows a compilation of the sunset experiments.

The controls (right distribution) showed a very significant, unimodal response directed a little S of W clearly influenced by the setting sun (on the average a little N of W). Clearly, a standard direction towards SSW-SW has much less influence on the sample mean direction than a sunset taxis.

The experimentals (left distribution) showed a significant but much less clear WSW orientation apparently less influenced by the setting sun than the controls.

The difference between the two sample concentrations is significant ($P < 0.01$; Batschelet 1981).

Fig. 2 shows a compilation of the night experiments. Both controls and experimentals show S-orientation, and perhaps unexpectedly the controls more orientations in the reverse sector (if influence of an inclination compass the majority of orientations in the experimentals should have been in the reverse sector).

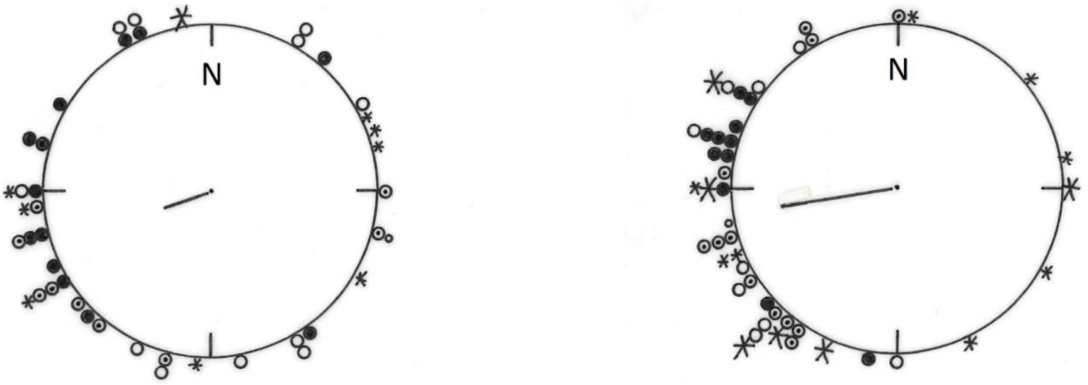

Fig. 1. Six sunset experiments 14 through 21 September 2013. The large dots refer to orientations on an individual activity level on at least “Small” (see Rabøl 2014). Black, dotted and white dots refer to high, medium and low concentrations. Small dots refer to orientations coupled to very small activities. Small stars to pairwise bimodal activities with about equal sized peaks. Large crosses to dominant peaks in a bimodal activity pattern. Both small dots and large stars are included in the calculation of the sample mean vector. The streak from the centre shows the sample mean vector; direction and concentration (r = 1.00 corresponds to length of radius). The sample mean vector of the controls (right distribution) is 262º - 0.719 (N = 39, P < 0.001), and of the experimentals (left distribution) 252º - 0.306 (N = 35, P < 0.05). The latter distribution looks a little bimodal but doubling the angles leads to no increase in sample concentration (249º/(69º) – 0.218, N = 39).

Resultaterne af seks solnedgangs-forsøg. Til højre ses kontrollerne testet i det normale, uforstyrrede magnetfelt. Fuglene er meget signifikant orienterede mod WSW-W og under klar indflydelse af en solnedgangs-taxi lidt N for W. Til venstre ses forsøgs-fuglene, der var udsat for et inverteret magnetfelt (hvor den lodrette komponent i hældningen peger opad). Orienteringen er i WSW og mindre påvirket af solnedgangen. Der er også mere spredning på, så det inverterede magnetfelt påvirker diffust, men resulterer slet ikke i omvendt orientering som forventet ud fra inklinationskompas-hypotesen.

