



HAL
open science

Biological Effects of Electric, Magnetic, and Electromagnetic Fields from 0 to 100 MHz on Fauna and Flora: Workshop Report

Blanka Pophof, Bernd Henschenmacher, Daniel R Kattnig, Jens Kuhne, Alain
Vian, Gunde Ziegelberger

► To cite this version:

Blanka Pophof, Bernd Henschenmacher, Daniel R Kattnig, Jens Kuhne, Alain Vian, et al.. Biological Effects of Electric, Magnetic, and Electromagnetic Fields from 0 to 100 MHz on Fauna and Flora: Workshop Report. *Health Physics*, 2023, 124 (1), pp.39-52. 10.1097/HP.0000000000001624 . hal-04292569

HAL Id: hal-04292569

<https://hal.inrae.fr/hal-04292569v1>

Submitted on 17 Nov 2023

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.



Distributed under a Creative Commons Attribution - NonCommercial - NoDerivatives 4.0
International License

Biological Effects of Electric, Magnetic, and Electromagnetic Fields from 0 to 100 MHz on Fauna and Flora: Workshop Report

Blanka Pophof,¹ Bernd Henschenmacher,¹ Daniel R. Kattinig,² Jens Kuhne,¹
Alain Vian,³ and Gunde Ziegelberger¹

Abstract—This report summarizes effects of anthropogenic electric, magnetic, and electromagnetic fields in the frequency range from 0 to 100 MHz on flora and fauna, as presented at an international workshop held on 5–7 November in 2019 in Munich, Germany. Such fields may originate from overhead powerlines, earth or sea cables, and from wireless charging systems. Animals and plants react differentially to anthropogenic fields; the mechanisms underlying these responses are still researched actively. Radical pairs and magnetite are discussed mechanisms of magnetoreception in insects, birds, and mammals. Moreover, several insects as well as marine species possess specialized electroreceptors, and behavioral reactions to anthropogenic fields have been reported. Plants react to experimental modifications of their magnetic environment by growth changes. Strong adverse effects of anthropogenic fields have not been described, but knowledge gaps were identified; further studies, aiming at the identification of the interaction mechanisms and the ecological consequences, are recommended. *Health Phys.* 124(1):39–52; 2023

Key words: electromagnetic fields; electrostatic field; environmental impact; radiation, nonionizing

INTRODUCTION

IN MANY COUNTRIES, the expansion of power grids and the construction of new high voltage power lines have led to

changes in exposure conditions to static and extremely low frequency electric and magnetic fields (ELF-EMFs) that affect the animal and plant populations in terrestrial, freshwater, and marine environments.

Based on recognized scientific evidence, compliance with the guidelines of the International Commission on Non-Ionizing Radiation Protection (ICNIRP 2009, 2010) ensures protection against scientifically substantiated adverse health effects of static and ELF-EMFs. However, these guidelines are established for the protection of humans. While it is generally assumed that animals, plants, and ecosystems are protected if humans are protected (ICNIRP 2000), different actual exposure conditions and interaction mechanisms could give rise to specific effects on flora and fauna. Firstly, flying animals, like insects, birds, or bats, and also high trees may approach closer to sources of ELF-EMFs, such as power lines, and may thus be exposed at intensity levels exceeding the accepted limits. Furthermore, exposure conditions in underwater environments may strongly differ from those in air. Secondly, animals and plants possess receptors and structures not existing in humans, which could give rise to additional biological effects occurring at lower thresholds than effects established for humans.

In view of these issues, the scientific knowledge on the effects of ELF-EMFs on flora and fauna is still limited. The last comprehensive summary was provided by ICNIRP (2000). In order to review the current state of knowledge and to identify research needs, the German Federal Office for Radiation Protection organized the international workshop “Environmental Effects of Electric, Magnetic, and Electromagnetic Fields: Flora and Fauna” in Munich, 5–7 November 2019. This report summarizes the current knowledge of bioeffects of electromagnetic fields with frequency below 100 MHz, as it was discussed at this meeting. The frequency range (0–100 MHz) has been chosen to include the effects of weak radiofrequency electromagnetic fields (RF-EMFs) on the orientation of animals in the geomagnetic field, which are well documented. Biological effects of anthropogenic RF-EMFs at frequencies above 100 MHz are discussed in an accompanying article. We focus on topics

¹Competence Centre for Electromagnetic Fields, Department of Effects and Risks of Ionizing and Non-Ionizing Radiation, Federal Office for Radiation Protection, 85764 Oberschleißheim, Germany; ²Department of Physics and Living Systems Institute, University of Exeter, Stocker Road, Exeter, EX4 4QD, United Kingdom; ³Univ Angers, Institut Agro, INRAE, IRHS, SFR QUASAV, F-49000 Angers, France.

The authors declare no conflicts of interest.

For correspondence contact: Blanka Pophof, Competence Centre for Electromagnetic Fields, Department of Effects and Risks of Ionizing and Non-Ionizing Radiation, Federal Office for Radiation Protection, Ingolstädter Landstraße 1, 85764 Oberschleißheim, Germany, or email at bpophof@bfs.de.
(Manuscript accepted 5 August 2022)

0017-9078/22/0

Copyright © 2022 The Author(s). Published by Wolters Kluwer Health, Inc. on behalf of the Health Physics Society. This is an open-access article distributed under the terms of the Creative Commons Attribution-Non Commercial-No Derivatives License 4.0 (CCBY-NC-ND), where it is permissible to download and share the work provided it is properly cited. The work cannot be changed in any way or used commercially without permission from the journal.

DOI: 10.1097/HP.0000000000001624

presented at the workshop, documented by publications of the speakers (see acknowledgements) and references in their presentations and abstracts (BfS 2020). Additionally, peer-reviewed publications co-authored by the presenters and/or directly related to the topics presented at the workshop and published between the workshop (November 2019) and January 2022 were considered. The literature search was based on the database EMF-Portal, which systematically summarizes scientific research data on the effects of EMFs and covers most of the relevant databases (e.g., Medline/Pubmed and IEEE Explore).

The key questions to be addressed by the participants of the workshop were as follows:

- What are the effects of natural electric and magnetic fields on animals, plants, and ecosystems?
- Are reactions of animals and plants to natural electric and magnetic fields disturbed by anthropogenic EMFs?
- Are there any adverse effects of anthropogenic EMFs on animals, plants, and ecosystems?
- What are the most significant research gaps?
- How can such gaps in the research be closed?

RESULTS

Anthropogenic EMFs

Detailed knowledge about EMF exposure is necessary to assess possible EMF-related effects on animals and plants. The spatiotemporal distribution of fields emitted by an EMF-source depends on various parameters, such as frequency, modulation, source configuration (e.g. type, voltage, current, phasing and spacing on power lines; type of current and configuration of electromagnetic coils; type, power and directionality of RF antenna emissions) and topography around the source. Therefore, distance to the source alone is a poor proxy for exposure, and measurements and/or calculations are a prerequisite for a valid exposure determination.

In most cases, a biological response will not be directly elicited by the ambient EMF outside of the body (e.g., external electric field strength, external magnetic flux density, incident power density, etc.) but by the EMF coupled into or induced in the exposed object (e.g., induced electric field strength, tissue-internal magnetic flux density, SAR, etc.). The coupling efficiency into the organism depends on the considered internal exposure metric and on various parameters (e.g., organism size and anatomy, dielectric tissue parameters, characteristics of incident EMF). Which body/tissue internal exposure metric is most correlated with a given outcome depends on the (putative) biophysical action mechanism.

In a power grid, overhead power lines or underground cables are used to distribute the electrical energy generated in power plants. Depending on technology, the surrounding environment of the conductors is exposed to static (0 Hz, direct current, DC) or ELF (16.7/25 Hz for traction power or

50/60 Hz for domestic current, alternating current, AC) EMFs. Underground cables only produce external magnetic fields, as the outer layer of cable isolation and the surrounding soil shield the electric field. In the marine environment, high-voltage AC cables emitting a low-frequency sinusoidal field are used for short distance and high-voltage DC cables emitting a static field are in use for long distance power transport. When an animal or water current causes motion, secondary induced electric fields are generated as a result of the high conductivity of sea water (Gill et al. 2014; Gill and Desender 2020).

Wireless power transfer (WPT) systems for electric vehicle charging will become widespread in future automotive applications. Inductive resonant WPT systems have turned out as the most promising technology, as they allow for efficient power transfer over a separation distance (gap) between transmitter and receiver coil of up to approximately 20 cm. Transmission frequencies are usually in the range 20–90 kHz (for passenger vehicles typically 85 kHz), and power ratings range from several kW up to 100 kW. Within the gap between transmit and receive coils, the magnetic flux densities may reach several tens of mT (Wang et al. 2018), i.e., far exceeding the reference and action levels applied presently in human exposure guidelines. Even outside the gap, stray fields may reach flux densities exceeding the mentioned reference levels.

In practice, it can be expected that small animals (rodents, cats, small dogs, etc.) may approach the WPT system, or if there is no appropriate non-metallic object detection implemented in the WPT system, they may even move into the gap during charging. High exposures of animals may occur in such situations. Accounting for the spatiotemporal field distribution, exposure geometry, and electrical properties of the animal, Wang et al. (2018) estimated an induced electric field of 22 V m^{-1} in the skin of a cat placed laterally to the gap. This value is close to the human occupational basic restriction of 23 V m^{-1} (ICNIRP 2010) but below the stimulation threshold of mammalian nerve cells, assumed at 100 V m^{-1} (Reilly 1998). If metallic implants are present (e.g., in pets after injuries), severe thermal tissue damage may still occur due to the induction heating of the implant.

Strong sources of RF-EMFs at frequencies below 100 MHz are AM and FM broadcast stations that transmit data (e.g., time signal stations), video, and audio signals (e.g., TV and radio stations) over large distances. Radiofrequency emissions can also be an unintentional by-product of operating electric and electronic devices and infrastructure, often leading to broadband radiofrequency interference (RFI).

Action mechanisms of EMFs in living organisms

A well-known action mechanism of ELF-EMFs is the induction of an electromotive force and hence currents in conductive tissues, which can ultimately lead to the activation of nerve cells. This effect is well established and represents the basis of present exposure guidelines (ICNIRP 2010).

Far less understood is magnetoreception, the ability of many organisms to perceive the direction and intensity of the geomagnetic field (20–60 μT) and use it for orientation/navigation (Wiltschko 1995; Mouritsen 2018). It is a well-recognized phenomenon, but the biophysical principles underpinning this “sixth sense” are still under investigation (Nordmann et al. 2017). At present, the best established hypotheses involve magnetite and the radical pair mechanism (RPM). The former is thought to underpin a light-independent magnetic sense, while the latter is commonly attributed to light-dependent magnetoreceptive traits. A third mechanism based on electromagnetic induction has been discussed for electrosensitive elasmobranchs (Jungerman and Rosenblum 1980) and recently also proposed for pigeons (Nimpf et al. 2019); however, except for highly specialized electrosensitive species, the evidence is scant, so it will not be discussed further.

