RIN 19

10th RIN Conference on Animal Navigation

10-12 April 2019

Royal Holloway College, UK

Abstracts

Hosted by the Royal Institute of Navigation's Animal Navigation Group (ANG)

S1 Magnetic Compass

Magnetic compass orientation in the presence of RF fields: zebra finches can be trained to Larmor-frequency, but not broadband RF fields

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Magnetoreception of the avian magnetic compass is suggested to be based on a light-dependent process involving a radical pair mechanism. Both Larmor-frequency and broadband radio-frequency electromagnetic fields (RF fields) in the lower MHz range have been shown to interfere with the magnetic compass in birds and lead to disorientation. However, it has been questioned whether RF fields at the Larmor frequency can affect the singlet-triplet interconversion of the radical pair substantially enough to affect the product yield. I show that zebra finches can be successfully trained to orient using the magnetic compass in the presence of low-intensity (peak at 10 nT) Larmor-frequency RF fields, which otherwise lead to disorientation in birds unfamiliar with these conditions. Birds trained in the presence of broadband RF fields, on the other hand, are not able to use their magnetic compass. These findings demonstrate that low-intensity, single-frequency RF fields at the Larmor frequency do not totally abolish magnetic compass orientation. More likely they change the perception of the magnetic field to such a degree that birds familiar with the pattern can use the information for orientation, while birds unfamiliar with the pattern are disoriented. On the contrary, higher intensity and broadband RF fields alter the perception of the magnetic field to such a degree that the birds no longer can extract directional information.

The sensitivity threshold of magnetic orientation of a long-distant migrant bird to radio-frequency magnetic fields

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We report the study aimed at determination of the minimum amplitude of oscillating magnetic field that would disrupt magnetic orientation of songbird migrants. Garden warblers, Sylvia borin, were placed in coils and subjected to oscillating magnetic fields at the frequency of 1.403 MHz with amplitudes 0, 0.4, 1, 2.4, 7 and 20nT. Orientation tests were conducted double-blind, according to the standard method, with the use of plastic Emlen funnels. Garden warblers were found to loose orientation in RF fields with amplitudes above 2 nT. Experiments with European robins, reported earlier by Ritz et al. (2009), showed higher sensitivity threshold, in between 5 and 15 nT. This may be related to the fact that garden warblers, as distinct from robins, are long-distance migrants and might have more sensitive magnetoreception system. The high sensitivity of the magnetic compass of migratory birds to high-frequency magnetic perturbations does not find explanation within the radical-pair model of magnetoreception. We discuss possible mechanisms that could provide such an extreme sensitivity.

Garden warblers are not disoriented by oscillating magnetic fields applied to their eyes

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It was shown previously that long-distance migrants, garden warblers (*Sylvia borin*), were disoriented in the presence of narrow-band oscillating magnetic field (OMF). The sensitivity threshold of the magnetic compass to the OMF was determined to be around 2–3 nT under 1.403 MHz. In this work, we used miniaturized portable magnetic coils, which generated the OMF with amplitude just above the sensitivity threshold (ca. 5 nT) to localize the compass-related magnetoreception in the organism of a bird. We performed behavioural experiments on orientation of first-year garden warblers in round arenas with local application of OMF to the area of retina, the most likely location of magnetoreceptors. The OMF in other parts of the birds head (upper beak and inner ear (lagena)), which might be involved in magnetoreception, was considerably lower than the sensitivity threshold. Surprisingly, the birds with local application of OMF to the area of retina were not disorientated and showed the seasonally appropriate migratory direction. On the contrary, the same birds placed in a homogeneous 5nT OMP generated by coils 0.75 m in diameter showed disorientation. We conclude that the disruption of magnetic orientation of birds by oscillating magnetic fields is not related to its effect on the magnetoreceptor allegedly situated in the eye. This work was supported by Russian Science Foundation (grant no. 16-14-10159).

Magnetic declination as a map tool in songbird migrants

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Determining East-West position is a classical problem in human sea navigation. Prior to the use of GPS satellites, extraordinarily accurate clocks were needed to measure the difference between local time and a fixed reference. Birds do not appear to possess a time-difference clock sense. Nevertheless, experienced night-migratory songbirds can correct for East-West displacements to unfamiliar territory. Consequently, migratory birds must solve the longitude problem in a different way. We showed that adult Eurasian reed warblers (*Acrocephalus scirpaceus*) can use magnetic declination (the difference in direction between geographic and magnetic North) to solve the longitude problem under clear night skies. Reed warblers migrating through Rybachy, Russia, were exposed to a declination change of 8.5° while all other cues remained unchanged. This corresponded to a virtual magnetic displacement to Scotland where such magnetic cues occur. Adult birds responded by changing their heading in Emlen funnels from WSW to ESE, consistent with a compensatory response. Juvenile birds without developed navigational skills oriented towards the WSW at the capture site and became randomly oriented after the declination treatment. However, European robins tested in the same way did not respond to the changed declination and were always oriented in their species-specific direction. This study suggests significant variation in how navigational maps are organised in different songbird migrants.

S2 Other Compasses

Experimental Systems Analysis - Understanding the factors that drive navigation in Homing Pigeons

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Our new project NavMap applies novel analytical techniques in combination with experimental manipulation of navigational factors to investigate the cues with which pigeons navigate. Past studies have produced conflicting reports on effects of individual experimental treatments when attempting to investigate specific sensory cues. If anything these past experiments already hint at a rather complex system involving multiple redundant cues. Recent developments in mathematical analysis of GPS tracks have not only provided direct evidence for this, but have also produced new methods, that allow us to take a direct look at the underlying mechanisms of the navigational process. NavMap aims to combine these new methods, with experimental treatments to investigate in detail the involvement of individual sensory modalities in the pigeon's navigational process. Here we present a first look at the initial findings from a larger ongoing study that has a broad focus on investigating, the involvement compass, route and map information. In this presentation we are going to focus on the involvement of the sun compass, magnetic and olfactory map information and are going to look if we can find general evidence for the long held presumption that birds in different areas in the world, occupying fundamentally different visual environments are prone to use different strategies to home.

Anosmic migrating songbirds demonstrate a compensatory response following long-distance translocation: a radio-tracking study

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A few studies have shown that migrating birds can navigate to their goals even from unfamiliar territory. It has been demonstrated that Eurasian reed warblers (Acrocephalus scirpacues) captured in spring in SE Baltic, displaced 1,000 km eastward and tested for orientation in orientation cages, show an orientation tendency towards their breeding grounds. It requires the ability to determine a new geographic position relative to the goal. The natural cues used for this behaviour remain controversial with both magnetic and olfactory cues proposed. Virtual displacement experiments have shown that the geomagnetic information alone is sufficient for reed warblers to find their geographic position but the role of olfaction was not explicitly tested. We displaced anosmic reed warblers together with untreated controls between the same capture and displacement sites where the Emlen funnel tests were previously performed. Following release, we radio-tracked birds for the first few kilometres using an array of automated radio towers. The result strongly suggests a navigational response of both anosmic and intact birds (re-orientation towards migratory corridor), unlike some other experiments testing the effect of anosmia on migrating birds. This result supports the hypothesis that, at least in this species, the olfactory system is not crucial for determining geographic position and the zinc sulphate anosmia treatment is unlikely to have any non-specific effects on navigational abilities.

Stellar compass of European robins Erithacus rubecula is time-independent

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It is known that birds can use different compass cues for orientation during migration, such as magnetic field of the Earth, the movement of the sun, polarized light and also the stars. Whereas the necessity of birds` internal clock for successful sun orientation has been claimed earlier, its role to the star orientation has remained unproven as all such experiments were carried out in the natural magnetic field, which could provide additional compass information and under the artificial stars. To clarify this we have caught European robins Erithacus rubecula on the Courish Spit during autumn migration, kept them indoors in a windowless room under the imitated local photoperiod and tested for their migratory orientation in Emlen funnels under the natural clear starry sky in the artificial vertical magnetic field in Merritt four-coil magnet system. After birds have shown orientation directions consistent with their normal autumn migratory direction, we changed the local photoperiod in the room where the birds were kept to the artificial photoperiod, clock-shifted four hours forward. When birds` activity rhythms were synchronized to the new photoperiod, their orientation was again tested under the natural clear starry sky in the artificial vertical magnetic field. The new distribution was not significantly different from the direction shown before clock-shift. Our data have independently proven that star compass of European robins is time-independent.

Reliance on familiar visual landmarks by anosmic pigeons

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The olfactory navigation hypothesis predicts that homing pigeons learn the association between wind-borne odours and wind direction at the home loft, so to develop an olfactory map of the surroundings. The prevalent local odours were shown to provide the birds spatial information for determining the home direction after displacement. Consistently, birds deprived of their sense of smell are impaired at homing when challenged to navigate over unfamiliar areas. However, anosmic birds are able to home when released within their familiar area. In order to assess whether the lack of olfactory cues during training releases may affect the birds' navigational strategies, we subjected two experimental groups of intact birds to one release from each of three sites located in different directions with respect to home. Prior the second release from any of the three sites, a group of birds was made anosmic. The development of route fidelity during repeated training releases in both experimental groups was studied. In the second release from each site the anosmic birds displayed unimpaired homing abilities, suggesting that a modest familiarity with the release site area is sufficient for unimpaired navigation. During training the anosmic birds displayed a greater fidelity to previously over-flown locations compared to the intact birds, providing a direct evidence that familiar visual landmarks constitute a critical source of navigational information when olfactory cues are not available.

S3 Cryptochromes

Magnetic Compass in Animals: Why is it so fragile to noise and what is the role of cryptochromes?

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It has been nearly two decades since the suggestion of cryptochrome as a magnetoreceptor candidate sparked a renewed interest in the radical pair mechanism as a potential mechanism underlying magnetic orientation. In this time, two set of insights have been gained into the workings of the magnetic compass, in addition to the previously found effects of ambient light on magnetic orientation: 1) In a few invertebrate species amenable to genetic approaches, functional cryptochromes are required for magnetic orientation and 2) the magnetic compass turns out to remarkably fragile to certain kinds of perturbations, in particular to radio frequency oscillating magnetic fields.

Here, I will first show that even a simple model linking light-dependent activation of cryptochromes to magnetic signaling can rationalize many of the observed light effects on the avian magnetic compass. However, I will also argue that the genetic experiments so far are entirely consistent with cryptochrome being simply a part of the magnetic signal transduction network rather than it being the magnetic receptor itself and discuss what future experiments may be most helpful to shed light about the exact role of cryptochromes.

Secondly, I will highlight the need to incorporate variations and noise in models of radical pair compasses rather than focusing exclusively on how to enhance the signal. I will show that even small amounts of noise can dramatically modify or abolish the signals of certain radical pair compass types, while other compasses are more robust against noise. Intriguingly, the signals of the recently discussed quantum needle compass type appear to be enhanced rather than reduced by noise. I will argue that identifying the fragility or robustness to noise may be a crucial and so far overlooked aspect that may hold the key for understanding how extremely weak artificial fields can disrupt magnetic orientation.