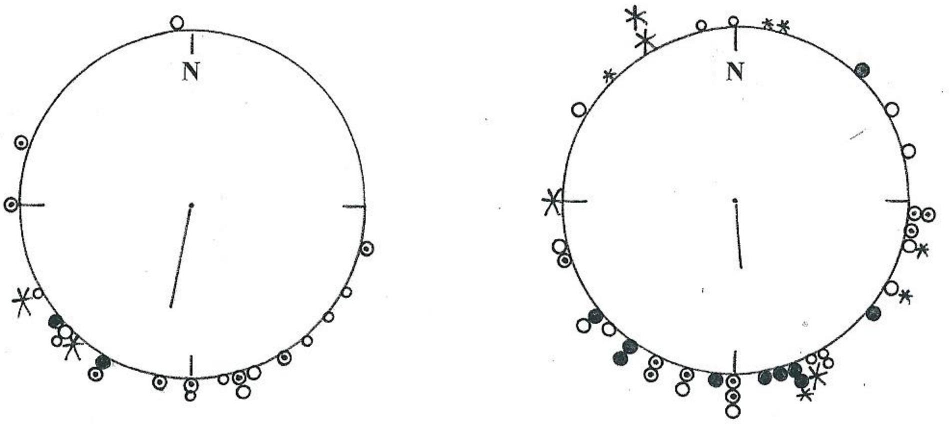

Fig. 2. Night experiments 25 September through 2 October 2013. The left figure shows the experimentals tested in inverted magnetic fields. The sample mean vector is 192º - 0.626 (N = 23, P < 0.001). The right figure shows the controls. The sample mean vector is 175º - 0.407 (N = 38, P < 0.01). According to the Mardia-Watson-Wheeler test there is no difference between the two samples (0.50 < P < 0.70).

Natforsøg. Fugle testet i inverterede magnetfelter (venstre figur) og kontrollerne (højre figur). Begge grupper viser signifikant sydlig orientering, og der er intet, der tyder på brugen af et inklinationskompas (faktisk tværtom; kontrollerne har forholdsvis flest mod nord).

Discussion

In general

The question is whether it is a proven fact that migrating birds make use of a magnetic inclination compass, or whether it is a phantom among people belonging to the group of W. and R. Wiltschko. Outside that group are presented very few confirmations of the hypothesis, which at present ranks close to a law-of-nature. In such a situation it is a legal and logical requirement to re-test the hypothesis.

This is not the same as claiming that something is wrong about the inclination compass, nor with Wiltschko & Wiltschko. Different people and groups treat their birds differently, and this may in principle be at least part of the reason for the discrepancies. As an example, Wiltschko & Wiltschko (2017) mentioned homing pigeons *Columba livia* from different lofts raised and trained differently were clearly influenced differently in their orientation in reference to olfaction.

Specifics concerning Christiansø, autumn 2013

The Robins were mostly significantly oriented in about the standard direction and there were no consistent signs of reverse orientation in the inverted magnetic fields, i.e. the results are not indicative of a magnetic inclination compass in action.

The results are compatible with a) the outcome of a magnetic polarity compass, or b) steering by an un-appreciated (migratory) compass (not celestial, i.e. not rooted in the sun or stars), or c) it could be considered as a taxis towards ‘something’ such as a light pattern, the coil frames, or (the noise from) a bird in another funnel too close (Rabøl 2019). Obviously, c) is a good – partial – explanation in case of the influence of the sunset (Fig. 1). In the night experiments (Fig. 2) c) is non-existent (the funnels were not close to each other; there was no asymmetric light-pattern, and the birds could not see the frame nor the stars. Here, a) seems to be the only probable and reasonable explanation.

Clearly, a) could be further elucidated comparing the orientation in two experimental groups where magnetic N is deflected towards geographic E or geographic W, respectively. In both, the combined magnetic inclination vector should be directed 70º downwards and the total intensity should be as in Denmark. In fact, I already made a lot of such experiments, apparently without influence/steering of a magnetic compass but almost all were under a contemporary clear starry sky, i.e. the orientation was perhaps steered/dominated by a stellar compass (Rabøl 2010). However, sometimes when the birds were kept for days and nights in cages within deflected magnetic fields and then were transferred to funnels and tested within the deflected fields, the magnetic compass took partly over and dominated the stellar compass, but then reverse orientation appeared in reference to magnetic N.