Magnetic sensors based on magnetite. The magnetite hypothesis for sensory perception of the geomagnetic field assumes specialized cells containing ferrimagnetic or superparamagnetic particles (Kirschvink and Gould 1981; Shaw et al. 2015). Minerals in the magnetite-maghemite solid solution series ($\text{Fe}_3\text{O}_4 - \gamma\text{-Fe}_2\text{O}_3$) and greigite (Fe_3S_4) are the only ferrimagnetic minerals known to be produced by organisms (Faivre and Schuler 2008). Therefore, these minerals are the most suitable primary interaction candidates to realize an effective sensor of the weak ambient magnetic field. A straightforward way of detecting the magnetic field in an animal would be via single-domain magnetite (approximate particle size: 50 nm) connected to mechanosensitive ion-channels, which could directly transduce the reorientation of the particles into a neuronal signal (Kirschvink and Gould 1981; Winklhofer and Kirschvink 2010). Other mechanisms based on superparamagnetic nanoparticles (less than 10 nm particle size) are feasible (Davila et al. 2003) but generally less efficient.

The experimental observations that magnetic orientation depends on the polarity of the ambient magnetic field in salmon (Quinn et al. 1981), subterranean mole-rats (Marhold et al. 1997), honey bees (Kirschvink and Kobayashi-Kirschvink 1991), and bats (Wang et al. 2007) is consistent with a mechanism based on single-domain magnetite. Furthermore, effects of a strong (100–500 mT) but brief (0.1–5 ms) magnetic pulse (with the potential to change the axis of magnetization of permanent magnetic particles) on magnetic orientation in honeybees (Kirschvink and Kobayashi-Kirschvink 1991), arthropods (Ernst and Lohmann 2016), fish (Fitak et al. 2020), turtles (Irwin and Lohmann 2005), birds (Wiltschko et al. 1994), mole-rats (Marhold et al. 1997), and bats (Holland et al. 2008) have been interpreted to support a ferrimagnetic sensory system in these species. Neither induction of electric fields nor radical-pair mechanisms (see below) are thought to lead to a prolonged effect on animal orientation from

magnetic pulses, as observed in these experiments. The trigeminal nerve, as part of the somatosensory system, has been shown to be involved in the magnetic sensing pathway in both fish (salmonids) (Walker et al. 1997) and migratory birds (Heyers et al. 2010; Pakhomov et al. 2018; Kobylkov et al. 2020). The trigeminal nerve innervates mechanosensory nerve endings in the periphery, and it is conceivable that it also transmits magnetic information from magnetically gated mechanosensitive ion channels. Structural evidence for a magnetite-based sensor was found in trigeminally innervated tissue in the nose of the rainbow trout (Diebel et al. 2000); however, the exact cell type hosting the magnetite particles remains to be identified, even 20 y after it has been described. Also, note that for migratory birds, a dual mechanism is thought to exist whereby magnetic compass information (as derived putatively from a radical pair-based sensor) uses visual but not trigeminal mediation (Zapka et al. 2009).

Magnetic sensing based on magnetite may be affected, at least in theory, by extremely low-frequency magnetic fields of moderate strength (<100 Hz, 1 μT) (Polk 1994) or even by radiofrequency fields (Kirschvink 2014). In contrast, heating through magnetic relaxation effects is practically negligible under weak radio-frequency magnetic fields (<1 μT , <10 MHz), as used in testing for radical-pair based magnetoreception (Shcherbakov and Winklhofer 2010). However, candidate cells, which are not directly accessible yet (Shaw et al. 2015), will be required to quantitatively assess effects of magnetic fields of any frequency on magnetoreceptor cells.

Magnetic sensors based on radical pairs. The radical pair mechanism (RPM) is widely considered as the canonical model for the magnetosensitivity of chemical reactions in weak magnetic fields (Hore and Mouritsen 2016). As the name suggests, the magnetosensitivity results from a pair of radicals, i.e., reaction intermediates with unpaired electrons, which can undergo different chemical reactions depending on their overall spin state. Only if the electron spins of the two radicals are antiparallel, i.e., give rise to a singlet state, the radical pair can recombine. On the other hand, triplet states, in which the electron spins add to a non-zero total spin, cannot directly produce closed-shell products as this would violate the conservation of angular momentum and the Pauli Exclusion Principle.

The magnetosensitivity arises because the singlet and triplet states can interconvert as the electron spins, in a semi-classical picture and undergo a precession motion in the local magnetic field. This field comprises the applied, e.g., geomagnetic, field and the field due to magnetic nuclei in the radicals (a result of so-called hyperfine interactions). In reality, this process is quantum in nature, as the system is to be described as a superposition of spin states that coherently evolve to reveal only their singlet and triplet character stochastically when “measured” by a spin-selective reaction process. Furthermore, the dynamics can show quantum

features that go beyond the picture of precessing spins described above and has put the mechanism at the forefront of the emerging field of quantum biology (Hiscock et al. 2016). Overall, these processes implicate that the ratio between the singlet and triplet products depends on the direction and intensity of the magnetic field. Interestingly, this effect is measurable—even if the magnetic interactions are orders of magnitude smaller than thermal energies—because for a short time, the radical pair is in a non-equilibrium spin state.

The RPM might underpin the magnetic compass attributed to many migratory birds in the form of the blue-light sensitive flavo-protein (binding flavin adenine dinucleotide, FAD) cryptochrome located in the retinae of the animals (Hore and Mouritsen 2016). For the cryptochromes of the fruit fly (*Drosophila melanogaster*) and the thale cress (*Arabidopsis thaliana*), in vitro experiments show that magnetosensitivity can result from a radical pair that involves the flavin anion radical and the radical cation of the third tryptophan of the so-called tryptophan triad (in plant cryptochromes) or tetrad (animal cryptochromes), a highly conserved electron transfer pathway linking the protein surface and the FAD cofactor (Maeda et al. 2012; Sheppard et al. 2017). For the European robin cryptochrome 4, a swift reversible electron transfer reaction involving the two outermost tryptophan residues was suggested (Xu et al. 2021). On the other hand, Type II cryptochromes, such as mammalian cryptochromes, regulate circadian rhythms and are thought to lack the structural features to securely bind the photoactive flavin cofactor (Kutta et al. 2017).

This view has, however, been contradicted by the study of Zeng et al. (2018), which demonstrated flavin binding and a photo-activated magnetic field effect on human cryptochrome 1 in vitro. In vivo, the situation appears to be potentially even more complex, and how/if magnetosensitivity could ensue is currently fiercely debated, whereby besides the photo-reduction, the reoxidation of the flavin cofactor is being considered (Pooam et al. 2019). The RPM is also discussed in the context of putatively adverse health effects in humans resulting from the exposure to weak static and oscillatory magnetic fields (Juutilainen et al. 2018). Several questions concerning the RPM of magnetoreception, e.g., details of the signaling cascade, the amplification of the very small effects, decoherence phenomena, and the suppressive effect exerted by inter-radical interactions (in particular, the electron-electron dipolar coupling), still remain unresolved (Babcock and Kattinig 2020). In any case, to elicit sensitivity to the applied magnetic field, quantum coherences must be sustained for at least the time of a Larmor precession period of the electron spins, which equates 600 ns to 1.8 μ s depending on local geomagnetic field intensity, and the reaction rates must be matched to the spin dynamics. A detailed study of spin relaxation in cryptochrome revealed characteristic decoherence times in the order of microseconds under physiological conditions (Kattinig et al. 2016).

This is confirmed by behavioral studies (Kobylkov et al. 2019) and the lifetime of spin-correlation of radical pairs in isolated cryptochromes, as studied by time-resolved electron paramagnetic resonance (EPR) spectroscopy (Biskup et al. 2009).

In behavioral experiments, the ability of animals to orient in the geomagnetic field has often been found to be deprived in the presence of weak oscillatory magnetic fields in the range from 0.1 to \sim 100 MHz (Ritz et al. 2004; Engels et al. 2014; Malkemper et al. 2015; Leberecht et al. 2022). This effect is usually construed as indicative of radical-pair based magnetoreception/sensitivity, the idea being that RF-EMFs alter the spin-dynamics of the radical pair when resonant with (at least) one of the frequencies of singlet–triplet interconversion. While these effects have been demonstrated in a chemical model system and are supported by theoretical analysis, the tiny magnetic field amplitudes used in these experiments (e.g., amplitudes of the order of 1 nT for monochromatic fields or mean noise densities of the order of 1 pT ($\sqrt{\text{Hz}}^{-1}$ for broadband noise), necessitate unphysically long coherent lifetimes in order to manifest in the radical pair spin dynamics (Hore and Mouritsen 2016; Kobylkov et al. 2019). On the other hand, the frequency dependence of the disruptive effect and the modeling of spin relaxation times of cryptochromes suggest coherent lifetimes of no longer than \sim 10 μ s, which is orders of magnitude too short for a radical pair to respond to such weak RF perturbations (Kattinig et al. 2016; Hiscock et al. 2017). Thus, the RF effect has remained a mystery. If the radical pair model truly applies, it will require an additional amplification of the magnetic field to explain the effect. It is puzzling though that this RF effect, which is most widely accepted as a decisive indicator of a radical pair-based sensor, cannot be explained within this framework without resorting to unphysical parameters with respect to the coherent lifetime of the radical pair. Therefore, a different model could be required, possibly by still building on the radical pair premise.

The governing principle of the RPM is the coherent interconversion of the singlet and triplet spin states of a radical pair, the key ingredient to which is their hyperfine interaction. However, according to recent research, the hyperfine interaction is not a categorical requirement to realize magnetosensitivity to weak magnetic fields. Instead, in systems comprising more than two radicals, electron-electron dipolar interactions could provide an alternative, so far mostly unexplored, pathway for magnetic field effects (Keens et al. 2018). A model of this effect demonstrates a directional sensitivity to fields weaker than the geomagnetic field, and remarkable spikes in the reaction yield as a function of the magnetic field intensity that can be tuned by the exchange interaction. Studies so far suggest that the effect could be relevant to magnetic field effects on lipid autoxidation (Sampson et al. 2019) and potentially enhance the magnetosensitivity of the cryptochrome sensor (Babcock and Kattinig 2020).