Retinal horizontal cells express Cry4: a new take on the avian light-dependent magnetic compass

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Birds can detect the Earth's magnetic field and use a light-dependent, radical-pair-based magnetic compass for orientation. Cryptochromes (Cry) located in the retina of birds have been suggested as the magnetoreceptors, since they are the only known vertebrate photopigments known to form radical-pairs upon photo-activation. Vertebrate-type Cry1 and Cry2, however, seem to not bind FAD, the photosensitive cofactor of cryptochromes, and may thus not be involved in light-dependent magnetoreception. Cry4, on the other hand, has retained the ability to bind FAD in vivo, thus is intrinsically photosensitive, which is crucial for the radical-pair mechanism to work. To investigate the location and distribution of Cry4 in the avian eye, we used immunohistochemistry on thin sections of zebra finch retinas. These birds use a light-dependent magnetic compass and express Cry4 in their retinas at constant levels. We found Cry4 expression in a subpopulation of horizontal cells in the retina, known to modulate the input from rods and cones to enhance contrast and aid in colour opponency. The involvement of horizontal cells in light-dependent magnetic compass reception provides intriguing evidence for a direct interaction of magnetic compass information with the visual system. Moreover, the observed distribution of Cry4 in only parts of the retina suggests a mechanism that provides orientation information but does not interfere with important visual tasks (feeding, predator avoidance).

The Molecular Landscape of the Pigeon Cryptochromes

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The ability to detect magnetic fields is a sense that is employed by a diverse array of animals on the planet to aid navigation. The mechanistic basis for this sense is unknown, but has been proposed to rely on the generation of radical pairs in photosensitive molecules. The cryptochromes are considered to be the most promising candidate proteins for such a light based magnetoreceptor. Five cryptochromes are present in the pigeon, which are broadly expressed and can be found in all major tissues. An important issue when considering the plausibility of cryptochromes as putative magnetoreceptors is their anatomical localisation and their interaction partners, and previous work revealed that cryptochrome transcript levels alter with time of day and are present in all major retinal layers. Accordingly, if cryptochromes are indeed the molecular mediators of the magnetic sense, they would need to interact with an adaptor molecule that confers both stability and specificity to a magnetosensitive complex. To this end, we generated monoclonal antibodies against all major cryptochromes found in the pigeon; clCRY1a, clCRY2, and clCRY4, and validated their specificity. Employing these unique tools we have performed co-immunoprecipitation experiments for each cryptochrome, defining it's interactome in the retina, liver and brain. This approach has identified retina specific cryptochrome interactors that may play a role in the magnetic sense.

Experimental Confirmation of Radical-pair-based Magnetic Field Effects in an Avian Cryptochrome

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It is well established that migratory birds use the Earth's magnetic field for navigation. The photoactive protein cryptochrome in the birds' retinas is proposed as the primary geomagnetic field sensor based on the radical pair mechanism. In this work, we expressed and purified an avian cryptochrome in order to study the magnetic field-dependence of its photochemistry. Various spectroscopic techniques were applied to investigate the photophysical behaviour of this protein. Picosecond transient absorption measurements and electron paramagnetic resonance spectroscopy on the wild-type cryptochrome and a series of carefully selected single-site mutations indicate that the flavin and a tetrad of tryptophan residues are involved in the photochemically-induced electron transfer cascade, consistent with previous observations of the photocycles of other animal cryptochromes. Furthermore, we report the first ever magnetic field effects on an avian cryptochrome. These results were obtained using highly sensitive cavity ring-down spectroscopy, and confirmed by transient absorption measurements. This work represents the first detailed experimental evidence that the radical pair mechanism can give rise to magnetosensitivity in an avian cryptochrome.

Studying cryptochromes through the computational microscope

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Clearly, the laws of physics hold and are exploited in living organisms. Speaking as a physicist, most biological characteristics stem from the laws of classical physics that students learn in their first year. However, crucial characteristics in organisms are governed by quantum physics. The latter characteristics are those in which biological processes involve the jumps of electrons from one state to another. The quantum behavior of electrons covers all chemical transformations, for example it arises in optical transitions induced through light absorption by biomolecules. The mechanism by which night-migratory songbirds sense the direction of the Earth's magnetic field appears to possibly rely on the quantum spin dynamics of light-induced radical pairs in cryptochrome proteins located in the retina. Cryptochrome binds internally the flavin cofactor, which governs it signaling through light-induced electron transfer involving a chain of four tryptophan residues. I will discuss the state-of-the-art computational tools available for studying cryptochrome-based magnetoreception, and that are qualified to be named as the computational microscope. In particular, I will introduce VIKING (Scandinavian Online Kit For Nanoscale Modeling) – a web-based service for automating computational modeling of biophysical systems. I will discuss the essentials of VIKING, and will then demonstrate how it can be used to study structure and dynamics of avian cryptochromes in silico.

Double-cone localisation and seasonal expression pattern suggest a role in magnetoreception for European robin cryptochrome 4

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The primary sensory molecule underlying light-dependent magnetic compass orientation in migratory birds has still not been identified. The cryptochromes are the only currently known class of candidate proteins which could mediate this mechanism in the avian retina. They are ubiquitously expressed in various animal tissues and some of them are involved in circadian clock regulation. Here, we report the identification of the complete cryptochrome 4 (Cry4) sequence isolated from the retina of the night-migratory songbird European robin. By quantitative RT-PCR, we find that Cry1a, Cry1b and Cry2 mRNA display robust circadian oscillation patterns, whereas Cry4 shows no obvious circadian fluctuation. When comparing the relative mRNA expression levels of the cryptochromes during the migration season relative to the non-migratory season in both migrating European robins and non-migrating chickens, we observe that Cry4 is significantly higher expressed during the migratory season only in the migratory birds. In immunohistochemistry double-stainings, we find Cry4 protein specifically located in photoreceptor outer segments of double-cones and long-wavelength cones, which would be an ideal location for light-dependent magnetoreception. Furthermore, our predicted structure of erCry4 protein suggests that erCry4 should bind flavin. In combination, these results lead us to suggest that avian retinal Cry4 could be the primary sensory protein mediating radical-pair-based magnetoreception.

S4 What if not Cryptochromes?

What if it's not cryptochrome?

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There is near universal agreement that cryptochromes play a central role in a light-dependent magnetic compass. Among epigean rodents, support for a radical pair mechanism (RPM) includes: (1) disruption of magnetic compass orientation by low-level radio frequency fields (e.g., Malkemper et al. 2015; Painter 2017), (2) a complex, axially-symmetrical pattern of magnetic input (Painter et al. 2013) and (3) the presence of light-dependent magnetoreceptors in the retina (Olcese 1990). Furthermore, both fly and human cryptochromes rescue light-dependent responses to magnetic cues in flies (Drosophila) that lack a wild-type cryptochrome gene (Foley et al. 2011). However, evidence for a RF-sensitive magnetic compass in murine rodents, consistent with a RPM, argues against cryptochrome's role in magnetoreception. Contrary to the conclusions of early investigators, mammalian (Type II) cryptochromes do not bind the flavin chromophores that are necessary to initiate light-dependent electron transfer reactions, and therefore are unlikely to be involved in magnetoreception (Kutter et al. 2017). Coupled with findings of the rescue experiments, this suggests that cryptochrome's role in magnetoreception needs to be reconsidered not only in mammals, but in other organisms as well. The remainder of the talk will discuss new evidence that a non-cryptochrome photopigment may be involved in the light-dependent magnetic compass. Literature Cited available upon request.

Exploring the minimal functional unit of magnetoreceptor (MagR) and a roadmap to MagR2.0

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Previously, a putative magnetoreceptor (MagR) and its complex with Cryptochrome (Cry) were identified, and a rod-like structure of MagR polymer assembled by twenty monomers was reported. Structural analysis indicated that a plate-like MagR tetramer might serve as the minimal functional unit for both protein assembly and magnetoreception. Here in this study, a single chain tetramer MagR fusion protein (SctMagR) was designed, expressed and purified to explore the dynamical assembly process of MagR, and to study the connections between MagR assembly and magnetic sensing. Hierarchical assembly of MagR polymer was visualized and a series of different assembly status was identified, indicating that SctMagR could be the basic structural unit of MagR polymer. Obvious paramagnetism was observed with cells expressing SctMagR in magnetic field, stronger response to magnetic field using purified SctMagR protein was recorded in different experiments, suggesting SctMagR may represent the minimal magnetic unit and improved version for magnetosensing.

Antibiotics effect migratory restlessness orientation in a migrating passerine: first experimental support for the symbiotic magnetoreception hypothesis

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Magnetoreception is a sense which allows the organism to perceive and act according to different parameters of the magnetic field. This magnetic sense plays part in many fundamental processes in various living organisms. Much effort was expended in finding the 'magnetic sensor' in animals. While some experiments show a roll of the ophthalmic nerve in magnetic sensing, others show that effects of light on processes in the cornea are involved. According to these inconclusive and puzzling findings, the scientific community has yet to reach an agreement concerning the underlying mechanism behind animal magnetic sensing. Recently, the symbiotic magnetotaxis hypothesis has been forwarded as a mechanistic explanation to the phenomena of animal magnetoreception. It suggests a symbiotic relationship between magnetotactic bacteria (MTB) and the navigating host. Here we show that opposed to the control group, antibiotic treatment caused a lack of clear directionality in an Emlen funnel experiment. Moreover, the effect of antibiotics on orientation was also apparent in significantly reduced individual repeatability of directional preference in a cage setup. These effects of antibiotics on magnetic sensing associated behavior may be interpreted as the first experimental support of the symbiotic magnetotactic hypothesis. To the best of our knowledge this is the first reported effect of antibiotics on animal orientation.

Magnetic compass in pigeon retina: electroretinographic study

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There is a large body of indirect evidence suggesting that avian magnetic compass is localized in the retina We studied whether changes in external magnetic field (MF) can modulate visual signals in avian retina. Study was performed on pigeons. Photoresponses were recorded using ex vivo electroretinography (ERG). MF (amplitude 50 μT) was modulated by Helmholtz coils. Light stimuli (blue and red) were applied under two different inclinations of MF – 0° and 90°. We performed 2 series: 1) with intact isolated retina and 2) with pharmacological isolation of photoreceptor responses (adding aspartate + BaCl2). 1st series: Comparison of responses to blue flashes under two directions of MF showed that response amplitude under MF with 0° inclination was significantly higher than under 90° inclination (t-test, $n = 20$, $p = 0.023$). Responses to red flashes showed no difference under two directions of MF. 2nd series: No significant effects of MF direction change on photoreceptor responses to blue or red flashes were found. Conclusion: We found that changes in MF modulate amplitude of ERG-responses of intact retina to blue but not to red flashes. It is in a good agreement with behavioral data about birds ability to orient under blue but not red light. Effect of MF change was not observed on isolated photoreceptor responses. One explanation could be that magnetic compass is localized in other retinal cells, not in photoreceptors. Study was supported by grant 16-14-10159 from the RSF.