Specifics concerning Rabøl et al. *(2002)*

This important contribution received very little attention probably because it brought confusion on the scene. The initial question was whether migrant birds are endowed with a magnetic inclination compass, and whether such a compass should be considered as only a first choice, i.e. the magnetic compass in use following soon after the transfer from the cage in the normal magnetic field to the funnel/cage in an inverted magnetic field. This has been the standard procedure in almost all experiments such as those carried out by Wiltschko & Wiltschko. The intriguing question is whether the magnetic compass in use continues to be an inclination compass after several days and nights caged in an inverted field, or whether a polarity compass in such a situation takes over. Here we shall only consider the European Pied Flycatcher *Ficedula hypoleuca* experiments, which were especially designed for that purpose.

In these indoor experiments from autumn 1992 the birds were trapped as migrants on Christiansø and transported to Strødam N of Copenhagen. 16 birds were first kept and tested for six nights (10 birds) or four nights (6 birds) in the natural magnetic field, and then for four nights in the inverted magnetic field. The first test in the inverted field (night 0) was immediately following the transfer from the natural magnetic field. The next tests in the inverted field were on following nights 1, 3 and 5. The expectation was reverse orientation (following use of a magnetic inclination compass) on at least night 0, and then perhaps also on nights 1, 3 and 5. However, there was no such development. Therefore, I just combined all orientations in two samples: controls in the natural magnetic field, and experimentals in the inverted magnetic field. The sample mean vector of the controls was 100º - 0.254 (N = 84, P < 0.01), and of the experimentals 115º - 0.485 (N = 64, P < 0.001). The corresponding grand mean vectors were 107º - 0.380 (N = 16) and 118º - 0.645 (N = 16, P < 0.001). Clearly there was no significant difference in mean directions which, however, were surprising easterly (standard direction about SSW). Surprisingly, the sample concentration was much smaller in the controls: 32 directions out of 84 are situated in the reverse half of the circle in reference to the mean direction. The same figure is 10 out of 64 in the experimentals. The difference is significant (chi-square test, P < 0.01). This is the opposite trend of the expected if an inclination compass had been prevailing in some of the birds. In conclusion, no influence of a magnetic inclination compass was found, whereas the results are in accordance with orientation in reference to a magnetic polar compass.

Homing pigeons

The question is whether homing pigeons are endowed with a magnetic compass of the inclination type. Wiltschko & Wiltschko (1995) write about the often cited, but much less understood, magnetic coil experiment performed by Wallcott & Green (1974): “When magnetic north of the induced field pointed upwards, so that the resultant field roughly corresponded to an inversion of the vertical component, the test birds showed a tendency to fly away from home […]. These findings suggest that the magnetic compass of pigeons, too, is an inclination compass.” Probably, the designations NUP and SUP (North up, and South up) and drawings of pigeons sitting with heads held high up led Wiltschko & Wiltschko and other people erroneously to believe that magnetic N of the coil field also in the bird on the wings was directed vertically up- or downwards, and that the inclination of the combined field in the NUP-condition was negative. However, as pointed out by Rabøl (1988) – unfortunately in Danish – this was not so. The coil field of the pigeon on the wings forms an angle to the horizontal on about 30º, and according to the specifications of Wallcott & Green the inclination of the combined field in both the NUP- and SUP-condition will be positive, and therefore if pigeons have an inclination compass, it is of a different type than the one hypothesized for passerine birds: both when flying due N and S, a ‘classic’ inclination compass tells the pigeons that they are flying N. When flying E or W, the inclination is also directed downwards (i.e. positive) with a strong northerly component. So, the pigeons are apparently not endowed with a ‘classic’ inclination compass.