Additionally, there is another surprising effect that can boost the magnetosensitivity of radical pairs in the putative magnetosensory protein cryptochrome (Kattinig and Hore 2017; Kattinig 2017). Magnetic field effects can be vastly amplified if one of the radicals of the primary pair undergoes a spin-selective electron transfer reaction with a spin-bearing scavenger (chemical Zeno effect). This three-radical scheme offers clear and important benefits over the RPM, such as a greatly enhanced sensitivity to the orientation of a 50 μT magnetic field and immunization of the sensor to fast decoherence processes in one of the radicals. Consequently, magnetic field effects on radical pairs involving swiftly spin-relaxing species, such as superoxide, are no longer to be precluded. This is remarkable insofar as some evidence has recently emerged in favor of a magnetosensitive reoxidation reaction in cryptochrome involving superoxide (Pooam et al. 2019).

Biological effects

Invertebrates. Many insect species perceive electric and magnetic fields and use them for communication and orientation (Greggers et al. 2013; Vacha 2017). Honeybees (*Apis mellifera*) perceive electric fields via the mechanosensitive Johnston's organ located on their antennae. They react behaviorally to both constant and modulated electric fields. Under natural conditions, bees emit electric fields during motion and during the waggle dance and use them for social communication (Greggers et al. 2013).

Effects of a high voltage power-line on honeybees have been investigated in a field study (Greenberg et al. 1981). The E-field strength was 7 kV/m, which is above the current limit recommendation of 5 kV/m (ICNIRP 2010). Depending on the height of the hives (1 or 1.5 m), the currents induced within the hives were 59 μA and 85 μA , respectively. After 8 or 16 wk of exposure, the weight gain and the brood declined, which was associated with enhanced queen loss and colony failure and reduced overwinter survival (Greenberg et al. 1981). The bees are not disturbed directly by the perception of the E-field but by electric shocks and contact currents at magnitudes above about 275–350 nA (Bindokas et al. 1988).

Bumble bees (*Bombus terrestris*) detect electric fields via mechanosensitive body hairs, which react to air motion as well as to electric fields (Sutton et al. 2016). Insect bodies gain positive charge during flight, while flowers tend to be negatively charged (Clarke et al. 2017). The flower charges become modulated by the natural field of a visiting forager. Bumble bees and bees can therefore use electric fields to judge the reward contained in flowers they are visiting (Clarke et al. 2013). Opposite electric charges between bees and flowers are further involved in pollen collection, transportation, and subsequent pollination of the next visited flower (Clarke et al. 2017).

Many arthropod species, beyond insects, are capable of electroreception. Spiders not only perceive electric fields

via mechanosensitive body hairs but also disperse via “ballooning:” they climb to the top of a prominence, produce a silk thread, and float away using the wind and thermal air currents for transportation. The mechanism, however, cannot be fully explained by aerodynamic models. The global atmospheric electric circuit and the resulting atmospheric potential gradient provide an additional force that the spiders make use of. Behavioral experiments have shown that spiders are stimulated to take off in the presence of an electric field. The silk is charged, and the atmospheric potential gradient can provide sufficient Coulomb force to enable transport using electrostatic forces (Morley and Robert 2018).

Many insect species can perceive Earth's magnetic field and use it for orientation (Vacha 2017). The underlying mechanism(s) are not completely understood. In the fruit fly (*Drosophila melanogaster*), a cryptochrome-based light-dependent radical pair magnetosensor has been proposed (Gegear et al. 2008). Cryptochromes are not only blue light receptors but also circadian oscillators necessary to maintain the circadian rhythm in animals (Chaves et al. 2011). In cockroaches (*Blattella germanica*), the circadian rhythm is affected by static magnetic fields as well as by weak broadband RF-EMFs (Bartos et al. 2019). Low frequency magnetic fields also exert an influence on the activity levels and circadian period of fruit flies (Fedele et al. 2014). In both species, data support a light dependent magneto-sensor involving cryptochrome.

Honeybees can be conditioned to discriminate the presence and absence of localized magnetic anomalies superimposed on Earth's magnetic field (Walker and Bitterman 1989a and b; Kirschvink and Kobayashi-Kirschvink 1991). The results in honeybees point to the perception of magnetic field polarity suggested to proceed via magnetite (Lambinet et al. 2017). Honeybees can also perceive ELF-EMFs but with a lower sensitivity than shown for static fields (Kirschvink et al. 1997).

During their foraging flights, honeybees can be exposed to relatively high levels of 50 Hz magnetic fields in proximity to powerlines, ranging from 20–100 μT at ground level below powerline conductors to several mT within 1 m of the conductors. In two experimental studies, behavioral reactions of honeybees to 50 Hz magnetic fields between 20 μT and 7 mT in comparison to sham exposures were investigated to simulate these situations. The learning performance, tested by the proboscis extension reflex in response to olfactory cues, was slightly decreased at 20 μT and significantly reduced at 100 μT and 1 mT. Magnetic fields were applied between the conditioning and the testing session, e.g., during memory consolidation. Flight behavior was affected in the presence of magnetic fields, and the number of successful outward flights was reduced; however, the returning flights were not affected at 100 μT . Furthermore, the feeding of the foraging bees was reduced after exposure to magnetic

fields of 100 μT (Shepherd et al. 2018). In a follow-up experiment, exposure to 100 μT or 1 mT reduced aversive learning performance, as tested by the sting extension response, by over 20%. Furthermore, the aggressive response to intruder bees from foreign hives increased at magnetic fields of 100 μT by about 60% (Shepherd et al. 2019). These results indicate that short-time exposure to magnetic fields, at levels that could be encountered in beehives placed under power lines or during foraging flights, could affect the ability of bees to forage and pollinate crops and to respond appropriately to environmental stimuli, therefore having wider ecological implications. In a combinatorial experimental approach, neonicotinoid insecticides (e.g., clothianidin) were toxic to honey bees, but there was no synergistic effect with ELF-EMFs on flying behavior and learning. Neonicotinoids seemed even to attenuate partially the effects of ELF-EMFs (Shepherd et al. 2021).

On the other hand, field investigations (Lupi et al. 2020, 2021) have shown negative effects of electric and magnetic fields from power lines in combination with pesticides on various biomarkers of bee health, separately as well as in combination. The strongest negative effects on vital parameters were observed in combined multistress situations. Laboratory studies on effects of acute exposure to ELF-EMFs on bee behavior require independent replication. Furthermore, long term exposure should be investigated in field experiments to test whether bees can adapt to ELF-EMFs under power lines in the absence of pesticides.

Marine animals. Anthropogenic ELF-EMFs are emitted into the marine environment by substations and cables, potentially interfering with natural magnetic (e.g., the geomagnetic field) and electric fields (e.g., bioelectric fields). The number and power of wind turbines and offshore wind parks is steadily increasing in recent years, as measures to counteract climate change. As a consequence, more subsea cables carrying more power are deployed in coastal waters worldwide, resulting in increased intensity and coverage of anthropogenic ELF-EMFs.

Many marine organisms from bacteria to mammals are able to detect and respond to natural magnetic and electric fields. At a large scale, they use the geomagnetic field for orientation and migration (Walker et al. 1992).

Migrating fish species, such as European eels (*Anguilla anguilla*) or salmonids, have been reported to slow down their motion and/or change the direction when crossing sea cables (Westerberg and Lagenfelt 2008). Chinook salmon smolts (*Oncorhynchus tshawytscha*) and adult green sturgeon (*Acipenser medirostris*) regularly migrate via the San Francisco Estuary, crossing the Trans Bay Cable and several bridges producing strong magnetic anomalies, but they appear not to present a strong barrier to the natural seasonal movement patterns of these species (Klimley et al. 2017). In chinook salmon, the cable did not affect the migration success but

caused a slight modification of the migration route (Wyman et al. 2018). Importantly, these single events did not seem to affect the migration as a whole. The number of subsea cables, however, is steadily increasing, and more frequent encounters might result in a slower and energetically more costly migration affecting the population. Studies designed to test how anthropogenic magnetic fields may affect magnetic orientation have only started recently and should be further prioritized (Klimley et al. 2021).

Several species of sharks and rays can perceive the bioelectric field of prey and use it for prey location, as has been shown in behavioral experiments (Kalmijn 1971). Sharks, skates, and rays receive electrical information not only on the position of their prey but also on the drift of ocean currents and their magnetic compass headings. They react to artificial electric fields designed to mimic prey with a threshold of about 5 nV cm^{-1} (Kalmijn 1982). The underlying sensory organs are the ampullae of Lorenzini, which operate on the basis of positive feedback driven by conductance, employing voltage-sensitive ion channels as excitable elements (Kalmijn et al. 2002). Various species possess several ampullary clusters with different location and morphology, suggesting specialized ampullary functions for processing weak bioelectric fields or geomagnetic induced fields (Rivera-Vicente et al. 2011).

Seabed species, closer to the source, are most likely to encounter higher intensities of anthropogenic ELF-EMFs. The benthic small-spotted catshark (*Scyliorhinus canicula*) learned quickly under laboratory conditions to use electric stimuli to locate food and habituated to the stimuli if unrewarded (Kimber et al. 2014). Little skates (*Leucoraja erinacea*) increased substantially their exploratory and foraging activity close to subsea high voltage DC cables (Hutchison et al. 2020). Furthermore, embryos of thornback rays (*Raja clavata*) reduced their ventilation as a reaction to electric field stimuli, which resembled the presence of a predator (Ball et al. 2016).

The few available findings in marine invertebrates provide variable results. Under natural conditions, a modest increase of foraging activity was observed in American lobsters (*Homarus americanus*) close to a high voltage DC cable (Hutchison et al. 2020). On the other hand, juvenile European lobsters (*Homarus gammarus*) did not show any behavioral changes under laboratory conditions during exposure to static magnetic fields of 200 μT (Taormina et al. 2020). The edible crab (*Cancer pagurus*) preferred shelter exposed to static magnetic fields of several mT over an unexposed shelter and over freely roaming within the experimental area (Scott et al. 2018). In contrast, spiny lobsters (*Panulirus argus*) avoided a shelter with a strong magnetic anomaly in a laboratory setting (Ernst and Lohmann 2018). The same species uses local signatures of Earth's magnetic field for navigation (Boles and Lohmann 2003); thus it has to be taken into consideration that any magnetic disturbance can have profound effects on their

distribution. Long-term exposures to magnetic fields did not significantly affect survival and reproduction in several species of crustaceans and molluscs (Bochert and Zettler 2004). Altogether, magnetic fields and induced electric fields apparently have physiological and behavioral effects on marine vertebrates and invertebrates, but the ecological consequences for species abundance and distribution remain largely unknown and need to be followed up, especially in the context of continuously increasing intensity and coverage of anthropogenic subsea ELF-EMFs.

Magnetic compass of night-migratory songbirds.