S5 Brain

Different structure same function: avian hippocampus and spatial memory

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Birds' hippocampus, contrary to its mammalian homolog, lacks a layered structure. However also in birds this structure is crucial for spatial orientation. The question of how such different structures can support similar functions requires to investigate the avian hippocampus in ways that can be directly compared to mammalian studies. Here I will present the results of a series of experiments with two species of birds (zebra finches and domestic chicks), which questioned how far theories developed for mammalian hippocampus can also be applied to the avian hippocampal formation, using experimental setups equivalent to those used for rodents. In zebra finches (Taeniopygia guttata) we demonstrated the role of the avian hippocampus in learning and recall of a spatial task based on allocentric cues, in contrast to orientation on local cues, which, like in rodents, does not involve hippocampus. We also found enhanced hippocampal activation (by visualizing c-Fos to map neuronal activity) of domestic chicks (Gallus gallus) that used the geometrical shape of the environment to orient, compared to chicks trained to discriminate local features. Another study with chicks revealed a change in the neural representation of two different environmental shapes in the hippocampus, pointing to a remapping-like effect, in line with rodents' studies. This work has implications for the understanding hippocampal representations in birds and the evolutionary history of spatial cognition.

Cluster N activity in migrating nocturnal birds: Circadian control or facultative regulation?

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The navigation of avian migration in part relies on the use of a geomagnetic compass. Cluster N, a forebrain region thought to be involved in geomagnetic processing, is active at night when birds are active with migration. However, no comparison of Cluster N activation within the same species has been made between birds exhibiting or not exhibiting nocturnal migratory restlessness (Zugunruhe). Question: Is Cluster N activity under circadian control regardless of migratory behavior, or is it facultatively regulated? We housed nocturnal migrating white-throated sparrows (Zonotrichia albicollis) in outdoor aviaries. W-t sparrows are also the first species of western hemisphere migrant examined for Cluster N activation during migration. Brains were collected during the day or at night. At night, brains were collected from birds that were exhibiting migratory restlessness as well as those that were inactive, as observed with IR video. Three different groups were employed: day (n=5), night active (n=7) and night inactive (n=6). We used immunohistochemistry to quantify immediate-early gene (ZENK) expression in Cluster N. Night migratory active birds had a significantly greater number of ZENK-active neurons in Cluster N than those in the day, and more importantly, night migratory inactive groups. We conclude that Cluster N is behaviorally regulated on a night to night basis, and given the importance of retinal stimulation, likely reflects "eyes open" during nights with migration.

The cortival visual pathway is necessary for landmark anchoring of head direction cells in the rat

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In order for an animal to navigate, the brain must form and update spatial maps to represent the world. One such representation is produced by head direction (HD) cells - a population of neurons that modulate their activity depending on the bearing of the animal's head, forming a 'neural compass' that may underlie an animal's sense of direction. On a neural level, in order to accurately reflect the animal's continually changing head direction, the HD cell population is believed to integrate idiothetic (self-motion) and allothetic (external) sensory information into a single abstracted representation of direction. Accordingly, the population of HD cells is seen to 'anchor' to visual features in an environment, and use these landmarks to reorient the animal. Recent work in our lab aimed to elucidate the brain pathway that provides visual information to HD cells. We present HD cells recorded from rats with lesions of a key nucleus in the cortical visual pathway, one of two predominant visual processing pathways in the brain. In rats with impaired cortical vision, HD cells are unable to use visual scenes to reorient their firing activity relative to the external environment. In these rats, HD cells remain directionally modulated, but may have wider tuning curves, indicating a reduction in the precision of the directional code. These results suggest that navigation circuits in the brain may require intact cortical visual areas to align accurately with the external visual world.

Evidence for a separate brain pathway processing magnetic map information in migratory birds

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Displacement experiments have shown that birds can not only derive directional ("compass") but also positional ("map") cues from Earth´s magnetic field parameters to navigate during their migratory journeys. Input from the ophthalmic branches of trigeminal nerves (V1) is required for magnetic map-based but not magnetic compass orientation and was shown to induce magnetic field-dependent activation in ventral parts of the principle trigeminal brainstem nuclei (PrVv). These findings make the PrVv a likely primary brain relay for magnetic map information. Where and how is magnetic map information further processed in a bird´s brain? While trigeminally perceived somatosensory information is transmitted from the dorsal PrV to the telencephalic basorostral nucleus (NB) any connections from the magnetically activated PrVv have remained elusive. Using neuronal tract tracing and morphometric analyses in the trigeminal brainstem of migratory Eurasian blackcaps (Sylvia atricapilla), we here present the first evidence that PrVv is a part of a morphologically distinct neuronal subpopulation, which seems to form the origin of an exclusive projection to the frontal telencephalon. This discrete connection seems to be a part of a previously unknown avian brain pathway that could exclusively be dedicated to transmit trigeminal magnetic map information to higher-order forebrain centres in order to calculate navigational goals.

S6 Genetics Approaches

The molecular signatures of magnetite-based magnetoreception: evidence from transcriptomics

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Despite numerous animals utilizing Earth's magnetic field for orientation and navigation, the underlying mechanism of this magnetic sense remains unclear. A majority of what is known regarding magnetoreception results from decades of behavioral research in many canonical long-distance migratory species. Our research, however, has been utilizing advances in next-generation sequencing and transcriptomics to identify candidate magnetoreception genes and locate tissues containing probable magnetoreceptors. This presentation summarizes results from trout (Oncorhynchus mykiss) demonstrating that a magnetic pulse elicits gene expression changes in the brain, but has little to no effect in the retina. Although both tissues have been suggested to contain putative magnetoreceptors, these findings indicate that the brain is a more likely location. We also found that the expression of genes associated with iron regulation (e.g. frim) and the development and repair of photoreceptive structures (e.g. crygm3, purp, crabp1) was altered; implicating them in either a magnetic sense or as a consequence of pulse magnetization. Finally, we discuss ongoing work further characterizing these genes and others linked to iron regulation in the brain of Chinook salmon (O. tshawytscha) using a time-series approach. These studies are the first to use transcriptomics to identify candidate genes that respond to pulse magnetization and has important implications for the characterization of a magnetic sense.

Whole brain clearing and imaging reveals magnetically activated brain regions in the mouse

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Magnetoreception is the ability to sense and respond to the Earth's magnetic field and is used by animals to solve a large variety of spatial tasks. Although knowledge about the magnetic sense is growing, and magnetic sensitivity seems to be commonplace in the animal kingdom, the neurobiological basis and location of the magnetoreceptor(s) remain unknown. Multiple behavioral studies indicated that rodents, including mice, possess a magnetic compass. Here, we employ male C57/BL6 mice as a model system to identify brain regions involved in processing magnetic information by focusing on intermediate early gene expression (C-fos). In order to generate an unbiased picture of brain activation in response to magnetic field changes we used whole brain clearing, immunostaining (iDISCO), light sheet microscopy and voxel based comparative analysis. We report magnetically induced neuronal activation in several brain regions of interest in both head-fixed awake animals and anaesthetized mice. In the future we will exploit the powerful genetic tools in mice to ablate putative magneto-sensitive molecules of interest.

The chromatin accessibility landscape in the brain of a migrant songbird

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Bird migration is a fascinating behaviour of journeys between breeding and wintering grounds. This behaviour relies on multiple adaptations for optimized flight, timing and navigation. Such adaptations have been shown to be heritable, but the identity of the molecular mechanisms is largely unknown. Population genomics approaches have shown associations of regions in the genome differentiating between populations with different patterns of migration. Nonetheless, the underlying demographic and evolutionary variables of these approaches, makes it difficult to find functional associations with migration. To overcome this, our approach expands beyond genomic sequence to identify the gene regulation networks and pathways of migration. We have designed a common garden experiment with populations of European blackcaps (*Sylvia atricapilla*) known to have different orientation patterns. We sampled brain areas based on the assumption of relevance with seasonal and orientation/navigational features. We focus on i) the suprachiasmatic nucleus (SCN), a brain region controlling circadian and circannual regulatory processes, ii) hippocampus a brain region involved in spatial navigation, and iii) cluster N a brain region involved in magnetic compass orientation. In these brain areas, we used ATAC-seq to obtain the genome-wide landscape of chromatin accessibility and identify cis-regulatory components changing between different migratory seasons and orientation patterns.

S7 Independent Replication & New Technologies

The importance of independent replication: a study of magnetic field effects on Drosophila melanogaster

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Independent replication of published studies is a core feature of science. In our case, we wanted to replicate two influential studies of magnetic field effects on Drosophila: Gegear et al. 2008 and Fedele et al., 2014. Both studies were performed to shed light on the mechanisms of magnetoreception (Hore & Mouritsen, 2016). Drosophila are the only animals whose behaviour has been claimed to be affected by magnetic fields in a cryptochrome-dependent fashion, in accordance with the radical pair mechanism. In the first study it was reported that flies, following a classic Pavlovian paradigm, could associate a magnetic field with a sucrose reward in a T-maze assay. The second claimed that negative geotaxis (the ability to climb against gravity) was disrupted when the flies were exposed to a magnetic field. We redid both studies at the University of Oldenburg inside one of the truly non-magnetic and radiofrequency-screened chambers described by Schwarze et al., 2016. Both were conducted using double-blind protocols in a more controlled manner than the original studies and with much larger sample sizes (n = 79,000 and n = 11,000, respectively). Both investigations failed to reproduce the reported effects of 500 mT static magnetic fields on the flies' behaviour. Our results question whether Drosophilae are actually capable of sensing magnetic fields.

Searching for magnetite in the pigeon lagena

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It is well established that an array of Avian species senses the Earth's geomagnetic field and uses this information for orientation and navigation. While the existence of magnetic sense can no longer be disputed, the underlying cellular and biophysical basis remains unknown. It has been proposed that pigeons exploit a magnetoreceptor based on magnetite crystals (Fe3O4) that are located within the lagena, a sensory epithelium of the inner ear. It has been hypothesised that these magnetic crystals form a bed of otoconia, that stimulate hair cells transducing magnetic information into a neuronal impulse. We performed a systematic high-sensitivity screen for iron in the pigeon lagena using synchrotron X-ray fluorescence microscopy coupled with the analysis of serial sections by transmission electron microscopy. We find no evidence for extracellular magnetic otoconia or intracellular magnetite crystals suggesting that if an inner ear magnetic sensor does exist it relies on a different biophysical mechanism.

New technologies to address old questions of magnetic orientation in free-roaming animals

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The recent emergence of biologging technologies are providing powerful opportunities to collect a wealth of information from free-roaming animals for studies of animal behavior and movement ecology. We take advantage of miniaturized tri-axial accelerometer and magnetometer sensors, integrated with GPS technology, to further characterize magnetic alignment responses reported across a range of wild animals. Specifically, raw accelerometer signatures, synced with ground-truth video records, are used to create machine learning classifiers to identify discrete behaviors in free-roaming wild boar (Sus scrofa), shown previously to exhibit spatial behaviors consistent with magnetic alignment responses. Magnetometer data are combined with the behavioral classifiers to create 'magnetic ethograms' used to evaluate magnetic orientation in wild boar without the need for direct observation. In addition, we have designed radio frequency antennas that broadcast in the frequency range shown to disrupt magnetic orientation in a variety of animals. Combining these antennas with the biologging collars will provide a unique test for the involvement of a quantum related biophysical mechanism mediating magnetic alignment in wild boar. These technologies will help to revolutionize studies of magnetic orientation in free-roaming animals, and will offer new possibilities to investigate a range of behavioral and ecological processes across spatiotemporal scales never before possible in wild animals.