Simulated equator-crossings

Wiltschko & Wiltschko (1992) considered two groups of Garden Warblers *Sylvia borin* tested in the magnetic field of Germany (0.46 G, +66º of inclination). The orientation of both groups was about S in August/September. Then on 1 October one of the groups, the experimentals were placed in a horizontal magnetic field (0.46 G, 0º inclination) for two days and nights. The two groups were tested again in October/November in the unchanged magnetic field of Germany (0.46 G, +66º inclination). The control group still oriented about S. However, the experimentals now oriented about N, i.e. reversed their orientation about 180º.

What then follows are two one-sided interpretations by Wiltschko & Wiltschko: a) the treatment of the experimentals is perceived by the birds as a signal of an equator crossing; b) the compass reference in operation must be an inclination compass which following the 'equator crossing' is adjusted to turn the orientation 180º for the birds to continue about S heading for the African wintering ground well south of the equator.

Now, reverse orientation is a common reaction following various treatments or circumstances, and though Wiltschko & Wiltschko of course may be right in their interpretation, they should have considered the possibility of reverse orientation, too, as the result of a motivational shift due to 'discomfort' or confusion with the treatment (the horizontal magnetic field applied for two days and nights was much stronger than the natural magnetic field at the equator). Surely in order to elucidate whether the reverse orientation is motivationally conditioned we need more experiments with more species (also species, such as the Robin, that do not ordinarily cross the magnetic equator) and other kinds of magnetic treatments such as e.g. two days and nights placement in a vertical field. The interpretation of Wiltschko & Wiltschko also rests on the repeated performances of only four birds in particular, and this seems too small a sample size for a broad generalization. In conclusion, the claim of a magnetic inclination compass in action in Wiltschko & Wiltschko (1992) is weakly founded.

Beason (1986) reported on orientation-experiments with Bobolinks *Dolichonyx oryzivorus* clearly indicative of use of a polar magnetic compass. However, these experiments were soon forgotten by both Beason and Wiltschko & Wiltschko. Instead, Beason (1992) followed Wiltschko & Wiltschko (1992) in their interpretation of a magnetic inclination compass in work in a simulated equator-crossing experiment.

Beason (1992) tested a group of Bobolinks over nine nights where the inclination changed gradually from +67.5º over horizontal inclination to -67.5º. The orientation remained southerly on all nights. The interpretation of Beason of the unchanged orientation rests on the assumption that the single night of horizontal inclination was a signal that magnetic equator was crossed and from then on, orientation established with an inclination compass as the reference should reverse 180º (the unchanged and not bimodal orientation on the night of horizontal inclination is explained as delayed and maintained in relation to the stationary 'stellar sky' of the planetarium in which the birds were tested). One may wonder why Beason (1992) never discussed the simplest explanation: the compass in operation was a polarity compass. Apparently, his trust in an inclination compass was so strong that it could not be doubted.

Wiltschko & Wiltschko on the move?

Wiltschko & Wiltschko (1995) do not consider the possibility of the presence of both types of magnetic compasses in migrant birds: without exceptions, the magnetic compass in birds is of the inclination type. However, after many years of stagnation Wiltschko & Wiltschko allowed themselves in cautious ways to be more spacious – or did they really change?

According to the summary in Wiltschko *et al.* (2011): “The avian magnetic compass is an inclination compass that appears to be based on radical pair processes. It requires light from the short-wavelength range of the spectrum up to 565 nm green light; under longer wavelengths, birds are disoriented. When pre-exposed to longer wavelengths for 1 h, however, they show oriented behaviour. This orientation was analysed under 582 nm yellow light and 645 nm red light in the present study: while the birds in spring prefer northerly directions, they do not show southerly tendencies in autumn. Inversion of the vertical component does not have an effect whereas reversal of the horizontal component leads to a corresponding shift, indicating that a polar response to the magnetic field is involved. Oscillating magnetic fields in the MHz range do not affect the behaviour but anaesthesia of the upper beak causes disorientation. This indicates that the magnetic information is no longer provided by the radical pair mechanism in the eye but by the magnetite-based receptors in the skin of the beak. Exposure to long-wavelength light thus does not expand the spectral range in which the magnetic compass operates but instead causes a different mechanism to take over and control orientation.” This is an interesting paper which possibly means that Wiltschko & Wiltschko – as rather usual – were too early out with their generalizations extending these into laws of nature. There is no reference to Rabøl *et al.* (2002) where a magnetic inclination compass could not be demonstrated. Clearly, the results of the 2011 paper are a bomb under their repeated claim that the magnetic compass is of the inclination type. However, the claim is happily saved at least for a while by another claim that not all kind of oriented responses should be considered as migratory compass orientations.