Night-migratory songbirds use a magnetic compass to find their way, sometimes over thousands of kilometers (Mouritsen 2018; Hore and Mouritsen 2022). Neuroanatomical and behavioral data suggest that magnetic compass information in European robins (*Erithacus rubecula*) is detected in the eye and then processed in the brain in part of the visual pathway terminating in “Cluster N” (Mouritsen et al. 2005; Zapka et al. 2009). When Cluster N is experimentally deactivated, birds can no longer use their magnetic compass, whereas their star compass and sun compass abilities remain unaffected (Zapka et al. 2009). A wealth of evidence suggests that migratory birds use a light-dependent, radical pair-based mechanism to sense magnetic compass directions (Hore and Mouritsen 2016, 2022). Cryptochromes are the only vertebrate proteins known to form suitable, spin-correlated radical pairs upon photoexcitation, with coherent lifetimes sufficient to respond to the geomagnetic field (i.e., of $\sim 1 \mu\text{s}$ or longer; see above). Cryptochrome 4 has recently been highlighted because it is expressed in the bird retina, and it binds flavin and forms magnetosensitive radical pairs (Günther et al. 2018; Hochstoeger et al. 2020; Xu et al. 2021); cryptochrome 1 has also been implicated (Wiltshcko et al. 2021), but two recent studies failed to replicate its supposed light-dependent activation (Pinzon-Rodriguez and Muheim 2021; Bolte et al. 2021). Cryptochrome 2 is also expressed in bird retina, but its localization points to a role in the circadian clock rather than an involvement in magnetoreception (Einwich et al. 2022). Additionally, birds may possess another magnetosensitive pathway involving the ophthalmic branch of the trigeminal nerve, which has been hypothesized to be innervated by a magnetite-based sensor (Heyers et al. 2010). However, a magnetic pulse of 100 mT, able to disrupt magnetite-based sensors, failed to affect the migratory behavior of northern wheatears (*Oenanthe oenanthe*) (Karwinkel et al. 2022), so if this sensor exists in birds, it is not used for migration, at least in this species.

The bird magnetic compass is perturbed by weak broadband (0.1–85 MHz, $0.085 \mu\text{T}$) and single-frequency (7 MHz, $0.47 \mu\text{T}$) oscillating magnetic fields, suggesting a resonance effect (Ritz et al. 2004). A series of carefully controlled double-blinded laboratory experiments demonstrated that in the presence of broadband anthropogenic RF-EMFs (400 kHz

to 10 MHz) in the nT-range ($\sim 1,000$ times weaker than the current recommended limits) birds are unable to use their magnetic compass (Engels et al. 2014). This finding has been repeatedly replicated (Schwarze et al. 2016; Kobylkov et al. 2019), documenting a reproducible effect of low-intensity anthropogenic electromagnetic noise on the behavior of a vertebrate. A recent study has shown that RF fields at even higher frequencies (75–85 MHz) prevent a night-migratory songbird from using its magnetic compass in behavioral experiments. These results have been interpreted to indicate that a flavin-tryptophan radical pair could be the magnetic sensor (Leberecht et al. 2022). Power lines (16.7 Hz or 50 Hz fields) or mobile phone signals (100 MHz to GHz frequencies) are not expected to disrupt the magnetic sense of birds, since these frequencies do not interfere with the assumed radical-pair mechanism (Hiscock et al. 2017).

Most of the fundamental knowledge of magnetoreception and orientation/navigation in migratory birds is based on cage experiments under controlled laboratory conditions studying the intended take-off direction. Studies addressing magnetic cues in free flying birds are scarce. Such studies require equipping birds with sensors and coils, to employ magnetic manipulations, and measure behavioral responses. Despite the progress in miniaturization, this still represents a major challenge in small migratory birds. Consequently, the question whether anthropogenic RF-EMFs affect bird migration in the long run has not yet been investigated.

Magnetic sense in mammals. The magnetic sense is less investigated in mammals than in other taxa (Burda et al. 2020). One of the better studied mammalian groups are bats, the only mammals with powered flight, enabling them to move over hundreds of kilometers during foraging and ranging flights. Some migratory bats move thousands of kilometers between breeding and wintering sites, facing similar ecological challenges as migratory birds. While it has been established for more than 50 y that birds have a magnetic sense, in bats this sense was demonstrated for the first time only 15 y ago (Holland et al. 2006). Studies suggest that their magnetic compass differs from that of birds, relying on polarity rather than inclination as the key physical parameter of the magnetic field. Pulse remagnetization tests, argued to be diagnostic of a magnetic particle based magnetic sense, support the presence of this system in bats (Holland et al. 2008). To date there is no evidence that bats have a radical-pair based compass, making it unlikely that they are affected by weak environmental RF-EMFs, although the effect of radiofrequency noise on bats has not been directly tested. Bats calibrate their magnetic compass at sunset (Holland et al. 2010), using polarized light patterns (Greif et al. 2014) or the sun disk as a reference (Lindecke et al. 2015, 2019). Thus, when considering the possible effects of EMFs on bats, the time of exposure and weather conditions must be considered.

Studies on rodents have provided evidence for a magnetic sense in several species. Many of these studies have been performed in the laboratory, ensuring control of magnetic stimuli and other confounding factors. Early studies have shown that African mole-rats (*Fukomys sp.*) preferentially build their nests in the southeast direction of an arena, and that this behavior can be predictably modulated by artificial rotation of the magnetic field (Burda et al. 1990). The preferred direction differs between mole-rat species, and it remains unclear if it is an innate or learned behavior (Oliveriusova et al. 2012). Similar to bats, the magnetic sense of mole-rats is sensitive to magnetic field polarity rather than inclination, and it does not require light (Marhold et al. 1997). Furthermore, it is not affected by radiofrequency noise of the same frequencies and intensities known to perturb the avian magnetic compass (Thalau et al. 2006). Taken together, these findings support the hypothesis of a compass based on magnetic particles, but the location of the receptive organ is unknown. The Middle East blind mole rat (*Spalax ehrenbergi*), which is more closely related to hamsters and rats than to African mole-rats, also possesses a light-independent magnetic sense (Kimchi and Terkel, 2001), supporting the idea that the polarity compass represents an adaptation that aids navigation in the underground environment.

Aboveground living (epigeic) rodents with well-developed vision, such as the wood mouse (*Apodemus sylvaticus*), have also been suggested to use Earth's magnetic field for orientation (Mather and Baker 1981). In a nest building assay, wood mice showed an innate bimodal north-south preference, which in contrast to mole-rats was susceptible to RF-EMFs. This finding was interpreted to suggest the involvement of the RPM (Malkemper et al. 2015). A magnetic sense was further demonstrated in other epigeic rodents, e.g., Djungarian hamsters (*Phodopus sungorus*) (Deutschlander et al. 2003) and the Roborovski hamster (*Phodopus roborovskii*) (Malewski et al. 2018a), the bank vole (*Clathronomys glareolus*) (Oliveriusova et al. 2014), and even in laboratory C57BL/6 J mice (Muheim et al. 2006; Painter et al. 2018). Some of these species did not show a spontaneous preference for nest building but could be trained to respond to magnetic field directions. Laboratory mice are further suggested to be able to use magnetic field cues for orientation in a Morris water maze (Phillips et al. 2013). Interestingly, magnetic experiments on epigeic rodents were only successful in the absence of weak radiofrequency noise, i.e., when the laboratory was electromagnetically shielded (Phillips et al. 2013; Malewski et al. 2018b). Phillips et al. (2022) provide a comprehensive summary of light-dependent magnetic compass orientation in murine rodents, its sensitivity to low-level RF-EMFs, and methodological problems caused by anthropogenic RF-EMFs in laboratory settings. Thus, current data have been interpreted to suggest that epigeic mammals might use a radical pair mechanism, while mole-rats and bats likely use a light-independent magnetic particle-based mechanism.

Evidence for a magnetic sense in other mammalian taxa is indirect and predominantly based on field observations of magnetic alignment, a preference of animals to align their body axis with the field lines of Earth's magnetic field. This behavior has been observed (with the help of Google Earth) in ruminants like domestic cattle (*Bos primigenius*) and roe deer (*Capreolus capreolus*) during resting and grazing (Begall et al. 2008) and was later independently confirmed (Slaby et al. 2013). When startled, roe deer prefer to escape in the north or south direction (Obleser et al. 2016). Power lines (50/60 Hz) appear to disturb the alignment behavior in both cattle and deer in a distance-dependent manner (Burda et al. 2009). There are some indications that whales, which are related to ruminants, may use Earth's magnetic field for orientation (Kirschvink et al. 1986; Walker et al. 1992; Horton et al. 2011) and might be affected by radiofrequency noise (Granger et al. 2020), but evidence for a causal relationship is lacking so far. Alignment in the north-south direction has also been observed in two suid species, wild boars (*Sus scrofa*) in Europe and warthogs (*Phacochoerus africanus*) in Africa (Cervený et al. 2016). The preference of red foxes (*Vulpes vulpes*) to perform their hunting jumps toward the northeastern direction is also discussed as a manifestation of magnetic alignment. Their hunting success was shown to depend critically on the jumping direction, increasing toward north or south, in comparison to east or west (Cervený et al. 2011). Domestic dogs (*Canis lupus domesticus*) tend to align their body along the north-south direction during defecation and urination, but only if the geomagnetic magnetic field is stable (Hart et al. 2013). Dogs can also be trained to find a hidden bar magnet (Martini et al. 2018), and seem to use the magnetic field for orientation to aid path integration (Benediktova et al. 2020). While these observations have the heuristic potential to extend the list of magneto-sensitive mammalian species, the evidence is purely correlative and yields limited insight into the properties and mechanisms of the magnetic sense.

Humans seem to have no magnetic sense or at least are not consciously aware of the (geo-) magnetic stimuli encountered in everyday life. In the early 1980s, studies suggested that at least some humans may be able to perceive Earth's magnetic field and use it for orientation (Baker 1980, 1981), but these results were not replicable when applying proper blinding protocols and controls (Gould and Able 1981; Westby and Partridge 1986). It is possible that humans lost the magnetosensory system shared by many of our animal relatives or that a system still exists but lacks potent output to elicit perceptual awareness; i.e., the perception remains subconscious. A recent study supports the existence of a subconscious human magnetic sensory system (Wang et al. 2019). Under strictly controlled double-blind experimental conditions, brief, ecologically relevant rotations of Earth-strength magnetic fields produced specific and repeatable decreases

in the EEG alpha band (8–13 Hz) power in human volunteers. Such alpha-band power responses are termed alpha event-related desynchronizations and typically arise from visual, auditory, or tactile stimuli. The data are in line with a human geomagnetic sense that responds to polarity, can operate in darkness, and is not based on electrical induction or radical-pair-based effects (Wang et al. 2019). These results render a system based on magnetite particles as the most likely. It remains to be seen if these findings can be replicated independently.