A brain-wide screen for magnetically-induced activity in the pigeon

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The remarkable navigatory abilities of the rock pigeon (*Columba livia*) are facilitated by a sensory system that allows the detection of magnetic fields. While there is compelling behavioral evidence demonstrating the existence of a magnetic sense, the primary sensory cells have yet to be identified, and the neuronal circuits that process magnetic information in the brain are largely unknown. To address these issues, we have developed tissue clearing coupled with light sheet microscopy to quantitate the expression of immediate early genes in the pigeon. We adapted existing open source software to map individual brain scans to custom-built reference templates, allowing us to compare neuronal activity between treatment groups at a cellular resolution on a brain wide scale. As a proof-of-principle, we exposed pigeons to high-frequency sounds and show that our analysis pipeline detects significant activity in the major stations of the central auditory pathway. This experimental platform represents an important tool to globally assess sensory-driven immediate early gene expression in the avian brain. We anticipate that it will shed light on the pigeon's central magnetosensory circuit and will provide key insides for the localization of primary magnetoreceptive cells in the periphery.

S8 It's Not All About Birds (Insects)

Virtual reality exploration of bumblebees' scanning behaviour in a 3D flight arena during object discrimination

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A fundamental visual theory of object recognition stipulates that, in humans, objects are memorized as arrangements of simple parts (vertices and edges) and their relationships (Biederman, 1987). Because this solution economizes on storage capacity, it might be even more viable in small-brained animals such as bees, which possess a brain of just 1mm3 comprising 960 000 neurons, yet exhibit remarkable cognitive and navigational capabilities. However, little is known as to how bees store visual patterns in memory. We developed a bee tracking system with stereoscopic imaging which was processed to recover 3D flight path data that we subsequently explored within an immersive Virtual Reality presentation. Studies on human vision showed deletion of vertices results in a larger decline in object recognition performance than the deletion of edges (Biederman & Cooper, 1991; Szwed, Cohen, Qiao, & Dehaene, 2009). Using a simple discrimination task between a square and a triangle, we found that, although there are individual differences between bees trained to associate a reward with square or triangle, all bees tend to rely on vertices to discriminate and distinguish the objects, as humans do. Moreover, by exploring the data in the VR environment, in particular the Z-coordinate (distance from the target), we can better appreciate and reconstruct the appearance of the stimuli, noticing that the bees preferentially scanned the bottom of the shapes and exhibit a visual lateralization.

The Earth's Magnetic Field and Visual Landmarks Steer Migratory Flight Behavior in the Nocturnal Australian Bogong Moth

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The Australian Bogong moth is a remarkable nocturnal navigator, undertaking a yearly migration over enormous distances from the Southern Queensland to the alpine regions of New South Wales and Victoria. After emerging from their pupae in early Spring, adult Bogong moths embark on a long (~ 1000km) southerly journey towards the Australian Alps. Once in the Mountains, Bogong moths (in hundreds of thousands) seek out the shelter of high ridge-top caves. Towards the end of the summer, the same individuals that arrived months earlier emerge from the caves and begin their long return trip to their place of birth. Once there, moths mate, lay eggs and die. The moths that hatch in the following Spring then repeat the migratory cycle afresh. But how do the moths find their way to the desired regions? Animals need external cues to perform compass orientation that allows them to migrate through unknown territories or environments. By tethering migrating moths in an outdoor flight simulator, we found that their flight direction turned predictably when dominant visual landmarks and a natural Earth-strength magnetic field were turned together, but that the moths became disoriented when these cues were set in conflict. Our results suggest a navigational strategy whereby moths use their magnetic compass to find their inherited migratory direction but use one or more visual landmarks as orientation beacons, apparently rechecking landmark fidelity with the compass every few minutes.

Interactions of navigational strategies during the learning of environmental information in ants

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Effective navigation is a multimodal process taking into account information from different sources tuned to the sensory ecology of a navigator. For ants, the combination of innate navigational strategies and the learning of environmental information is a key to their success, with the main innate strategy being Path Integration (PI). We recorded ants being guided by PI and found that (i) ants' walking speed decreases significantly along homing paths and stays low during subsequent search paths and (ii) ants are influenced more strongly by novel or learnt visual cues the further along their homing path they are. These results suggest that PI modulates speed along the homing path in a way that might help ants search for, utilise or learn environmental information at important locations. Ants walk more slowly and sinuously when encountering novel or altered visual cues and occasionally stop and scan the world, this might indicate the re-learning of visual information. We also investigated how two learned sensory modalities interact by looking at visual and olfactory guidance in navigating ants. We see that multiple cues lead to more accurate and efficient ants, but with more complex paths. Moreover, if olfactory and visual cues are learnt together, both of the cues are necessary for successful navigation. However, this binding seems to depend on the 'usefulness' of the available cues.

Resolving the heading-direction ambiguity in vertical-beam radar observations of migrating insects

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Each year, massive numbers of insects fly across the continents at heights of hundreds of metres, carried by the wind. These migrations not only bring benefits but can also lead to serious economic and social impacts. To investigate the insects' flight behavior and their response to winds, entomological radar is one of the most important tools, but its observations of insect orientation are ambiguous with regard to the head/tail directions and this greatly hinders interpretation of the migrants' behavior. We have developed two related methods of using wind data to resolve the head/tail ambiguity and we have compared their outputs with those from a method used previously, by applying all three methods to radar observations of Australian Plague Locust migration. For the study dataset, some of the headings selected by the previous method are shown to be clearly incorrect. The two new methods reveal a significantly different, and presumably much more accurate, relationship of heading direction to track direction. However, use of these methods leads to quite a large proportion of the sample being lost, as they eliminate occasions when the available wind values are identified as being unreliable. The two new methods produce similar results and appear to be a significant improvement on the previous method. These new methods have moreover demonstrated that locusts are frequently oriented at a large angle to their track, and that quite often their movement is slightly 'tail-first'.

S9 It's Not All About Birds

Biophysics of Magnetoreception Evidenced from Alpha Waves in the Human Brain

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Magnetoreception, the perception of the geomagnetic field, is a sensory modality well-established across all major groups of vertebrates and some invertebrates, but its presence in humans has only been tested rarely, yielding inconclusive results. We report here a strong, specific human brain response to ecologically-relevant rotations of Earth-strength magnetic fields. Following geomagnetic stimulation, a drop in amplitude of EEG alpha oscillations (8-13 Hz) occurred in a repeatable manner; termed alpha event-related desynchronization (alpha-ERD), such a response has been found to arise from sensory and cognitive processing of external stimuli in visual, auditory, and somatosensory domains. Biophysical tests showed that the neural response was sensitive to the dynamic components and axial alignment of the field, but also to the static components and polarity of the field. The pattern of these results rules out electrical induction or quantum-compass based mechanisms as the biophysical basis for the sensory transduction, but are compatible with ferromagnetism.

Planarians possess a light-independent, circadian time-dependent magnetic inclination compass

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As there is the need in the magnetoreception field for simpler animal models, we have focused our efforts on planarians, a well-studied invertebrate in the field of regeneration. We set-up a simple behavioural test consisting of a 14.5 cm diameter arena surrounded by a 3D Helmholtz coils system encased in a Faraday cage. After a 2 minute-habituation period, the worm (D. dorotocephala, Dd) was released at the centre of the arena. Under IR illumination, Strasbourg magnetic field (SMF) and during the dark period, Dd showed a preferential westward orientation (μ: 266.7+/-68.3°, $p<0.001$). Such behaviour was abolished either during cancelation of the SMF. Reversal of the horizontal component did not affect Dd's orientation, whereas shifting the vertical component by 180° triggered a full eastward orientation (μ: 86.8+/-68.1°, $p<0.001$). Pushing the idea further, it was found that the worms only oriented with SMF inclination +/- 11°. The principle of an inclination compass was later supported by experiments carried out on other planarian species. Besides, we were also able to narrow down the magnetosensitive behaviour to a small area of the tail region of Dd. On the other hand, testing Dds during the subjective day resulted in a NE orientation (μ: 52.0+/-76.4°, $p<0.001$) suggesting a 360° turn over a day period. This was later confirmed by testing the same population of worms over a 48 H-interval. A possible use of this circadian time-dependent compass would be for homing behaviour.

Lassie come home: Homing strategies in hunting dogs

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There are many anecdotal reports about astonishing homing abilities in domestic dogs, yet this phenomenon was never studied systematically. Hunting dogs (scent hounds) have been bred for sencturies to search for the game in the forest, to stop („tree“) it and attract the hunter by barking. During tracking they might depart for several hundred meters or kilometers in an unknown terrain. If they fail to find the game or if the hunter does not come they have to find the way back and to return. We equipped 26 dogs dogs with GPS collars and action cams and recorded their homing strategies in more than 700 trials. We found that in 42 % of trials dogs did not returned following their own scent trail but used a novel inbound route. Interestingly, this „scouting“ for a new way home started in most cases , i.e. significantly, with a short route along the north-south axis, independently in which direction the goal actually was. We suggest that initial locomotion along the north-south axis serves to organize and read the cognitive map. In analogy, we reported already previously, that roe deer, if surprised, prefer to start ist escape along the north-south axis.

Tadpole transporting frogs use map-like spatial memory to navigate the rainforest

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The ability to take optimal routes between any two locations within a familiar area without directly perceiving the goal is a hallmark of flexible, map-like spatial memory. It is widely accepted that mammals and birds use such spatial representations when navigating in their local area, but how widespread such ability is among other vertebrates remains an open question. We experimentally tested the flexibility of the spatial memory in a small rainforest frog under natural conditions. Males of Allobates femoralis shuttle their tadpoles from terrestrial territories to small pools tens to hundreds of meters away, relying on spatial memory to locate them. We displaced the frogs and quantified their ability to find artificial pools using tracking. To test if the frogs flexibly adjust their trajectory after displacement en route, we translocated tadpole carrying frogs captured at the pools. We also displaced frogs from their territories and released them in an area that was familiar or new to them. We experimentally induced their pool searching behavior by placing tadpoles on frogs, and we manipulated direct cues associated with pools, such as the odor by covering and removing the pools. Local frogs in all conditions navigated straight to pool sites, even when direct cues were not available. Most frogs unfamiliar with the area were unable to locate even the nearby pools. These results strongly suggest that A. femoralis use map-like spatial memory to navigate in the rainforest.

Going home magnetically: geomagnetic imprinting in sea turtles and salmon

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Various marine animals, including sea turtles, fish, and mammals, migrate across vast expanses of ocean before returning as adults to reproduce in the areas where they originated. How animals accomplish such feats of natal homing has remained an enduring mystery, but growing evidence suggests that sea turtles and salmon imprint on the magnetic field of their home area when young and use this information to return as adults. Both turtles and salmon have the sensory abilities needed to detect the unique 'magnetic signature' of a coastal area. Analyses have revealed that, for both groups of animals, subtle changes in the geomagnetic field of the home region are correlated with changes in natal homing behavior. In turtles, a relationship between population genetic structure and the magnetic fields that exist at nesting beaches has also been detected, consistent with the hypothesis that turtles recognize their natal areas on the basis of magnetic cues. Salmon likely use a biphasic navigational strategy in which magnetic cues guide fish through the open sea and into the proximity of the home river where chemical cues allow completion of the spawning migration. Similarly, turtles may also exploit local cues to help pinpoint nesting areas at the end of migrations. During most of the migration, however, magnetic navigation appears likely to be the primary mode of guidance during long-distance natal homing in both sea turtles and salmon.