According to the introduction of Wiltschko *et al.* (2011): “The avian compass is an inclination compass: the birds do not use the polarity of the magnetic field […] This inclination compass could be demonstrated “only under light from the short-wavelength end of the spectrum, from below 370 nm ultraviolet to about 567 nm green light […]. From 580 nm yellow light onward, birds were no longer oriented […]. Interesting, when migratory birds had been pre-exposed to red light for 1 h prior to testing, they were oriented also under red light – the exposure to red light seemed to have conferred the ability to detect magnetic directions under longer wavelengths […].” Wiltschko & Wiltschko refer to so called ‘fixed direction responses’ which are “a second type of directional response to the magnetic field [which] has been observed under extreme light conditions, such as bright monochromatic light, bichromatic lights combining short-wavelength and yellow light or in total darkness." "They differ from normal migratory orientation, being fixed in the sense that they do not show the seasonal change between spring and autumn" … "they are indeed fundamentally different from normal compass: they are polar responses to the magnetic field."

Wiltschko & Wiltschko end up with a kind of proposal that the upper beak magnetite polarity-based receptors are an old compass mechanism which now is taken over by an eye-based inclination compass ("Some authors like, e.g. Kirschvink and colleages, propose that they also provide the directional information for the avian magnetic compass."). Apparently, they still believe in magnetite based gradient navigation mediated from the upper beak region. Their conclusion is "The magnetite-based receptors thus do not seem to be involved in the magnetic compass; they normally provide information on the magnetic intensity, and only under very unusual light conditions not occurring in nature, do they appear to make birds head into specific directions."

The paper by Wiltschko *et al.* (2003) is about the orientation in high-intensity lights. Apparently, the birds (Silvereyes *Zosterops lateralis*) oriented WNW in both the normal and in the inverted magnetic field, i.e. an inclination compass was not in charge. Wiltcshko & Wiltschko (2002) is a pre-runner showing change to W/(E) orientation under sixfold increased intensities.

Apparently, we know less about the nature and complexity of the magnetic compass in birds than formerly claimed by Wiltschko & Wiltschko.

Other investigations of the type of magnetic compass

Swedish investigators such as S. Åkesson, R. Muheim and R. Sandberg carried out several experiments in deflected or vertical magnetic fields, but according to Åkesson (in litt.) none in inverted magnetic fields.

The group of H. Mouritsen in Oldenburg apparently only published a single experiment (Engels *et al.* 2012) supporting the hypothesis of the magnetic compass being of the inclination type. Fig. 3B in that publication shows reverse orientation under condition of an inversion of the magnetic field in Robin, autumn. The sample mean vector was 37º - 0.55 (N = 22, P < 0.001). Anyway, the distribution looks a little bimodal and doubling the angles – on the base of measuring angles on the figure – lead to 21º/(201º) – 0.39 (N = 22, P < 0.05). Mouritsen does not belong to the tribe of Wiltschko & Wiltschko. Therefore, this finding of Engels *et al.* could be considered an independent and important confirmation of the presence/action of an inclination compass. However, a single swallow makes no summer. Therefore, it would be interesting to know whether Mouritsen and his team have further results confirming the inclination compass hypothesis. Schwarze *et al.* (2016) found random orientation at 0º inclination, whereas normal orientation was found down to 5º inclination. Certainly, this result is indicative of the action of a magnetic inclination compass and not a polar compass. Anyway, the birds of Schwarze *et al.* (Eurasian Blackcaps *Sylvia atricapilla*) were long-time caged birds and perhaps a magnetic compass of the inclination type better show off in such birds deprived of other stimuli for a long time.

