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Review Paper

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

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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.**
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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

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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 ($Fe_3O_4 - \gamma\text{-}Fe_2O_3$) 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 feld 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 Kattnig 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 μs 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 (Kattnig 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 ~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 ~10 μs, which is orders of magnitude too short for a radical pair to respond to such weak RF perturbations (Kattnig 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 Kattnig 2020).

Additionally, there is another surprising effect that can boost the magnetosensitivity of radical pairs in the putative magnetosensory protein cryptochrome (Kattnig and Hore 2017; Kattnig 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 (*Blatella 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., clothiatidin) 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 ~1 μs 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 (Wiltschko 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 μT) and single-frequency (7 MHz, 0.47 μT) 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 (~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 adaption 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 (*Clathreonomys 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 (Cerveny 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 (Cerveny 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.

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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.

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