Distance estimation in a coral reef fish, Rhinecanthus aculeatus

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The Picasso Triggerfish, Rhinecanthus aculeatus is a territorial coral-reef fish of the Indo-Pacific Ocean. Their territories are large and visually complex and they spend much of their day foraging for small fish. An ability to navigate efficiently is crucial to their survival and success. One mechanism by which they could move between patches and return home is path integration. This involves the animal continuously updating its distance and direction travelled such that it can follow a direct vector home. To understand how the path integration system in these animals works, we must explore how they collect this distance and direction information. Previous studies have looked at directional sensing in fish in the context of a long-range compass, with evidence that different species can use a time compensated sun compass, magnetosensation or polarised light to discern their direction of travel. However, the cognitive and mechanistic basis of distance estimation remains entirely unexplored in fish. Using the Picasso Triggerfish as my model system, I present the results of an operant conditioning task providing the first direct evidence that fish can keep track of their linear distance travelled. I also test the hypothesis that these fish rely on optic flow cues in their odometers, extending previous research with bees, ants and spiders as well as humans and rats. These results bridge the gap between our understanding of path integration in fish and terrestrial animals.

Diversification of the neural substrate of mental maps in primates

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Comparative studies of the hippocampal formation (HF) are used to approximate the evolution of mental navigational abilities; species with larger HF are thought possess greater navigational abilities. HF, however, is composed of subregions with distinct navigational functions, and little is known about evolution of these subregions. We investigate size changes in these HF subregions between two primates groups inhabiting different navigational niches: diurnal anthropoids (humans and our closest relatives) and nocturnal strepsirrhines. HF subregions are scaled against the functionally independent medulla to create a cross-species measure of relative volume. As complex foraging decisions (increased navigational ability) are thought to have driven anthropoid brain expansion, we hypothesized that anthropoids would possess larger HF subregions than strepsirrhines. Results instead indicate that anthropoids experienced a selective decrease across HF subregions compared to the strepsirrhine-like ancestral condition. We propose two explanations. Either strepsirrhines possess greater navigational abilities than anthropoids, or navigational processing in anthropoids has greatly shifted to the neocortex. Humans deviate from other anthropoids in displaying enlargement across HF subregions, suggesting that humans co-opted the HF navigational system for additional functionality. Neurological work points toward human's expanded capacity for mental time travel, which is also controlled by HF.

Sensory Transduction of Radio Waves by Biogenic Magnetite: An alternative to the Cryptochrome Quantum Compass Hypothesis of Magnetoreception

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In laboratory experiments, many migratory and homing animals fail to orient normally to earth-strength magnetic fields when exposed to weak radio waves (Rf) in the 0.2-9 MHz range. The phyletic diversity argues that this is a primitive feature of the animal magnetosensory system, which is often interpreted as the 'smoking gun' proof for a magnetic quantum compass receptor. However, the sensitivity of the system (~ 1 nT) and broad-band nature of the effects are difficult to explain. Two separate studies lead us to propose that biological magnetite alone might be able to account for the radio wave effects. Kellnberger et al. (2016) demonstrated experimentally the magnetoacoustic effect, in which the energy of an incipient radio wave acting on single-domain magnetite is converted to ultrasound at the second harmonic of the radio frequency. Second, Kubanek et al. (2016) discovered a class of trans-membrane ion channels that were activated by ultrasound in this same frequency band. If those ion channels were expressed in the lipid-bilayer membranes surrounding magnetosomes, they could constitute the biological radio-wave receptor. By making use of the Stoner-Wohlfarth model for magnetic moment behavior of single-domain particles, we place quantitative constraints on the magnetite crystal size, shape, and spatial distribution needed to reach the thermal noise barrier at such weak fields, and with a broad-band response. Rf is no longer the 'smoking gun' for a quantum compass.

Blue light-dependent human magnetoreception in geomagnetic food orientation

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Magnetic fields, including the Earth's geomagnetic field (GMF), are known to influence a wide phylogenetic range of creatures with magnetoreception, from bacteria to mammals, as a sensory cue or a physiological modulator. Despite some previous evidence, it is largely accepted that humans cannot sense magnetic fields. Here, we show that humans sense the GMF to orient their direction toward food in a self-rotatory chair experiment. Starved men significantly oriented toward the modulated magnetic north or east, directions which had been previously food-associated, without any other helpful cues, including sight and sound. The orientation was reproduced under blue light but was abolished under a blindfold or a longer wavelength, indicating that blue light is necessary for magnetic orientation. Importantly, inversion of the vertical component of the GMF resulted in orientation toward the magnetic south, indicating that orientation is dependent on an inclination compass. Moreover, blood glucose levels resulting from food appeared to act as a motivator for sensing a magnetic field direction. The results demonstrated that humans can sense the GMF and use it for magnetic food orientation when starved, and suggest that a cryptochrome-mediated radical pair mechanism may underlie the magnetoreceptive behaviors.

Compensation for wind drift in the Thrushes during autumn nocturnal migratory flight

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The data collected on the Courish Spit of the Baltic Sea by the Electronic-optical system allowed to investigate the mechanism of wind drift compensation in the Thrushes during autumn nocturnal migration. Turdus spp (by 90% represented by one species the Song Thrush) were identified by their silhouettes, linear size, and wing-beat pattern. Our equipment allowed to receive images of flying birds in the dark at the altitude up to 800m, to measure track and heading direction, ground and airspeed. The results clearly showed that during autumn migration, when the bird flux consists mainly of young navigationally naïve birds, the thrushes compensate for lateral wind drift along the leading line of the Spite. The completeness of compensation depends not only on wind velocity but also on altitude. Below 300m thrushes compensate completely, between 300 and 600m partly, and above 600 m they don't compensate at all. The compensation is achieved by combination of air speed and heading adjustment. Increasing side wind component causes an increase of both airspeed and angle between track and heading (up to 70˚). The dynamic simulation models which imitate the migratory flux of thrushes from Baltic region to their winter quarters in SW Europe helped to estimate the contribution of wind drift compensation along the leading lines. The role of wind drift compensation seems to be not as essential as wind selection but enables birds to mitigate deviation from the route and avoid offshore drift.

A reinterpretation of "Homing pigeons' flight over and under low stratus" based on atmospheric propagation modeling of infrasonic navigational cues

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Pigeons flying above low-stratus layers apparently lacked important navigational cues, and a reinterpretation of Wagner's 1978 study suggests these cues were low-frequency acoustic signals (infrasound). Wagner conducted 6 releases from topographic highs that emerged like "islands" above a low-stratus "sea". This weather condition over the Swiss Plateau results from temperature inversions common during autumn and winter months. Wagner made the releases to see if his pigeons could locate their loft beneath it. Birds remaining above the clouds appeared lost: they flew towards other mountain "islands", flew away from home, and circled in "searching" flights for up to 40 min. Those birds that descended beneath the clouds returned home on the same day. Atmospheric propagation modeling of infrasonic waves was done using a Hamiltonian Acoustic Ray-tracing Program for the Atmosphere (HARPA). The input meteorological data for the release days was recorded at the Payerne station located ~40 km W of the loft. The resulting HARPA models show that infrasonic waves transmitted from the loft area would have been ducted beneath the inversion layers and would not have reached the release sites above them. Presumably, other putative navigational cues (geomagnetic, olfactory) would have been available there. The absence of infrasonic cues above temperature inversions could explain the disorientation of Wagner's birds, especially if such signals are the predominant ones used by pigeons to home.

Gravity vector theory of pigeon navigation: predicted release sites entail severe homing problems as revealed by GPS tracking

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The gravity vector theory holds that many avian species possess an imprinted memory of the gravity vector at their hatching site. If true, comparing the actual gravity vector with the remembered one enables a displaced bird to calculate direction and distance to home. Problems arise at the border zone of gravity anomalies where the gravity vector is horizontally „tilted". Thus, at such release sites, the birds will miscalculate their position and the position of the goal, and one can expect severe homing problems and losses. Following earlier studies in the central Ukraine, we here report that highly pretrained homing pigeons released from geophysically predicted difficult spots are severely impaired in returning to the loft or get lost. Moreover, directionally trained birds whose release sites were extended along the training directions into regions containing anomalies showed suddenly slow homing or highly deviant homing pathways. Based on a preliminary analysis of 521 tracks collected in 2012, 2013 and 2017, we conclude that the gravity vector theory could explain or predict homing problems in 5 out of 6 studies – a respectable consistency in the field of navigation research. Navigation problems were compounded by geomagnetic anomalies while we could not test olfactory influences. Nonetheless, our data point to an unknown sense for the direction of gravity – possibly related to intracellular structures depending on genes activated by gravity changes – the gravitome.

How to dig a straight tunnel? Magnetic field as heading indicator in subterranean rodents?

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Subterranean mammals are able to dig long straight tunnels. Keeping the course of such 'runways' is important in the context of optimal foraging strategies and natal or mating dispersal. These tunnels are built in the course of several weeks to years, and, in social species, by several animals. Although the ability to keep the course of digging was recorded in the 1950s, its proximate mechanism could still not be satisfactorily explained. Here, we analyzed the directional orientation of 40 burrow systems in three species of African mole-rats (Fukomys anselli, F. mechowii, Heliophobius argenteocinereus) on the base of detailed maps of burrow systems charted within the framework of other studies and provided to us. The directional orientation of the vast majority of all evaluated burrow systems on the individual level (94 %) showed a significant deviation from a random distribution. The second order statistics (averaging mean vectors of all the studied burrow systems of a respective genus or species) revealed significant deviations from random distribution with a prevalence of about north-south oriented tunnels. We suggest that the Earth's magnetic field acts as a common heading indicator, facilitating to keep the course of digging. This study provides a field test and further evidence for magnetoreception and its biological meaning in subterranean mammals. Furthermore, it lays the foundation for future field experiments.

Do songbird migrants use the magnetic field during the non-migratory season?

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There is a lot of experimental evidence that songbird migrants during migrations use the magnetic field as orientation and navigation cues. On the contrary, the usage of the magnetic field by songbirds during the non-migratory season is poorly understood. To investigate that we tried to modulate circadian rhythms in birds by changing the magnetic field. Long-distance migrant garden warbler (Sylvia borin) was chosen as a model species. All tests were performed from November to March in a special experimental setup: magnetic coils were placed inside a wooden house to reduce outdoor sound and light. Each bird cage was equipped with an infrared camera and activity sensor to record the behaviour of experimental birds. Birds were kept inside the coils under a constant dim light for two weeks in the normal magnetic field (NMF). When birds exhibited free-running locomotor activity, they were subjected to "superstimulus magnetic condition" (SMC). In this case all parameters of the magnetic field were changing for 12 hours every day at the certain time. We hypothesized that if birds are able to perceive the magnetic field during the non-migratory period, they could use this information to synchronize their circadian rhythms. However, birds continued to show free-running locomotor activity under a constant dim light in the SMC, and the question about using the magnetic field in the non-migratory season is still open to investigate. This study was supported by RSF grant № 17-14-01147.