According to D. Kishkinev (in litt.) the Russians never tested the inclination compass hypothesis.

In conclusion, no one seems to doubt the presence of a magnetic inclination compass or do not consider testing its presence rewarding for their scientific impact or carrier. However, as obvious from above we need a lot of follow-up testing.

Resumé

Rødhalse testet i inverterede magnetfelter ved solnedgang eller om natten uden synlige stjerner på himlen: Intet spor af et magnetisk inklinations-kompas i aktion

Siden 1972 har det været god latin at opfatte fuglenes magnetiske kompas som værende af inklinationstypen. På vore breddegrader går de magnetiske kraftlinjer skråt ned i jorden, i Danmark således i en ret stejl vinkel på 70º (benævnt hældningen eller inklinationen og angivet som +70º). Inklinationen kan opløses i en vandret og en lodret vektorkomponent. En kompasnål følger den vandrette komponent. Den lodrette komponent er ca. 2,.75 gange kraftigere end den vandrette (svarende til tangens 70º). Kompasnålen er et polært kompas, der peger mod magnetisk N. Nogle dyr – men altså ikke fugle (siger man, med henvisning til det toneangivende par W. og R. Wiltschko) – har et polært kompas. Fugle har et inklinationskompas, der bestemmer retningen mod magnetisk N ud fra hældningen af de magnetiske kraftlinjer. I Danmark er denne vinkel som nævnt 70º, når man vender sig mod magnetisk N, medens den er (180º – 70º) = 110º i retningen mod magnetisk S. Den vandrette komponent af inklinationen peger stadig mod magnetisk N som angivet af et polært kompas, men den mindste vinkel mellem inklinationen og magnetisk S findes nu i retningen mod magnetisk S. Trækfugle udstyret med et inklinations-kompas opfatter derfor magnetisk S som magnetisk N og vender deres orientering 180º. Det fandt Wiltschko & Wiltschko ud af i 1972 ved at teste Rødhalse i et magnetfelt med en opadstigende inklination (et såkaldt inverteret felt) svarende til, hvordan det ser ud på den sydlige magnetiske halvkugle. Siden har de og deres studenter og samarbejdspartnere lavet masser of orienteringsforsøg, hvor resultaterne falder ud som styret af et inklinationskompas. Forskere udenfor gruppen såsom mig selv har sjældent eller aldrig fået resultater, der tyder på, at magnetkompasset hos fugle er af inklinationstypen. Men det er der ikke nødvendigvis noget fordækt i. Forskere kan ofte ikke gentage udfaldet af andre forskeres forsøg. Fugle (og forskere) er komplicerede væsener og behandling, udstyr og testprocedurer er altid mere eller mindre forskellige.

W. & R. Wiltschko opfatter inklinations-kompasset som sansebaseret. Det er resultatet af processer i øjets nethinde (retinaen). Men man kunne også forklare den omvendte orientering i det inverterede magnetfelt med, at reaktionen er motivationsbetinget: Fuglen er i virkeligheden udstyret med et polært magnetkompas, men hvis fuglen anbringes i et inverteret felt udløses omvendt orientering, der (som de fleste fuglekikkere ved) i andre sammenhænge er et ret almindeligt fænomen fx blandt trækkende Sanglærker *Alauda arvensis* om foråret i SV-vinde op ad formiddagen efter et forudgående normaltræk mod NØ i morgentimerne (det kan også kaldes modvindstræk, men omvendt træk og modvindstræk er to sider af samme sag).