Plant growth in magnetic fields and the possible role of cryptochromes. The geomagnetic field affects plant growth and development (Maffei 2014). Even though the exact mechanism of magnetoreception remains unknown, several lines of evidence suggest that it could be mediated by phytochrome and/or cryptochrome. Exposing plants to 500 μT static magnetic field inhibited growth in *A. thaliana* under blue light (which excites cryptochromes) but not under red light (which excites phytochromes) or in total darkness (Ahmad et al. 2007). Xu et al. (2014) showed that plant exposure to 500 μT increased blue light-dependent phosphorylation of cryptochromes (CRY1 and CRY2), while phosphorylation of CRY2 decreased in a near null magnetic field (NNMF, ≤ 40 nT). Agliassa et al. (2018b) showed, using wild-type and photoreceptor-deficient seedlings of *A. thaliana* grown in darkness, blue, and red light, and exposed to NNMF or geomagnetic field, that the magnetic field significantly impacts the expression levels of genes, known to be regulated by cryptochrome and phytochrome, in both shoots and roots. These results suggest that further activation/repression of specific cellular pathways responsible for modification of plant growth or delay in flowering time could occur in NNMF (Xu et al. 2012, 2015; Agliassa et al. 2018a), possibly through the involvement of the phytohormones gibberellin and auxin (Xu et al. 2017a and b).

It is worth noting that the mineral content of *A. thaliana* was affected rapidly after placing the plant in NNMF (Narayana et al. 2018). The amounts of both cations (ammonium, potassium, calcium, and magnesium) and anions (chloride, sulfate, nitrate, and phosphate) were rapidly (10 min) and significantly up-regulated compared to control plants, then fluctuated over the time-course analyzed to display lower levels after 96 h. These observations were sustained by rapid (10 min) changes in the expression levels of the corresponding transporter genes, suggesting a very rapid response of plants to NNMF. Furthermore, the iron and zinc content of roots was significantly decreased in NNMF-grown plants, along with a decrease in root ferric reductase activity (Islam et al. 2020). These results concerning mineral nutrition in NNMF are consistent with a delay in plant development under this condition. The reversion of the geomagnetic field can lead to important changes in gene expression, especially a drastic inhibition of the antioxidant-related genes in roots and a reduction of plant

size (Bertea et al. 2015). This observation may support the hypothesis that reversals of the geomagnetic fields may contribute to establish a higher selective pressure that eventually can influence the evolutionary pattern of plants (Maffei 2014; Occhipinti et al. 2014).

DC power lines may produce magnetic fields of a similar strength as Earth's magnetic field. Therefore, in close vicinity of DC power lines and in dependency of the magnetic field vector, the resulting total magnetic field magnitude may vary between zero and about twice the geomagnetic field. One would expect that the possible biological effects of ELF-EMF originating from AC power lines at 50 Hz on plants should have been apparent after several decades of continued anthropogenic exposure. Indeed, the few existing studies confirm that plant growth remains largely unaffected and that the few observed changes (Soja et al. 2003; Li et al. 2019) were weak in comparison with those evoked by natural environmental factors.

CONCLUSION AND RESEARCH RECOMMENDATIONS

A wealth of evidence shows that diverse species across the animal kingdom perceive biogenic electric fields or Earth's magnetic field and use them in short and long-distance orientation and navigation. It is therefore conceivable that anthropogenic electromagnetic fields can affect the physiology, behavior, and ultimately the ecology of animals. The extent of these effects and how they depend on frequency, intensity, and duration of the anthropogenic fields, however, is not known, because there are many unknowns on the underlying mechanistic principles and sensory structures.

The identification of sensory structures appears to be key to the identification of mechanisms; i.e., the underpinning biophysical principles. This has been achieved for the electric sense in fish where the structure and threshold levels of the receptor structures are known, allowing for predictions on the impact of anthropogenic changes in the environment. Concerning magnetic fields, the primary magnetosensory structures have not been identified yet, and the situation is opaque. Indirect evidence, such as a polarity dependence of a compass sense or interference of RF-EMFs, can only provide limited insight in this respect. Competing sensing principles could at least in theory realize comparable sensing modalities, as has become apparent in the section on action mechanisms. Based on sensory characteristics, it appears that at least two fundamentally different receptors for the detection of magnetic fields have evolved, but the cellular location and molecular basis of these remain to be elucidated. Knowledge of the molecular underpinnings of the magnetic sense promises to offer explanations of the various observed effects of anthropogenic fields, e.g., the disorientation of migratory birds in radiofrequency fields, and would enable

robust predictions that can guide preventive measures to protect wildlife. To this end, more research on the mechanisms that govern cellular and molecular responses to magnetic fields under strictly controlled laboratory conditions is needed.

On the other hand, because a response in the laboratory does not necessarily mean that the animals are affected in their natural behaviors and ecology, more data from animals in their actual habitats are required as well. With this, new challenges with respect to exposure assessment and dosimetry are unavoidable. We expect that the collection of data derived from experimental studies in the natural environment will be empowered by technological advances such as the ongoing miniaturization of non-transmitting data loggers that allow studying the behavior of freely roaming animals in detail, while simultaneously recording environmental parameters including light, temperature and electromagnetic fields. This will allow researchers to study natural behaviors and identify large-scale changes such as shifts in habitat use or community composition that might be induced by anthropogenic fields and are impossible to observe in the laboratory. Ultimately, only the amalgamation of interdisciplinary insights from the laboratory and the field will allow us to assess reliably any impact of anthropogenic EMFs on animals.

Plants appear to react to variations of the geomagnetic field by modifying various parameters such as gene expression, DNA alterations, or growth. As in many animal species, the underlying mechanism has been linked to the RPM in cryptochromes. Magnetic field effects are usually weak in comparison to the influence of other environmental parameters. Overall, only few data on plants are available, and these do not point toward adverse effects of anthropogenic ELF-EMFs on plants.

Taken together, the effects of electromagnetic fields on individual organisms have now been widely investigated for a multitude of plant and animal species. However, this does not yet address the ecological consequences of this perception in the context of increased anthropogenic EMF emissions. This will require studies of natural populations in their natural habitat and entire ecosystems, including the evaluation of the relevant physical variables over Earth's surface, along the seabed, in space and time, and detailed biological information on the relevant states of populations. Besides deciphering the action mechanism, this is a field of great demand for assessing the actual environmental effects of steadily increasing EMF emissions. Finally, and importantly, many results from isolated but often paradigm-forming studies have to be independently reproduced.

In particular, due to the ongoing technological development, the following topics are of special importance:

- Wireless charging and safety of small animals;
- Ecological consequences of the known behavioral effects of electric and magnetic fields from widespread marine cables;

- Ecological consequences of electromagnetic noise, known to disrupt animal (e.g., migratory bird) orientation in the laboratory, on animal orientation in the natural environment;
- Ecological consequences of observed behavioral effects of ELF-EMFs from powerlines, e.g., on insects and mammals; and
- Pinpointing sensory structures and action mechanism, whereby it is expected that progress for one species can fertilize progress in others.

Acknowledgments—We thank the invited speakers Margaret Ahmad, John Bolte, Dirk Geschwendtner, Christopher Gordon, Michael Hässig, Amparo Lazaro, Henrik Mouritsen, Daniel Robert, and Michael Winklhofer for their contributions to the workshop, Andrew Gill, Richard Holland, Joseph Kirschvink, Massimo Maffei, Benjamin Paffhausen, Heiko Schmaljohann, Gernot Schmid, Arno Thielens, and Adam Vanbergen for their contributions to the workshop and comments on the manuscript, and especially Pascal Malkemper for his help with the preparation of this manuscript, several critical reads, and comments.

The workshop was funded by Federal Ministry for the Environment, Nature Conservation and Nuclear Safety. Grant No. 3619102420

We dedicate this work to the late Christopher J. Gordon (24 March 1953–15 June 2021). Chris gave one of his last scientific presentations during the international workshop that is summarized in this paper. Chris was a biologist by training and spent 30 y at the US Environmental Protection Agency as a research physiologist. During his career, he investigated the influence of various environmental factors, especially non-ionizing radiation on thermoregulation in animals and humans and authored numerous scientific articles on that topic. We will miss his wit and dedication to research.

REFERENCES

- Agliassa C, Narayana R, Berteau CM, Rodgers CT, Maffei ME. Reduction of the geomagnetic field delays *Arabidopsis thaliana* flowering time through downregulation of flowering-related genes. *Bioelectromagnet* 39:361–374; 2018a.
- Agliassa C, Narayana R, Christie JM, Maffei ME. Geomagnetic field impacts on cryptochrome and phytochrome signaling. *J Photochem Photobiol* 185:32–40; 2018b.
- Ahmad M, Galland P, Ritz T, Wiltshcko R, Wiltshcko W. Magnetic intensity affects cryptochrome-dependent responses in *Arabidopsis thaliana*. *Planta* 225:615–624; 2007.
- Babcock NS, Kattinig DR. Electron-electron dipolar interaction poses a challenge to the radical pair mechanism of magnetoreception. *J Phys Chem Lett* 11:2414–2421; 2020.
- Baker RR. Goal orientation of blindfolded humans after long-distance displacement: possible involvement of a magnetic sense. *Science* 210:555–557; 1980.
- Baker RR. Human navigation and the sixth sense. London: Hodder and Stoughton; 1981.
- Ball RE, Oliver MK, Gill AB. Early life sensory ability-ventilatory responses of thornback ray embryos (*Raja clavata*) to predator-type electric fields. *Dev Neurobiol* 76:721–729; 2016.
- Bartos P, Netusil R, Slaby P, Dolezel D, Ritz T, Vacha M. Weak radiofrequency fields affect the insect circadian clock. *J R Soc Interface* 16: 20190285; 2019.
- Benediktova K, Adamkova J, Svoboda J, Painter MS, Bartos L, Novakova P, Vynikalova L, Hart V, Phillips J, Burda H. Magnetic alignment enhances homing efficiency of hunting dogs. *Elife* 9:e55080; 2020.
- Begall S, Cervený J, Neef J, Vojtech O, Burda H. Magnetic alignment in grazing and resting cattle and deer. *Proc Natl Acad Sci USA* 105:13451–13455; 2008.
- Berteau CM, Narayana R, Agliassa C, Rodgers CT, Maffei ME. Geomagnetic field (GMF) and plant evolution: investigating the