Stay orientated: visual landmarks as dominant directional cues in the rat brain

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Maintaining a sense of direction is critical for self-localisation in space. However, built environments often have a twofold rotational symmetry, making them highly disorienting. Stable visual landmarks (e.g. doorways) and unique features (e.g. odours) in a local space can provide information salient enough to break the symmetry, and reinstate the sense of direction. We study how multi-sensory information, particularly visual landmark, is integrated in the brain and used as directional cue during reorientation in laboratory rats. We recorded the activity of single cortical neuron while rats foraged freely in a symmetrical black box that consists of two connected visually-identical compartments. Each compartment was adorned with a cue card on opposing sides of the wall and scented with a unique odour, enabling the rat to disambiguate the environment. We found unusual directionally-sensitive neurons, termed bi-directional (BD) cells, that fire when the rat faces either of two opposing directions in the box. To understand whether the anchoring of BD cell is driven purely by reversing visual landmarks, we further tested the activity of BD cells in a different asymmetrical arena with multiple visual landmarks in all directions. The majority of cells showed a degraded directional tuning or even became non-directional. We conclude that the specific activity of BD cells is visually dominant, and can be modulated by experiences of orienting in a visually ambiguous environment.

Navigation in visually ambiguous environments

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For efficient navigation, animals must disambiguate similar local environments and locate themselves globally. To facilitate disambiguation, a neural substrate that conjunctively encodes both local and global environments may exist. In a recent study, a subpopulation of directionally sensitive cells in dysgranular retrosplenial cortex (RSC) were found to be responsive bidirectionally in a symmetrical, visually rotated two-compartment box (Jacob et al., 2017), suggesting that such conjunctive encoding could exist in RSC. However, it is uncertain if the animals could disambiguate the two visually ambiguous compartments, or if place cells (cells that spike within a specific location) encode the environment globally or locally (as individual compartments). Here, we investigate the animals' ability to disambiguate the compartments and the type of encoding present in the place cell system. Behaviourally, we utilized an object-location-odour task, in which we found that rats can use context (odours) to detect the object that was moved to create an ambiguous environment, hence reflecting an ability to locate themselves globally. Place cell recordings also revealed a lack of 180° rotated, duplicated fields between the compartments, further supporting global encoding. These data indicate that the local bidirectional signals are integrated prior to the place cell system, thus helping the brain form a global map and enabling localization of the animal in visually ambiguous environments.

Alignment behaviour in dogs

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In recent years the description of alignment behaviour has emerged in a number of animals including cows, foxes, fish, birds and dogs. This appears to be spontaneous alignment to the Earth's Magnetic field. Most of the data collected has been by one research group and there have been surprisingly few attempts to replicate any of these studies given the relative ease of data collection that requires little more than the ability to observe the animal and measure its heading on multiple occasions. This coincidentally makes this an ideal student project and here we report the results of three studies of alignment behaviour in dogs during defacation and urination, collected by undergraduate students at Bangor University. The results are in general support of a north-south alignment behaviour previously reported, although the results of measurements under powerlines are not consistent with other studies and suggest that it is not clear that this is magnetically controlled.

Wind conditions affect nocturnal departure directions of Northern Wheatears (Oenanthe oenanthe) during autumn migration

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Nocturnal departure directions of migrating songbirds from stopover are not always directed towards the expected or seasonally appropriate migratory destination. Birds may adjust their trajectories to topographic features of the landscapes they encounter and follow detours when circumventing ecological barriers. Further, they adjust their behaviour to atmospheric conditions, like speed and direction of the wind. Birds may allow for drift in crosswinds, if possible, but compensate for these, if necessary. In this study, we investigated whether the prevailing wind conditions help explaining variation in the nocturnal departure direction of Northern Wheatears (Oenanthe oenanthe) from Helgoland, a small island in the south-eastern North Sea, during autumn. For this we used an automated radio-telemetry system to track the individual behaviour of free-flying birds setting off from the island. Northern Wheatears revealed a mean nocturnal departure direction of 176°. We found that variation in nocturnal departure directions was partly explained by the west-east component of the wind, indicating that birds allowed for wind drift. However, with increasing wind speed birds seemed to increasingly compensate to avoid further displacement. Such individual behavioural responses to wind conditions may help birds conserving energy during migratory flights. They require consideration when interpreting directional data from free-flying songbirds regarding their orientation during migration.

The use of spatial and local cues for orientation in domestic chicks (Gallus gallus)

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Birds have been widely used for studying spatial orientation. However, since different bird species rely on different types of visual information to find goal locations (e.g. spatial information from free standing objects vs. local cues, i.e. characteristics of a goal location like color, shape), it is important to investigate this aspect in each model species. The aim of the present study was to investigate whether domestic chicks, a ground-living bird and a widely used model for the comparative study of spatial orientation, are able to reorient in relation to free standing objects and if they preferentially follow local or spatial cues. Furthermore we also investigated whether monocular eye occlusion influences the ability of chicks to orient by spatial or local cues. Chicks were trained for one week, in a large circular arena with free standing objects providing relational spatial information, to find food in one of four feeders. We found that i) chicks are able to reorient in relation to the objects; ii) but they significantly prefer local cues (when both cues were available and put in conflict); iii) also in monocular tests chicks used local cues; iv) one eye-system is not sufficient to orient by spatial cues alone. These results clarify the nature of the information processed by chicks in this task and thus open the way to further experiments, on hemispheric specialization and the role of hippocampus.

A quantum needle can provide a highly sensitive and highly robust magnetic compass

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Many adult birds can travel 5,000km or more with a precision of centimeters. Earth's magnetic field provides an omnipresent source of information that aides in navigation. The mechanism by which animals sense the Earth's magnetic field remains one of the most important problems in sensory biology. The radical pair mechanism (RPM) proposes that the Earth's magnetic field influences a chemical pathway via electron spin's in a radical pair. Recently it has been shown that a particular, so-called ``quantum needle'' RP model can be extraordinarily sensitive to directional changes, thus potentially providing the basis for a highly sensitive magnetic compass (ref 1). However, it has also been shown that many compass systems are fragile, i.e. that even small, naturally occurring, variations in parameters can abolish effects that are observed in models without considering such noise (ref 2). Here, we ask what effects noise has on a quantum needle compass system. Surprisingly, rather than reducing the quantum needle, noise is found to either leave the needle intact or even enhance it in some systems. This suggest that a quantum needle based compass may not only be distinguished by a high sensitivity, but also by being unusually robust to noise, making it a highly optimized system for magnetoreception.

Does magnetic conditioning work on zebrafish?

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Many species of fish perform migratory movement on a regular basis, on time scales ranging from daily to annually, and with distances ranging from a few meters to thousands of kilometers. To reach distant feeding or breeding grounds, fish must have excellent navigation skills and keen sensory systems to detect and meaningfully interpret various orientation cues (e.g., magnetic field). Zebrafish (Danio rerio) and rainbow trout (Oncorhynchus mykiss) have previously been shown to be sensitive to geomagnetic stimulation. Here, we present magnetic conditioning attempts on zebrafish relying on negative (electric pulse) reinforcement. We have designed a Horner-type shuttle-box (two compartments separated by a hurdle) with fully automated stimulus application sequences and data acquisition procedures. As conditioned stimulus (CS), we applied a slowly oscillating magnetic field (sine wave with 1 sec period) of moderate amplitude (40000 nT), superimposed on the static background field. Weak electric pulses (unconditioned stimuli) were applied to punish fish that failed to escape upon magnetic field alterations (avoidance behavior). It turns out that individual zebrafish (n=5) were not responsive to the magnetic field stimulus presented, although other individuals (n=5) learned to respond to light as CS in otherwise identical conditions.

Unified Animal Navigation Theory and Einstein's Unified Field Theory

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The new Hypothesis of the navigation of animals can help physicists to search for a Unified Field, and the Unified Field Theory will help biologists to construct a Unified Animal Navigation Theory and to find a Biosensor of the Unified Field. The available Hypotheses confirmed by facts indicate that animals use the Magnetic (M), Gravitational (G), and Electric (E) fields of the Earth for the navigation. At first glance, Hypotheses of the M, G, and E-navigations of animals are disconnected completely. However, let us consider the Hypotheses of the navigation of animals from the viewpoint of Einstein's Unified Field Theory (UFT). It seems that they have a common base. This assumption is in agreement with UFT postulating the existence of the common basis for the Magnetic, Gravitational, and Electric fields. According to UFT, the Magnetic, Gravitational, and Electric fields are partial manifestations of the same field called Einstein's Unified Field (UF). In view of this reasoning, the M, G, and E hypotheses of the navigation of animals cannot be opposed and disconnected. So, Magnetic, Gravity and Electrical navigation theory are proper simultaneously. Based on Einstein's Hypothesis of the existence of UF, it is possible to advance a Hypothesis asserting that birds use Einstein's UF in their navigation.

Physical properties of a magnetoreceptor based on electromagnetic induction

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The mechanisms that underlie the magnetic sense of animals remain an unsolved mystery. Over the last few decades three hypotheses have emerged that attempt to explain this phenomenon. One idea is based on electromagnetic induction which predicts that an electric field produced by a changing magnetic field could directly activate an electrosensory cell. While this mechanism has primarily been considered with respect to aquatic organisms that are electroreceptive, an electric field could also be realized within the inner ear of a pigeon as it rotates its head. In such a model the endolymph would serve as a conductor, and a voltage would be induced as the orientation of the semicircular canals changes from a perpendicular to a parallel orientation with respect to the magnetic field vector. In this work we aim to assess the feasibility of this model employing both theoretical and experimental approaches that focus on the required size of the conductive loop, the conductivity of the endolymph, and the sensitivity of a putative electroreceptor.

Characterization of Pigeon Cry 4: a putative light-sensitive magnetosensor

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Cryptochromes (Crys) are blue-light photoreceptors that are homologous to photolysases and found throughout all domains of life. Crys have been shown to play an important role in circadian functions but are also believed to play a role in how organisms navigate using the geomagnetic field. Specifically, Crys have been suggested as the model protein for a light based radical-pair mechanism (RPM), a light-induced electron transfer reaction that is sensitive to magnetic fields. Expressing vertebrate Crys has proven to be challenging and prior data suggest they do not bind FAD like their homologues in plants and insects, an essential property for them to function as a magnetosensor under the current model. Here, we report the successful expression of pigeon Cry4 using an insect cell system, followed by its biophysical characterisation. We show that unlike mammalian cryptochromes pigeon Cry4 binds FAD in its native state.

In vivo 2-photon calcium imaging in the pigeon brain

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Magnetoreception is a sensory modality that permits the detection of magnetic fields and is a widespread phenomenon within the animal kingdom. Behavioral experiments have shown that the rock pigeon (Columba livia) employs the Earth's magnetic field to navigate, however the underlying cellular and molecular mechanism remains elusive. Recent studies in our lab have implicated the pigeon hippocampus, a brain region involved in navigation, orientation and spatial memory, in processing of magnetic field information. These results raise the possibility of "magnetic spatial cells" located in the pigeon hippocampus, which might aid during navigation by inferring position and/or direction from the geomagnetic field to generate a "magnetic map" of the environment. To investigate the role of the hippocampus in magnetoreception I developed 2-photon calcium imaging in awake pigeons. This method enables simultaneous recording of neuronal firing from potentially hundreds of cells while exposing the bird to magnetic stimuli. This will allow us to investigate which properties of magnetic fields cause neuronal firing in the pigeon hippocampus and how this information is encoded and represented on a systems level.