For nu at resumere: Den omvendte orientering i et inverteret magnetfelt kan være betinget af 1) sansemåden eller 2) sansemåde + motivation. Dette er aldrig faldet W. & R. Wiltschko eller andre ind. Jeg har tænkt i de baner helt tilbage til i 1990erne. Jeg har også iblandt skrevet det, men som flere andre af mine ideer og hypoteser, har de ikke spiret i den stenede jord.

Tilbage i 2002 publicerede jeg og tre andre danskere en artikel i tidsskriftet Italian Journal of Zoology, hvor vi omtalte fire grupper af forsøg, hvor vi testede inklinationskompas-hypotesen. Forsøgene faldt alle negativt ud. Der var intet, der tydede på et inklinationskompas, men i princippet kunne orienteringen godt have været styret af et polært kompas. Denne ikke-paradigmebekræftende artikel er formentlig en af de mindst citerede artikler i orienteringslitteraturen. I en del af ovennævnte forsøg havde fuglene stjernehimlen til rådighed for deres orientering, så i de tilfælde var inklinationskompasset måske undertrykt af stjernekompasset. I en del år lod jeg det være ved det, men i efteråret 2013 gik jeg i gang igen og lavede orienteringsforsøg med Rødhalse på Christiansø i inverterede magnetfelter under en kunstig, overskyet himmel (tragtene dækket med lysgennemskinnelig men ikke gennemsigtig plastik). I en første periode i september blev fuglene testet omkring solnedgang. I en senere periode i slut september og oktober blev de testet om natten mindst to timer efter solnedgang og uden spor af solnedgangen. Fuglene kunne altså ikke se stjernehimlen om natten, men givetvis retningen mod solnedgangen i solnedgangsforsøgene. Solnedgangen formenes at være et brugbart kompas for træk-orienteringen, dog ikke som retningen mod solnedgangen i sig selv, men i forhold til den 'regnbue' af polariseret lys, der strækker sig hen over himlen gennem zenit vinkelret på solnedgangen. Denne bue kan de dog efter alle solemærker at dømme ikke se gennem det uigennemsigtige plastikdække. På den anden side kunne den kraftigere lysintensitet i retning af solnedgangen i solnedgangsforsøgene måske tjene som udgangspunkt for en lystiltrukket reaktion. Men i natforsøgene er ethvert spor af solnedgangen væk, og det eneste trækorienteringskompas, fuglene havde til rådighed, var magnetkompasset enten det nu var et inklinations- eller et polært kompas. Resultaterne er vist på figurerne. I solnedgangs-forsøgene er der klare spor af en lystiltrækning, der må antages at være trækorienteringen uvedkommende. Sådanne reaktioner er meget normale i solnedgangsforsøg, hvad der forties bravt af de fleste forskere. Der er meget lidt, der tyder på et inklinationskompas i aktion. I så fald burde fuglene testet i de inverterede felter have haft en dominerende eller sekundær ØNØ-top. De er dog mere spredte i orienteringen end kontrollerne, og det kan tydes, som at nogle af dem prøver at bruge et inklinationskompas, der så stort set overrules af lystiltrækningen. I natforsøgene er der intet spor af et inklinationskompas, men både kontroller og forsøgsfugle er stort set orienterede i normaltrækretningen. Den nærliggende konklusion er således, at de bruger et polært magnetkompas.

Det var så (stort set) slutbemærkningen: Trækfuglene (i hvert fald i mine forsøg her) bruger 1) et polært magnetisk kompas, eller 2) noget helt tredje (den anden mulige kompas-type baseret på sol- eller stjernehimlen var ikke til stede i natforsøgene to timer efter solnedgang). Dette tredje kunne være en form for inerti-orientering (Barlow 1964). Den fjerde mulighed (tiltrækning eller frastødning af ikke-trækorienteret natur (lyde, hældninger, synsindtryk o.a.)), mener jeg at kunne udelukke.

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