- effects of GMF reversal on *Arabidopsis thaliana* development and gene expression. *J Vis Exp* 105:53286; 2015.
- BfS. Internationaler Workshop zum Einfluss elektrischer, magnetischer und elektromagnetischer Felder auf die belebte Umwelt - Vorhaben 3619102420 [online]. 2020. (in German). Available at <http://nbn-resolving.de/urn:nbn:de:0221-2020050821802>. Accessed 15 December 2021.
- Bindokas VP, Gauger JR, Greenberg B. Mechanism of biological effects observed in honey bees (*Apis mellifera*, L.) hived under extra-high-voltage transmission lines: implications derived from bee exposure to simulated intense electric fields and shocks. *Bioelectromagnet* 9:285–301; 1988.
- Biskup T, Schleicher E, Okafuji A, Link G, Hitomi K, Getzoff ED, Weber S. Direct observation of a photoinduced radical pair in a cryptochrome blue-light photoreceptor. *Angewandte Chem* 48: 404–407; 2009.
- Bochert R, Zettler ML. Long-term exposure of several marine benthic animals to static magnetic fields. *Bioelectromagnet* 25:498–502; 2004.
- Boles LC, Lohmann KJ. True navigation and magnetic maps in spiny lobsters. *Nature* 421:60–63; 2003.
- Bolte P, Einwich A, Seth PK, Chetverikova R, Heyers D, Wojahn I, Janssen-Bienhold U, Feederle R, Hore P, Dedek K, Mouritsen H. Cryptochrome 1a localisation in light- and dark-adapted retinas of several migratory and non-migratory bird species: no signs of light-dependent activation. *Ethol Ecol Evol* 33:248–272; 2021.
- Burda H, Marhold S, Westenberger T, Wiltshcko R, Wiltshcko W. Magnetic compass orientation in the subterranean rodent *Cryptomys hottentotus* (Bathyergidae). *Experientia* 46:528–530; 1990.
- Burda H, Begall S, Cerveny J, Neef J, Nemecek P. Extremely low-frequency electromagnetic fields disrupt magnetic alignment of ruminants. *Proc Natl Acad Sci USA* 106:5708–5713; 2009.
- Burda H, Begall S, Hart V, Malkemper EP, Painter MS, Phillips JB. Magnetoreception in mammals. In: Fritsch B, ed. *The senses: a comprehensive reference*. Amsterdam: Elsevier: 421–444; 2020.
- Cerveny J, Begall S, Koubek P, Novakova P, Burda H. Directional preference may enhance hunting accuracy in foraging foxes. *Biol Lett* 7:355–357; 2011.
- Cerveny J, Burda H, Jezek M, Kusta T, Husinec V, Novakova P, Hart V, Hartova V, Begall S, Malkemper EP. Magnetic alignment in warhogs *Phacochoerus africanus* and wild boars *Sus scrofa*. *Mamm Rev* 47:1–5; 2016.
- Chaves I, Pokorny R, Byrdin M, Hoang N, Ritz T, Brettel K, Essen LO, van der Horst GTJ, Batschauer A, Ahmad M. The cryptochromes: blue light photoreceptors in plants and animals. *Ann Rev Plant Biol* 62:335–364; 2011.
- Clarke D, Whitney H, Sutton G, Robert D. Detection and learning of floral electric fields by bumblebees. *Science* 340:66–69; 2013.
- Clarke D, Morley E, Robert D. The bee, the flower, and the electric field: electric ecology and aerial electroreception. *J Comp Physiol A* 203:737–748; 2017.
- Davila AF, Fleissner G, Winklhofer M, Petersen N. A new model for a magnetoreceptor in homing pigeons based on interacting clusters of superparamagnetic magnetite. *Phys Chem Earth* 28:647–652; 2003.
- Deutschlander ME, Freake MJ, Borland SC, Phillips JB, Madden RC, Anderson LE, Wilson BW. Learned magnetic compass orientation by the Siberian hamster, *Phodopus sungorus*. *Animal Behaviour* 65:779–786; 2003.
- Diebel CE, Proksch R, Green CR, Neilson P, Walker MM. Magnetite defines a vertebrate magnetoreceptor. *Nature* 406:299–302; 2000.
- Einwich A, Seth PK, Bartolke R, Bolte P, Feederle R, Dedek K, Mouritsen H. Localisation of cryptochrome 2 in the avian retina. *J Comp Physiol A* 208:69–81; 2022.
- Engels S, Schneider NL, Lefeldt N, Hein CM, Zapka M, Michalik A, Elbers D, Kittel A, Hore PJ, Mouritsen H. Anthropogenic electromagnetic noise disrupts magnetic compass orientation in a migratory bird. *Nature* 509:353–356; 2014.
- Ernst DA, Lohmann KJ. Effect of magnetic pulses on Caribbean spiny lobsters: implications for magnetoreception. *J Exp Biol* 219:1827–1832; 2016.
- Ernst DA, Lohmann KJ. Size-dependent avoidance of a strong magnetic anomaly in Caribbean spiny lobsters. *J Exp Biol* 221: jeb172205; 2018.
- Faivre D, Schuler D. Magnetotactic bacteria and magnetosomes. *Chem Rev* 108:4875–4898; 2008.
- Fedele G, Edwards MD, Bhutani S, Hares JM, Murbach M, Green EW, Dissel S, Hastings MH, Rosato E, Kyriacou CP. Genetic analysis of circadian responses to low frequency electromagnetic fields in *Drosophila melanogaster*. *PLoS Genet* 10:e1004804; 2014.
- Fitak RR, Wheeler BR, Johnsen S. Effect of a magnetic pulse on orientation behavior in rainbow trout (*Oncorhynchus mykiss*). *Behav Process* 172:104058; 2020.
- Gill A, Desender M. State of the science report, chapter 5: risk to animals from electromagnetic fields emitted by electric cables and marine renewable energy devices. Richland, WA: Pacific Northwest National Lab: 87–103; 2020.
- Gill AB, Gloyne-Philips I, Kimber J, Sigray P. Marine renewable energy, electromagnetic (EM) fields and EM-sensitive animals. In: Shields MA, Payne AIL, eds. *Marine renewable energy technology and environmental interactions*. Dordrecht (Netherlands): Springer: 61–79; 2014.
- Gegeer R, Casselman A, Waddell S, Reppert SM. Cryptochrome mediates light-dependent magnetosensitivity in *Drosophila*. *Nature* 454:1014–1018; 2008.
- Gould JS, Able KP. Human homing: an elusive phenomenon. *Science* 212:1061–1063; 1981.
- Greenberg B, Bindokas VP, Frazier MJ, Gauger JR. Response of honey bees, *Apis mellifera* L., to high-voltage transmission lines 1. *Environ Entomol* 10:600–610; 1981.
- Greggers U, Koch G, Schmidt V, Durr A, Floriou-Servou A, Piepenbrock D, Gopfert MC, Menzel R. Reception and learning of electric fields in bees. *Proc Biol Sci* 280:20130528; 2013.
- Granger J, Walkowicz L, Fitak R, Johnsen S. Gray whales strand more often on days with increased levels of atmospheric radio-frequency noise. *Curr Biol* 30:R155–R156; 2020.
- Greif S, Borissov I, Yovel Y, Holland RA. A functional role of the sky's polarization pattern for orientation in the greater mouse-eared bat. *Nat Commun* 5:4488; 2014.
- Günther A, Einwich A, Sjulstok E, Feederle R, Bolte P, Koch K-W, Solov'yov I, Mouritsen H. Double-cone localization and seasonal expression pattern suggest a role in magnetoreception for European robin cryptochrome 4. *Curr Biol* 28:211–223; 2018.
- Irwin WP, Lohmann KJ. Disruption of magnetic orientation in hatchling loggerhead sea turtles by pulsed magnetic fields. *J Comp Physiol A* 191:475–480; 2005.
- Hart V, Novakova P, Malkemper EP, Begall S, Hanzal V, Jezek M, Kusta T, Nemecek V, Adamkova J, Benediktova K, Cerveny J, Burda H. Dogs are sensitive to small variations of the earth's magnetic field. *Front Zool* 10:80; 2013.
- Heyers D, Zapka M, Hoffmeister M, Wild JM, Mouritsen H. Magnetic field changes activate the trigeminal brainstem complex in a migratory bird. *Proc Natl Acad Sci USA* 107:9394–9399; 2010.
- Hiscock HG, Worster S, Kattinig DR, Steers C, Jin Y, Manolopoulos DE, Mouritsen H, Hore PJ. The quantum needle of the avian magnetic compass. *Proc Natl Acad Sci USA* 113:4634–4639; 2016.
- Hiscock HG, Mouritsen H, Manolopoulos DE, Hore P. Disruption of magnetic compass orientation in migratory birds by radiofrequency electromagnetic fields. *Biophys J* 113:1475–1484; 2017.
- Hochstoeger T, Al Said T, Maestre D, Walter F, Vilceanu A, Pedron M, Cushion TD, Snider W, Nimpf S, Nordmann GC, Landler L, Edelman N, Kruppa L, Dürnberger G, Mechtler K, Schuechner S, Ogris E, Malkemper EP, Weber S, Schleicher E, Keays DA. The biophysical, molecular, and anatomical landscape