The earth's magnetic field is an early compass in desert ants

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Central place foragers face the crucial challenge to find back home every time they leave the nest. To do so, they use an impressive navigational toolkit including celestial compass cues, landmark guidance, and olfactory cues. However, when leaving the nest for the first time, it is essential to calibrate and learn navigational cues. Therefore, ants, bees and wasps perform so called learning walks and flights – short excursions around the nest entrance. We use Cataglyphis desert ants as experimental model to study this behavior. During naïve learning walks, Cataglyphis desert ants look back to the nest entrance repeatedly. Although the celestial compass provides the main directional cue during far-ranging foraging runs, the ants do not use them for navigation during learning walks. Instead, the ants use a geomagnetic compass during first walks outside the nest. By rotating the horizontal field component of the earth's magnetic field in the natural habitat, we altered the gaze directions during the look-back behavior from the nest entrance to a predicted fictive nest point. This shows that the geomagnetic field provides input to the path integrator during learning walks, adding a new compass cue to the ants' navigational toolkit. As celestial compass input triggers neuroplasticity in the ant's brain after learning walks, we conclude that the geomagnetic field provides an earthbound reference system for calibration of visual compass systems. Funded by DFG RO1177/7-1 to WR.

Bogong moth central complex neurons respond to the Milky Way

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The Australian Bogong moth *Agrotis infusa* is known for its remarkable ability to precisely navigate under low-light conditions. During their spring migration, these nocturnal moths fly over 1000 km to reach their estivation sites in the Australian alps, before returning to their breeding ground by the same route in autumn. This yearly migration event has become iconic in Australia, yet we are only beginning to understand how these small moths navigate so precisely. Behavioural experiments on tethered flying moths showed that Bogong moths can use the geomagnetic field in combination with visual cues to select a flight direction. One of the most prominent visual cues in the nocturnal Australian landscape is the Milky Way, which has been shown to be sufficient for the moths to maintain oriented flight even in the absence of the geomagnetic field. Using intracellular sharp-electrode recordings, we identified several neuron types in the Bogong moth brain that show a strong and specific response to the Milky Way. Many of these neurons are associated with the central complex (CX), the substrate of the insect brain's internal compass. The neurons presented here did not differ in their response patterns when tested in a nulled magnetic field compared to a normal local magnetic field, and thus the neural basis of the magnetic compass remains unclear. Nevertheless, this study is a first step towards understanding how the different compass cues are processed and integrated in the Bogong moth brain to produce the reliable steering output necessary for maintaining a migratory direction.

Radiofrequency noise modifies the insect sense of time

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Insect orientation and circadian rhythms have been shown to be sensitive to weak magnetic field (MF). The molecule supposedly providing both behavioural phenotypes with magnetic sensitivity is Cryptochrome (Cry). In our previous work, we showed that Cry2 is indispensable for magnetoreception of cockroach Blatella germanica. Recently, we focused on circadian rhythm of Blatella measured in environment strictly devoid of radiofrequency (RF) noise from technical sources. We found that: i) 120uT MF slows the clock down under 460nm UV light, ii) UV light is necessary for magnetic sensitivity of the clock system and, surprisingly, iii) also weak RF fields slow the clock down. There is apparent congruent impact of light, RFs and MF on the rhythm albeit with limited additivity. Besides, possibly antagonistic interaction was found between RF and MF. Results enlarge the pool of known interactions between weak RF noise and animal magnetoreception.

The neurogenomics of avian migration

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The avian migratory phenotype is both spectacular and complex, encompassing a range of morphological, physiological, and behavioural traits such as pre-migratory fat storage, circannual rhythms, and sensory mechanisms for navigation. It is now well recognised that many of these traits have a strong genetic basis, however the identity of the genes and molecular mechanisms that underpin the migratory phenotype is still unknown. In order to shed light on this, I will be examining gene expression in brain areas that likely play a role in regulating features of migratory behaviour such as hormonal regulation, navigation and orientation in the blackcap, Sylvia atricapilla. Specifically, I will compare the gene expression profiles of these brain areas in birds that are in the migratory season, and during an off-season control period. Additionally, I make use of the fact that blackcap populations exhibit a wide variability in migratory phenotype and compare gene expression profiles of both these seasons in populations that differ in their migratory orientation strategies. With this approach, I intend to gain novel insights into the neural and genetic control of migratory behaviour.

Mobile ecosystem services: the orientation strategies of migratory hoverflies

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Many species of hoverflies (Diptera; Syrphidae) are highly beneficial: the adults are pollinators of numerous plant species while the larvae are important predators of serious pest insects. Some common European syrphids are also spectacularly migratory, with prodigious numbers arriving each year in Northern Europe before departing to overwinter in the Mediterranean Basin. Assessments of seasonal bioflows and associated orientation behaviours cannot be made by sporadic observations on the mass arrivals, because syrphids also fly unnoticed at high altitudes. In contrast, huge numbers of active migrants can be readily studied as they traverse high mountain passes in the Pyrenees during autumn. We combine UK-based insect-monitoring radars and data from the hoverfly recording scheme, with Pyrenees-based tethered flight experiments and video-counts, to quantify syrphid migration and orientation strategies. Our research provides evidence of the adaptive nature of the migratory circuit, for orientation based on a time-compensated sun compass, and for the ability to partially compensation for wind drift during flight.

Exploring the minimal functional unit of magnetoreceptor (MagR) and a roadmap to MagR2.0

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Magnetoreception is a sense for animal to detect the geomagnetic field. Animals rely on this sense to migrate over long distance, find home, build nest or to orient their bodies [1, 2, 3]. Previously, a putative magnetoreceptor (MagR) and its complex with Cryptochrome (Cry) were identified, and a rod-like structure of MagR polymer assembled by twenty monomers was reported [4]. Structural analysis indicated that a plate-like MagR tetramer might serve as the minimal functional unit for both protein assembly and magnetoreception. Here in this study, a single chain tetramer MagR fusion protein (SctMagR) was designed, expressed and purified to explore the dynamical assembly process of MagR, and to study the connections between MagR assembly and magnetic sensing. Hierarchical assembly of MagR polymer was visualized and a series of different assembly status was identified, indicating that SctMagR could be the basic structural unit of MagR polymer. Obvious paramagnetism was observed with cells expressing SctMagR in magnetic field, compared with that of wild type MagR, suggesting SctMagR may represent the minimal magnetic unit and improved version for magnetosensing.

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Magnetic response of the bird's lagena

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Birds and other vertebrates navigating through 3-D environments possess a lagena which is localized in the cochlear canal, distally with respect to the hearing organ. Bird's lagena contains masses of otoconia composed from calcium carbonate in a form of calcite in the matrix of organic molecules. Lagena was proposed to play a role in magnetoreception (Harada 2001, Wu and Dickman 2011, 2012). Substantial quantities of iron were found in lagenal otolith by X-ray fluorescence (Harada 2001), but it was not known whether it formed any magnetic structures. We apply the technique of nonlinear high-frequency magnetic response (Anisimov 1982) to characterize magnetic properties of birds lagenae. In our experiments, lagenae of birds (pigeons, robins) were dissected from previously fixed heads inside the bone sheath. Samples were placed inside radiofrequency (RF) magnetic coils and subjected to the RF field at 15.7 MHz. The second harmonic (at 31.4 MHz) of the magnetic response was recorded as a function of static magnetic field parallel to the RF field. The phase shift and amplitude of the detected signal as functions of the static field give information on the type of the magnetic material (superparamegnetic, single- or multidomain etc.). We discuss the results in view of the possible role of the lagena in navigational magnetoreception.

Species and sex differences in wild poison frog homing ability

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Understanding how life history shapes the navigational abilities and movement strategies of animals is among the key challenge in the field of animal navigation. Poison frogs and their close relatives routinely navigate through the rainforest understory when shuttling their tadpoles from land to small and widely dispersed pools. Recent studies have revealed that some poison frogs can home back after translocations of several hundred meters. In this study, we used tracking to quantify the species and sex differences in homing performance in two poison frog species with contrasting life histories. We found that most males and females of both species returned to their home areas via a direct path after being released 50 m away. In contrast, strong species and sex differences become apparent when frogs were displaced for 200 m. Most males but no females of a smaller cryptic species Allobates femoralis returned via a direct path from 200 m. We found no such sex differences in homing performance of a larger aposematic species Dendrobates tinctorius. Interestingly, the two species also showed contrasting movement strategies. While A. femoralis mostly returned home via a direct path and remained stationary when not moving homewards, D. tinctorius showed wide-ranging search patterns and often returned home via an indirect path. We speculate that these species and sex differences reflect differences in life-history such as parental care roles and aposematism.

Do mole-rats use the daily fluctuations of the geomagnetic field (GMF) as a zeitgeber?

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The subterranean ecotope lacks typical environmental factors (e.g. daily changes of light-darkness or temperature) that its inhabitants could use as a zeitgeber. We proposed that the circadian rhythm of strictly subterranean African mole-rats (Bathyergidae) depends on daily fluctuations of the geomagnetic field. If this hypothesis is true, it would explain why previous studies have failed to demonstrate clear rhythms in subterranean mammals: all studies have been performed inside buildings where iron and electrical devices disturb the local geomagnetic field. We tested this hypothesis by keeping Ansell's mole-rats (Fukomys anselli) over months either in undisturbed, constant magnetic conditions or (reintroduced) controlled daily magnetic fluctuations in the range of a few hundred nanotesla. Here, we present preliminary results indicating that activity and body temperature change under different magnetic conditions. The findings constitute first evidence for a magnetic zeitgeber in a mammal with far reaching implications for research in chronobiology and magnetoreception.

Using brain clearing to study magnetoreception in the mole-rat

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Many species across the animal kingdom including mammals are able to sense the Earth's magnetic field and use this information for navigation. Although this has been proven in several behavioural studies, the position of the responsible receptors and the underlying mechanism of magnetoreception remain unclear. The two most commonly accepted hypotheses on sensing magnetic information are the magnetite-hypothesis relying on the presence of biogenic magnetite in receptor cells and the radical-pair hypothesis which is based on biochemical reactions in photoreceptors. Since biological tissue is permeable to magnetic fields the receptors could be localised anywhere in the body. Only a description of the primary receptor cells will solve the riddle on how magnetic stimuli are detected. In order to gather information about the magnetoreceptors we used a top-down neurobiological approach. Using the iDISCO+ technique for tissue clearing we can determine neuronal activity due to magnetic stimulation across whole brains in mole-rats. The active neurons are detected by immunohistochemical labelling of the immediate early gene c-fos. Afterwards the software ClearMap maps the distribution of active neurons onto a reference brain and identifies the differentially activated brain regions of different treatment groups. That way we want to gather new insights on the processing of magnetic signals in the brain which can provide important information about the location of downstream receptors.

Protein-protein interaction of the putative magnetoreceptor cryptochrome expressed in the avian retina

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Migratory birds can sense the Earth's magnetic field and use it for orientation tasks. A light-dependent radical-pair mechanism, which is associated with the visual system, is currently discussed as the underlying mechanism of the magnetic compass. The blue light receptor cryptochrome (Cry) has been considered as a potential primary sensor that detects the geomagnetic field. Moreover, Cry and its co-factor FAD are assumed to be the molecular components performing photo-chemical reactions leading to radical-pair intermediates. Here we used the yeast-two-hybrid system to screen avian cDNA libraries for possible interaction partners of Cry in chicken and European Robin. The UAS-GAL yeast two hybrid system was applied to confirm a group of candidate Cry interaction partners that were identified by the split-ubiquitin system. Several proteins from total of 59 candidates were selected as highly specific candidates for interacting with European robin Cry. Thus, we were able to uncover a Cry interaction network offering us clues about intracellular trafficking, function of Cry and down-stream targets in a signaling cascade of light-dependent magnetoreception. Furthermore, by comparing the differences of the interactome of the Crys in different species, we will enhance our understanding about their mediated signal pathways between migratory birds and non-migratory birds and further gain insight into the species evolution of this sort of conserved molecules.

Is Access to Celestial Cues in a Burrow-Nesting Seabird Essential for Fledging?

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Tied to land only by the necessity to breed, procellariiform seabirds are perhaps nature's greatest avian navigators. One such procelariiform, the burrow-nesting Manx Shearwater (Puffinus puffinus), will navigate from the west coast of the UK to the Patagonian Shelf every year of its breeding adult life. What sets Manx shearwaters apart from their terrestrially breeding counterparts, however, is their apparent naivety when setting off on their first migration. This is because, as burrow-nesting seabirds, access to celestial cues prior to fledging is extremely limited. However, given fledglings leave their burrow for a small amount of time in the nights prior to fledging, there is the possibility of timing fledging to maximize access to clear skies. Through the deployment of RFID readers on 70 Manx shearwater burrows, we observed the amount of time each chick spends on the surface through the fledging season. We report, for the first time, whether seabirds can fledge without access to celestial cues by informing on the amount of time spent in and out of the burrow. We suggest what this may mean with regards to the navigational mechanisms used to travel to and from their natal site, whilst commenting on how generalizable such mechanisms may be to movements over the entire migration route.

Analyzing the non-homing pigeon - a FlowR bundle for standardized quantitative dissection of pigeon GPS tracks

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Analyzing pigeon flight trajectories obtained by GPS-tracking reveals a bewildering variety of factors influencing the pigeons' homing performance. These include exposure to navigational cues at the release site, choice of initial direction, changes in directionality and speed en route, and the approach routes in the vicinity of the loft. While satellite, topographic and geophysical maps can reveal visual correlations of tracks with map features, there are many unmapped objects such as field roads, canopies and subtle terrain slopes that prevent straightforward quantitative matching. Another point is the individuality of pigeons: some birds leave release sites without circling and maintain a chosen flight course over long distances. Others within the same collective hesitate flying alone and wait for partners. To cope with such demands on data analysis, we are developing a FlowR bundle based on open-source R scripts, to achieve the following goals: i) digesting data from older and newer GPS loggers; ii) providing standard statistical analyses and plots of vanishing bearings, (iii) automatically analyzing graphically and statistically variation in speed and other flight parameters characterizing decision points en route; (iv) providing canonical correlations with release site properties or treatment discriminants. By conveniently bundling R-scripts together within the FlowR user interface, we will present a seamless automated approach to bird navigation analysis.

Magnetically induced immediate early gene activation in the fish brain

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Previous behavioral and magnetic conditioning studies have shown that fish can perceive the earth magnetic field and potentially use it for navigation. The trigeminal nerve, which innervates sensory structures in the snout of fish, seems to play a crucial role in detecting magnetic field changes. These findings were supported by recent immunohistological studies on freely swimming medaka, showing an increase in swimming activity and neuronal activation in the hindbrain under magnetic stimulation. Here we use immediate early gene expression levels to study neuronal activation in adult zebrafish and rainbow trout, each under two different magnetic field conditions, a strongly changing magnetic field of earth magnetic field strength and in a zero magnetic field in which no magnetic information were available to the fish. We find that one of the trigeminal nuclei in the hindbrain shows higher neuronal activity during the strongly changing magnetic field compared to the zero magnetic field condition. These findings support the hypothesis that fish are able to perceive earth magnetic field information and that the trigeminal nerve plays a crucial role.

Studying V-formation through the help of conservation and satellites

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An European conservation project leaded by Waldrappteam is trying to reintroduce a stable migrating population of Northern bald ibis (Geronticus eremita), after its extiction over 300 years ago. Every year chicks are hand-raised by two foster mothers and taught to follow a paraplane. Through this method it is possible to show the birds the migratory route from the breeding site (low Germany/Austria) to the wintering site in Tuscany. This conservation project offers a unique opportunity to study different aspects of migration flights, something that is very challenging with free migrating birds. For example, many aspects of formation flight during long-distance migration are still poorly understood. Even less studied is how the birds exchange their position inside a V-formation (e.g. from a more energy-demanding frontal position to a less energy-demanding back position) and whether social relationships among individuals may play a role. Previously these aspects were out of bounds because of the difficulty to keep track of all the individuals in a free-flying flock. The human guided migration gives the chance to address these questions, as it is possible to monitor all the birds in the formation. During the flight every bird is equipped with customized GPS data loggers with the purpose of collecting and storing satellites' raw data. The subsequent data post-processing allows to obtain cm-level precision in the calculation of the birds' relative position in the flock.

A magnetic pulse disrupts the magnetic sense of Chinook salmon

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Chinook salmon are perhaps one of the most iconic and competent ocean navigators, migrating distances of 3000 km across the open ocean to feed and grow, before returning to the same exact natal stream multiple years later. To assist in accomplishing this journey, Chinook salmon posses an inherited magnetic map, allowing them to extract positional information from EarthÕs magnetic field. Like all species, however, how this magnetic field information is detected and neurologically encoded remains unknown. Evidence from both histological and genetic studies suggests that a magnetite-based detection mechanism is likely in Chinook salmon. Behavior studies that involve treating animals with a strong magnetic pulse have long been used as a diagnostic tool for magnetite-based magnetoreception. However, the effect of a magnetic pulse on the behavior of any fish species remains untested, despite first being proposed with Chinook salmon over 30 years ago. To test the hypothesis that single domain magnetite is involved in magnetoreception, we treated Chinook salmon with a strong, but brief magnetic pulse capable of realigning the dipole moment of magnetite crystals. We report that the magnetic orientation of Chinook salmon was significantly different between our control and pulse groups. Pulsed fish were oriented to the northeast whereas fish from the control exhibited orientations that couldnÕt be distinguished from random. We show for the first time that a magnetic pulse disrupts the magnetic orientation of salmon providing the critical behavioral evidence for a magnetite-based mechanism is salmon and other fish.

Formation of foraging ground attachments

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Foraging ground fidelity, or a strong affinity to a specific foraging ground, is a phenomenon in which animals return to the same foraging area after migrating to distant sites. Juvenile sea turtles often demonstrate this sort of site fidelity: turtles have been shown to home to coastal foraging grounds following seasonal migrations or experimental displacements. Previous work has shown that turtles can use Earth's magnetic field to navigate to their foraging sites. We hypothesize that this navigation depends, in part, on the ability of turtles to sense two features of the magnetic field that vary geographically, similarly to latitude and longitude, and the combination of these two components likely functions as a bi-coordinate navigational system, in which each geographic location has a unique "magnetic signature". We further hypothesize that turtles learn to associate their foraging locations with magnetic signatures and retain this information to navigate back upon displacement. To assess whether turtles are capable of learning to associate a magnetic signature with food we classically conditioned sixteen hatchling loggerhead turtles (*Caretta caretta*) to a novel magnetic signature over the course of two months. Turtles were exposed to two novel magnetic signatures for equivalent amounts of time throughout the two months, but only received food in one of the magnetic signatures. In post-conditioning experiments, the food-seeking responses of the turtles demonstrated their recognition of the conditioned magnetic signature over the other novel field (*P=0.0008*). This study provides the first experimental evidence that sea turtles are capable of learning to associate a magnetic signature with a feeding location.

Ready for takeoff? A novel experimental assay to investigate the senses for navigation in migratory bats

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Navigational mechanisms of migratory mammals remain largely understudied compared to other taxa. To propel the study of magnetoreception and other mechanisms for long-distance orientation in mammals, we aimed to develop an experimental behavioural assay for bats. Bats recently advanced to models organisms of spatial cognition, and are promising to the field due to global abundance and high species diversity.

We hypothesised bats caught during summer migration would demonstrate directional preferences if their takeoff could be studied in an apparatus designed considering their needs. We conducted fieldwork in late summer at one of the major migratory corridors of bats in Europe, the shoreline of the Baltic Sea in Latvia. First, we tested whether takeoff would be a meaningful orientational behaviour producing non-random directional data. Once this could be established, we developed an easy-to-use apparatus which enables recording of takeoff orientation based on tracks a focal bat leaves on a thin layer of chalk. During an experiment, the animal is set free from distance inside a circular release box and can freely choose a preferred direction for takeoff.

In the last two years, we performed experiments using this technique in migratory species, *Pipistrellus nathusii* and *P. pygmaeus*. The behavioural assay proved to be applicable under field conditions and under semi-laboratory control, i.e., in a large tent.

First results imply that adult *P. pygmaeus* calibrate their (putatively magnetic) compass with the sun's azimuth at dusk, but that naïve migrants appear unable to take up a migratory heading. Takeoff orientation from adult *P. nathusii* showed to be unimodal if studied under controlled conditions, and mean direction is comparable with similar directional data from visual observations, VHF telemetry of departure flights, and long-distance ring recoveries.

We believe our assay is suitable for various habitats of bats worldwide. The setup can be easily customized for different bats and it could prove useful in laboratory settings and in a range of outdoor situations other than tested here, i.e. a migratory corridor. The circular release box could thus provide ultimately the background for testing navigational skills across taxa, such as bats, rodents and birds.

From open spaces to cluttered places: Straight-line orientation in different visual environments

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When a ball rolling dung beetle has found a suitable dung pile to feast on, it will shape a piece of dung into a ball and roll it away along a straight path. To keep its bearing, the beetle's compass processes directional information given by external celestial cues, such as the sun, polarised skylight, the intensity gradient or the chromatic gradient formed across the sky.

It has previously been shown that the diurnal savanna living beetle relies predominantly on its sun compass for straight line orientation. In a woodland biome, the visual ecology is vastly different from that of a savanna. This is partly due to its higher density of trees, where the canopy will frequently disrupt a beetle's view of the sun. In more closed habitats, sky wide compass cues, such as the celestial polarised light pattern, might better serve as reliable cues for orientation.

In this study, we explore straight line orientation in the woodland living beetle *Sisyphus fasciculatus* and compare its orientation strategies to the ones employed by the beetle *Scarabaeus lamarcki,* active on the open savanna. Through behavioural experiments we conclude that the woodland living beetles, in contrast to the savanna living beetles, rely predominantly on polarised skylight for straight line orientation. These results suggest that the dominant celestial compass cue is set by the cue most prominent in the habitat, indicating that the compass system network is highly affiliated to the visual ecology of the navigator.