- of pigeon cry4: a candidate light-based quantal magnetosensor. *Sci Adv* 6:eabb9110; 2020.
- Holland RA, Thorup K, Vohlfahrt MJ, Cochran WW, Wikelski M. Navigation: bat orientation using earth's magnetic field. *Nature* 444:702; 2006.
- Holland RA, Kirschvink JL, Doak TG, Wikelski M. Bats use magnetite to detect the earth's magnetic field. *PLoS One* 3:e1676; 2008.
- Holland RA, Borissov I, Siemers BM. A nocturnal mammal, the greater mouse-eared bat, calibrates a magnetic compass by the sun. *Proc Natl Acad Sci USA* 107:6941–6945; 2010.
- Hore PJ, Mouritsen H. The radical pair mechanism of magnetoreception. *Annu Rev Biophys* 45:299–344; 2016.
- Hore PJ, Mouritsen H. How migrating birds use quantum effects to navigate. *Sci Am* 326:26–31; 2022.
- Horton TW, Holdaway RN, Zerbin AN, Hauser N, Garrigue C, Andriolo A, Clapham PJ. Straight as an arrow: humpback whales swim constant course tracks during long-distance migration. *Biol Lett* 7:674–679; 2011.
- Hutchison ZL, Gill AB, Sigra P, He H, King JW. Anthropogenic electromagnetic fields (EMF) influence the behaviour of bottom-dwelling marine species. *Sci Rep* 10:4219; 2020.
- ICNIRP. Effects of electromagnetic fields on the living environment. In: Matthes R, Bernhardt JH, Repacholi MH, eds. Proceedings of the international seminar on effects of electromagnetic fields on the living environment, Ismaning, Germany, October 4 and 5 1999. Munich: International Commission on Non-Ionizing Radiation Protection; 2000.
- ICNIRP. Guidelines on limits of exposure to static magnetic fields. *Health Phys* 96:504–514; 2009.
- ICNIRP. Guidelines for limiting exposure to time-varying electric and magnetic fields (1 Hz to 100 KHz). *Health Phys* 99:818–836; 2010.
- Islam M, Maffei ME, Viganì G. The geomagnetic field is a contributing factor for an efficient iron uptake in *Arabidopsis thaliana*. *Front Plant Sci* 11:325; 2020.
- Jungerman RL, Rosenblum B. Magnetic induction for the sensing of magnetic fields by animals-an analysis. *J Theor Biol* 87:25–32; 1980.
- Juutilainen J, Herrala M, Luukkonen J, Naarala J, Hore PJ. Magnetocarcinogenesis: is there a mechanism for carcinogenic effects of weak magnetic fields? *Proc Biol Sci* 285:20180590; 2018.
- Kalmijn AJ. The electric sense of sharks and rays. *J Exp Biol* 55:371–83; 1971.
- Kalmijn AJ. Electric and magnetic field detection in elasmobranch fishes. *Science* 218:916–8; 1982.
- Kalmijn AJ, Gonzalez IF, McClune MC. The physical nature of life. *J Physiol Paris* 96:355–62; 2002.
- Karwinkel T, Winklhofer M, Christoph P, Allenstein D, Hüppop O, Brust V, Bairlein F, Schmaljohann H. No apparent effect of a magnetic pulse on free-flight behaviour in northern wheat-eaters (*Oenanthe oenanthe*) at a stopover site. *J Royal Soc Interface* 19:20210805; 2022.
- Kattnig DR. Radical-pair-based magnetoreception amplified by radical scavenging: resilience to spin relaxation. *J Phys Chem B* 121:10215–10227; 2017.
- Kattnig DR, Hore PJ. The sensitivity of a radical pair compass magnetoreceptor can be significantly amplified by radical scavengers. *Sci Rep* 7:11640; 2017.
- Kattnig DR, Solov'yov IA, Hore PJ. Electron spin relaxation in cryptochrome-based magnetoreception. *Phys Chem Chem Phys* 18:12443–12456; 2016.
- Keens RH, Bedkhal S, Kattnig DR. Magnetosensitivity in dipolarly coupled three-spin systems. *Phys Rev Lett* 121:096001; 2018.
- Kimber JA, Sims DW, Bellamy PH, Gill AB. Elasmobranch cognitive ability: using electroreceptive foraging behaviour to demonstrate learning, habituation and memory in a benthic shark. *Anim Cogn* 17:55–65; 2014.
- Kimchi T, Terkel J. Magnetic compass orientation in the blind mole rat *Spalax ehrenbergi*. *J Exp Biol* 204:751–758; 2001.
- Kirschvink JL. Radio waves zap the biomagnetic compass. *Nature* 509:296–297; 2014.
- Kirschvink JL, Gould JL. Biogenic magnetite as a basis for magnetic field sensitivity in animals. *Bio Systems* 13:181–201; 1981.
- Kirschvink JL, Kobayashi-Kirschvink A. Is geomagnetic sensitivity real? Replication of the Walker-Bitterman conditioning experiment in honey bees. *Am Zool* 31:169–185; 1991.
- Kirschvink JL, Dizon AE, Westphal JA. Evidence from strandings for geomagnetic sensitivity in cetaceans. *J Exp Biol* 120:1–24; 1986.
- Kirschvink J, Padmanabha S, Boyce C, Oglesby J. Measurement of the threshold sensitivity of honeybees to weak, extremely low-frequency magnetic fields. *J Exp Biol* 200:1363–1368; 1997.
- Klimley AP, Wyman MT, Kavet R. Chinook salmon and green sturgeon migrate through San Francisco Estuary despite large distortions in the local magnetic field produced by bridges. *PLoS One* 12:e0169031; 2017.
- Klimley AP, Putman NF, Keller BA, Noakes D. A call to assess the impacts of electromagnetic fields from subsea cables on the movement ecology of marine migrants. *Conserv Sci Pract* e436; 2021.
- Kobylkov D, Wynn J, Winklhofer M, Chetverikova R, Xu J, Hiscock H, Hore PJ, Mouritsen H. Electromagnetic 0.1–100 kHz noise does not disrupt orientation in a night-migrating songbird implying a spin coherence lifetime of less than 10 μ s. *J R Soc Interface* 16:20190716; 2019.
- Kobylkov D, Schwarze S, Michalik B, Winklhofer M, Mouritsen H, Heyers D. A newly identified trigeminal brain pathway in a night-migratory bird could be dedicated to transmitting magnetic map information. *Proc Biol Sci* 287:20192788; 2020.
- Kutta RJ, Archipowa N, Johannissen LO, Jones AR, Scrutton NS. Vertebrate cryptochromes are vestigial flavoproteins. *Scientific Reports* 7:44906; 2017.
- Lambinet V, Hayden ME, Reid C, Gries G. Honey bees possess a polarity-sensitive magnetoreceptor. *J Comp Physiol A* 203:1029–1036; 2017.
- Leberecht B, Kobylkov D, Karwinkel T, Doge S, Burnus L, Wong SY, Apte S, Haase K, Musielak I, Chetverikova R, Dautaj G, Bassetto M, Winklhofer M, Hore PJ, Mouritsen H. Broadband 75–85 MHz radiofrequency fields disrupt magnetic compass orientation in night-migratory songbirds consistent with a flavin-based radical pair magnetoreceptor. *J Comp Physiol A* 208:97–106; 2022.
- Li X, Liu X, Wan B, Li X., Li M., Zhu H, Hua H. Effects of continuous exposure to power frequency electric fields on soybean *Glycine max*. *J Environ Radioact* 204:35–41; 2019.
- Lindecke O, Voigt CC, Petersons G, Holland RA. Polarized skylight does not calibrate the compass system of a migratory bat. *Biol Lett* 11:20150525; 2015.
- Lindecke O, Elksne A, Holland RA, Petersons G, Voigt CC. Experienced migratory bats integrate the sun's position at dusk for navigation at night. *Curr Biol* 29:1369–1373; 2019.
- Lupi D, Tremolada P, Colombo M, Giacchini R, Benocci R, Parenti P, Parolini M, Zambon G, Vighi M. Effects of pesticides and electromagnetic fields on honeybees: a field study using biomarkers. *Int J Environ Res* 14:107–122; 2020.
- Lupi D, Palamara Mesiano M, Adani A, Benocci R, Giacchini R, Parenti P, Zambon G, Lavazza A, Boniotti MB, Bassi S, Colombo M, Tremolada P. Combined effects of pesticides and electromagnetic-fields on honeybees: multi-stress exposure. *Insects* 12:716; 2021.
- Maeda K, Robinson AJ, Henbest KB, Hogben HJ, Biskup T, Ahmad M, Schleicher E, Weber S, Timmel CR, Hore PJ. Magnetically sensitive light-induced reactions in cryptochrome are consistent with its proposed role as a magnetoreceptor. *Proc Natl Acad Sci USA* 109:4774–4779; 2012.

- Maffei ME. Magnetic field effects on plant growth, development, and evolution. *Front Plant Sci* 5:445; 2014.
- Malewski S, Begall S, Burda H. Learned and spontaneous magnetosensitive behaviour in the Roborovski hamster (*Phodopus roborovskii*). *Ethol* 124:423–431; 2018a.
- Malewski S, Begall S, Schleich CE, Antenucci CD, Burda H. Do subterranean mammals use the earth's magnetic field as a heading indicator to dig straight tunnels? *Peer J* 6:e5819; 2018b.
- Malkemper EP, Eder SH, Begall S, Phillips JB, Winklhofer M, Hart V, Burda H. Magnetoreception in the wood mouse (*Apodemus sylvaticus*): influence of weak frequency-modulated radio frequency fields. *Sci Rep* 4:9917; 2015.
- Marhold S, Wiltschko W, Burda H. A magnetic polarity compass for direction finding in a subterranean mammal. *Naturwissenschaften* 84:421–423; 1997.
- Martini S, Begall S, Findeklee T, Schmitt M, Malkemper EP, Burda H. Dogs can be trained to find a bar magnet. *Peer J* 6:e6177; 2018.
- Mather JG, Baker RR. Magnetic sense of direction in wood mice for route-based navigation. *Nature* 291:152–155; 1981.
- Morley EL, Robert D. Electric fields elicit ballooning in spiders. *Curr Biol* 28:2324–2330; 2018.
- Mouritsen H. Long-distance navigation and magnetoreception in migratory animals. *Nature* 558:50–59; 2018.
- Mouritsen H, Feenders G, Liedvogel M, Wada K, Jarvis ED. Night vision brain area in migratory songbirds. *Proc Natl Acad Sci USA* 102:8339–8344; 2005.
- Muheim R, Edgar NM, Sloan KA, Phillips JB. Magnetic compass orientation in c57bl/6j mice. *Learn Behav* 34:366–373; 2006.
- Narayana R, Fliegmann J, Paponov I, Maffei ME. Reduction of geomagnetic field (GMF) to near null magnetic field (NNMF) affects *Arabidopsis thaliana* root mineral nutrition. *Life Sci Space Res (Amst)* 19:43–50; 2018.
- Nimpf S, Nordmann GC, Kagerbauer D, Malkemper EP, Landler L, Papadaki-Anastasopoulou A, Ushakova L, Wenninger-Weinzierl A, Novatchkova M, Vincent P, Lendl T, Colombini M, Mason MJ, Keays DA. A putative mechanism for magnetoreception by electromagnetic induction in the pigeon inner ear. *Curr Biol* 29:4052–4059; 2019.
- Nordmann GC, Hochstoeger T, Keays DA. Magnetoreception-A sense without a receptor. *PLoS Biol* 15:e2003234; 2017.
- Obleser P, Hart V, Malkemper EP, Begall S, Hola M, Painter MS, Cerveny J, Burda H. Compass-controlled escape behavior in roe deer. *Behav Ecol Sociobiol* 70:1345–1355; 2016.
- Ochpinti A, De Santis A, Maffei ME. Magnetoreception: an unavoidable step for plant evolution? *Trends Plant Sci* 19:1–4; 2014.
- Oliveriusova L, Nemec P, Kralova Z, SedlaCek F. Magnetic compass orientation in two strictly subterranean rodents: learned or species-specific innate directional preference? *J Exp Biol* 215:3649–3654; 2012.
- Oliveriusova L, Nemec P, Pavelkova Z, SedlaCek F. Spontaneous expression of magnetic compass orientation in an epigeic rodent: the bank vole, *Clethrionomys glareolus*. *Naturwissenschaften* 101:557–563; 2014.
- Painter MS, Davis M, Ganesh S, Rak E, Brumet K, Bayne H, Malkemper EP, Phillips JB. Evidence for plasticity in magnetic nest-building orientation in laboratory mice. *Anim Behav* 138:93–100; 2018.
- Pakhomov A, Anashina A, Heyers D, Kobylkov D, Mouritsen H, Chernetsov N. Magnetic map navigation in a migratory songbird requires trigeminal input. *Sci Rep* 8:11975; 2018.
- Phillips JB, Youmans PW, Muhei R, Sloan KA, Landler L, Painter MS, Anderson CR. Rapid learning of magnetic compass direction by c57bl/6 mice in a 4-armed “plus” water maze. *Plos One* 8:e73112; 2013.
- Phillips J, Muheim R, Painter M, Raines J, Anderson C, Landler L, Dommer D, Raines A, Deutschlander M, Whitehead J, Fitzpatrick NE, Youmans P, Borland C, Sloan K, McKenna K. Why is it so difficult to study magnetic compass orientation in murine rodents? *J Comp Physiol A* 208:197–212; 2022.
- Pinzon-Rodriguez A, Muheim R. Cryptochrome expression in avian UV cones: revisiting the role of CRY1 as magnetoreceptor. *Sci Rep* 11:12683; 2021.
- Pooam M, Arthaut LD, Burdick D, Link J, Martino CF, Ahmad M. Magnetic sensitivity mediated by the *Arabidopsis* blue-light receptor cryptochrome occurs during flavin reoxidation in the dark. *Planta* 249:319–332; 2019.
- Polk C. Effects of extremely-low-frequency magnetic fields on biological magnetite. *Bioelectromagnetics* 15:261–270; 1994.
- Quinn TP, Merrill RT, Brannon EL. Magnetic field detection in sockeye salmon. *J Exp Zool* 217:137–142; 1981.
- Reilly JP. Applied bioelectricity. From electrical stimulation to electropathology. New York: Springer; 1998.
- Ritz T, Thalau P, Phillips JB, Wiltschko R, Wiltschko W. Resonance effects indicate a radical-pair mechanism for avian magnetic compass. *Nature* 429:177–180; 2004.
- Rivera-Vicente AC, Sewell J, Tricas TC. Electrosensitive spatial vectors in elasmobranch fishes: Implications for source localization. *Plos One* 6:e73112; 2011.
- Sampson C, Keens RH, Kattnig DR. On the magnetosensitivity of lipid peroxidation: two- versus three-radical dynamics. *Phys Chem Chem Phys* 21:13526–13538; 2019.
- Scott K, Harsanyi P, Lyndon AR. Understanding the effects of electromagnetic field emissions from marine renewable energy devices (MREDs) on the commercially important edible crab, *Cancer pagurus* (L.). *Mar Pollut Bull* 131:580–588; 2018.
- Schwarze S, Schneider NL, Reichl T, Dreyer D, Lefeldt N, Engels S, Baker N, Hore PJ, Mouritsen H. Weak broadband electromagnetic fields are more disruptive to magnetic compass orientation in a night-migratory songbird (*Erithacus rubecula*) than strong narrow-band fields. *Front Behav Neurosci* 10:55; 2016.
- Shaw J, Boyd A, House M, Woodward R, Mathes F, Cowin G, Saunders M, Baer B. Magnetic particle-mediated magnetoreception. *J R Soc Interface* 12:0499; 2015.
- Shcherbakov VP, Winklhofer M. Theoretical analysis of flux amplification by soft magnetic material in a putative biological magnetic-field receptor. *Phys Rev E* 81:031921; 2010.
- Sheppard DMW, Li J, Henbest KB, Neil SRT, Maeda K, Storey J, Schleicher E, Biskup T, Rodriguez R, Weber S, Hore PJ, Timmel CR, Mackenzie SR. Millitesla magnetic field effects on the photocycle of an animal cryptochrome. *Sci Rep* 7:42228; 2017.
- Shepherd S, Lima MAP, Oliveira EE, Sharkh SM, Jackson CW, Newland PL. Extremely low frequency electromagnetic fields impair the cognitive and motor abilities of honey bees. *Sci Rep* 8:7932; 2018.
- Shepherd S, Hollands G, Godley VC, Sharkh SM, Jackson CW, Newland PL. Increased aggression and reduced aversive learning in honey bees exposed to extremely low frequency electromagnetic fields. *PLoS One* 14:e0223614; 2019.
- Shepherd S, Lima MAP, Oliveira EE, Sharkh SM, Aonuma H, Jackson CW, Newland PL. Sublethal neonicotinoid exposure attenuates the effects of electromagnetic fields on honey bee flight and learning. *Env Adv* 4:100051; 2021.
- Slaby P, Tomanova K, Vacha M. Cattle on pastures do align along the north-south axis, but the alignment depends on herd density. *J Comp Physiol A* 199:695–701; 2013.
- Soja G, Kunsch B, Gerzabek M, Reichenauer T, Soja AM, Rippar G, Bolhar-Nordenkampf HR. Growth and yield of winter wheat (*Triticum aestivum* L.) and corn (*Zea mays* L.) near a high voltage transmission line. *Bioelectromagnetics* 24:91–102; 2003.
- Sutton GP, Clarke D, Morley ER, Robert D. Mechanosensory hairs in bumblebees (*Bombus terrestris*) detect weak electric fields. *Proc Natl Acad Sci USA* 113:7261–7265; 2016.

- Taormina B, Di Poi C, Agnalt AL, Carlier A, Desroy N, Escobar-Lux RH, D'Eu J-F, Freydet F, Durif CMF. Impact of magnetic fields generated by AC/DC submarine power cables on the behavior of juvenile European lobster (*Homarus gammarus*). *Aquat Toxicol* 220:105401; 2020.
- Thalau P, Ritz T, Burda H, Wegner RE, Wiltshcko R. The magnetic compass mechanisms of birds and rodents are based on different physical principles. *J R Soc Interface* 3:583–587; 2006.
- Vacha M. Magnetoreception of invertebrates. In: Byrne JH, ed. *The Oxford handbook of invertebrate neurobiology*. Oxford: Oxford University Press: 1–40; 2017.
- Walker MM, Bitterman ME. Honeybees can be trained to respond to very small changes in geomagnetic field intensity. *J Exp Biol* 145:489–494; 1989a.
- Walker MM, Bitterman ME. Conditioning analysis of magnetoreception in honeybees. *Bioelectromagnet* 10:261–276; 1989b.
- Walker MM, Kirschvink JL, Dizon AE, Ahmed G. Evidence that finwhales respond to the geomagnetic field during migration. *J Exp Biol* 171:67–78; 1992.
- Walker MM, Diebel CE, Haugh CV, Pankhurst PM, Montgomery JC, Green CR. Structure and function of the vertebrate magnetic sense. *Nature* 390:371–376; 1997.
- Wang CX, Hilburn IA, Wu D-A, Mizuhara Y, Cousté CP, Abrahams JNH, Bernstein SE, Matani A, Shimojo S, Kirschvink JL. Transduction of the geomagnetic field as evidenced from alpha-band activity in the human brain. *eNeuro* 6:0483–0418; 2019.
- Wang Q, Li W, Kang J, Wang Y. Electromagnetic safety evaluation and protection methods for a wireless charging system in an electric vehicle. *IEEE Trans Electromagn Compat* 61:1913–1925; 2018.
- Wang Y, Pan Y, Parsons S, Walker M, Zhang S. Bats respond to polarity of a magnetic field. *Proc Royal Soc B* 274:2901–2904; 2007.
- Westby GW, Partridge KJ. Human homing: still no evidence despite geomagnetic controls. *J Exp Biol* 120:325–331; 1986.
- Westerberg H, Lagenfelt I. Sub-sea power cables and the migration behaviour of the European eel. *Fisheries Manag Ecol* 15:369–375; 2008.
- Wiltshcko R. *Magnetic orientation in animals*. Berlin, Heidelberg: Springer; 1995.
- Wiltshcko W, Munro U, Beason RC, Ford H, Wiltshcko R. A magnetic pulse leads to a temporary deflection in the orientation of migratory birds. *Experientia* 50:697–700; 1994.
- Wiltshcko R, Nießner C, Wiltshcko W. The magnetic compass of birds: the role of cryptochrome. *Front Physiol* 12:667000; 2021.
- Winklhofer M, Kirschvink JL. A quantitative assessment of torque-transducer models for magnetoreception. *J Roy Soc Interface* 7:S273–S289; 2010.
- Wyman M, Klimley A, Battleson R, Agosta T, Chapman E, Haverkamp P, Pagel M, Kavet R. Behavioral responses by migrating juvenile salmonids to a subsea high-voltage DC power cable. *Mar Biol* 165:1–15; 2018.
- Xu C, Yin X, Lv Y, Wu C, Zhang Y, Song T. A near-null magnetic field affects cryptochrome-related hypocotyl growth and flowering in *Arabidopsis*. *Adv Space Res* 49:834–840; 2012.
- Xu C, Lv Y, Chen C, Zhang Y, Wei S. Blue light-dependent phosphorylations of cryptochromes are affected by magnetic fields in *Arabidopsis*. *Adv Space Res* 53:1118–1124; 2014.
- Xu C, Li Y, Yu Y, Zhang Y, Wei S. Suppression of *Arabidopsis* flowering by near-null magnetic field is affected by light. *Bioelectromagnet* 36:476–479; 2015.
- Xu C, Li Y, Yu Y, Zhang Y, Li Y, Wei S. Gibberellins are involved in effect of near-null magnetic field on *Arabidopsis* flowering. *Bioelectromagnet* 38:1–10; 2017a.
- Xu C, Zhang Y, Yu Y, Li Y, Wei S. Suppression of *Arabidopsis* flowering by near-null magnetic field is mediated by auxin. *Bioelectromagnet* 39:15–24; 2017b.
- Xu J, Jarocha LE, Zollitsch T, Konowalczyk M, Henbest KB, Richert S, Golesworthy MJ, Schmidt J, Déjean V, Sowood DJC, Bassetto M, Luo J, Walton JR, Fleming J, Wei Y, Pitcher TL, Moise G, Herrmann M, Yin H, Wu H, Bartölke R, Käsehagen SJ, Horst S, Dautaj G, Murton PDF, Gehrckens AS, Chelliah Y, Takahashi JS, Koch K-W, Weber S, Solov'yov IA, Xie C, Mackenzie SR, Timmel CR, Mouritsen H, Hore PJ. Magnetic sensitivity of cryptochrome 4 from a migratory songbird. *Nature* 594:535–540; 2021.
- Zapka M, Heyers D, Hein CM, Engels S, Schneider NL, Hans J, Weiler S, Dreyer S, Kishkinev D, Wild J, Mouritsen H. Visual but not trigeminal mediation of magnetic compass information in a migratory bird. *Nature* 461:1274–1277; 2009.
- Zeng Z, Wei JJ, Liu YY, Zhang WD, Mabe T. Magnetoreception of photoactivated cryptochrome 1 in electrochemistry and electron transfer. *ACS Omega* 3:4752–4759; 2018.

