UDK 577.359

INFLUENCE OF GEOMAGNETIC FIELD ON INSECT BEHAVIOR

V. V. Krylov[1*], Guijun Wan[2]
[1]*Papanin Institute for Biology of Inland Waters of the Russian Academy of Sciences,*
*Borok, Yaroslavl oblast 152742, Russia; *e-mail: kryloff@ibiw.ru*
[2]*Department of Entomology, College of Plant Protection, Nanjing Agricultural University, Nanjing 210095, China*

Revised 26.02.2024

The review presents contemporary data on the influence of the geomagnetic field and its variations on insect behavior. The most probable mechanisms of magnetoreception in different species are discussed. The prospects for studying insect electroreceptors as magnetodetectors are considered. Special attention is paid to studies investigating the impact of geomagnetic storms on insects. Differences in primary magnetoreception mechanisms are considered a potential cause for divergences in the reactions of different insect species to geomagnetic disturbances.

Keywords: magnetite; cryptochrome; geomagnetic activity; geomagnetic storm

DOI: 10.47021/0320-3557-2024-7-15

INTRODUCTION

The magnetic sense (magnetoreception) remains one of the most enigmatic among animals. Many species react to changes in the natural magnetic field, primarily manifested through alterations in behavior. Birds are the most studied in this regard [Wiltschko, Wiltschko, 2019]. Decades of research have yielded significant advancements in this field. The magnetic sense in invertebrate animals is less understood. We attempt to consolidate disparate data on insect orientation in the geomagnetic field and their responses to geomagnetic disturbances. However, before delving into this information, it is essential to discuss the characteristics of natural magnetic fields.

Natural magnetic fields have accompanied the evolution of life on the Earth. These fields can be characterized by the total magnetic vector, which integrates all magnetic forces originating from sources within the Earth's core and crust, as well as from the atmosphere [Akasofu, Chapman, 1972]. The Earth's magnetic field, also known as the geomagnetic field, originates from the movement of charged particles within the planet's liquid iron core. The intensity of the geomagnetic field varies from ~24 µT around the equator to ~66 µT near the poles [Alken et al., 2021]. The orientation of the Earth's magnetic field vector in the southern hemisphere opposes that of the northern hemisphere. In light of this review, the point is that the intensity and direction of the geomagnetic field vary from the equator to the poles. Therefore, each location has its specific direction and strength of the geomagnetic field. It enables animals to utilize Earth's magnetic field for orientation purposes.

The total magnetic vector is not constant. Regular, predictable magnetic variations occur approximately every day and year. These variations happen because the magnetic field components at a specific location deviate from their average values due to shifts in how the Earth is illuminated during its orbital motion and rotation around its axis [Kane, 1976]. Irregular natural magnetic fluctuations induced by various factors can also be registered. The most noticeable irregular disturbances of the natural magnetic environment are referred to as geomagnetic activity. It arises from disturbances in the geomagnetic field due to alterations in electric currents within the magnetosphere and ionosphere. These changes primarily stem from the influx of perturbed solar wind interacting with the geomagnetic field, thereby energizing the magnetosphere-ionosphere current system. Geomagnetic storms, substorms, and pulsations stand out as notable manifestations of geomagnetic activity [Jacobs et al., 1964; Akasofu, Chapman, 1972].

Various global and local indices are employed to evaluate geomagnetic activity. Global metrics encompass planetary geomagnetic indices (*Dst, ap, Kp, AE, etc.*) derived from magnetograms of multiple observatories placed at specific sites [Bartels, 1949; Davis, Sugiura, 1966; Sugiura, Kamei, 1991]. These indices reflect the generalized state of the magnetic field across the planet. Local magnetic fluctuations are primarily described by magnetograms recorded at specific locations and geomagnetic indices (*K, a, etc.*) derived from these magnetograms [Bartels et al., 1939; Berthelier, 1994]. It should be noted that the range of geomagnetic activity fluctuations is relatively weak and seldom exceeds 1% of the magnitude of the geomagnetic field.

Currently, the following mechanisms of direct or indirect perception of the magnetic field by specialized sensors are actively discussed:

1. perception of magnetic fields through the reception of electric fields induced by movement

in the geomagnetic field using electro-sensitive receptors;

2. perception of magnetic fields through iron compounds in cells;

3. perception of magnetic fields based on radical pair chemical reactions.

MAGNETIC FIELD RECEPTION THROUGH ELECTRORECEPTORS

Perception of magnetic fields through highly sensitive electroreceptors [Albert, Crampton, 2006; Hofmann, 2011] is extensively studied among elasmobranch fishes due to research performed by Kalmijn in the 1970s-80s [Kalmijn, 1974; Kalmijn, 1984]. The principle of electromagnetic induction suggests that uneven fish movement within the geomagnetic field generates an electric field sensed by electroreceptors. Even movement within a magnetic field gradient should produce a similar effect [Klimley, 1993]. This mechanism of magnetoreception was confirmed by direct experiments with elasmobranch fishes. Afferent nerves of electroreceptors on the wings (large pectoral fins) of the stingray *Trygon pastinaca* and corresponding brain areas responded to magnetic stimulation. Excitation and inhibition in the nerves were recorded when the magnetic field changed over time while the fish was stationary or when the animal moved in a constant magnetic field [Andrianov et al., 1974; Brown, Ilyinsky, 1978].

No research of this kind has been conducted on insects yet. However, we describe this mechanism for the following reasons. It is known that some insects, such as bumblebees *Bombus terrestris* [Clarke et al., 2013] and honeybees *Apis mellifera* [Greggers et al., 2013], can perceive weak electric fields. For example, bumblebees can orient themselves using electric fields generated by flowers, which helps them find nectar-bearing ones [Clarke et al., 2013]. Electroreceptor structures were identified in *B. terrestris* three years later, which turned out to be fine hairs covering their bodies [Sutton et al., 2016]. The antenna has been proposed to detect electric fields in honeybees [Greggers et al., 2013]. To date, we have not found studies on the influence of magnetic stimuli on insect electroreception. However, considering analogies with the magnetosensitivity of elasmobranch fishes, this direction appears promising. Experimental verification is awaited to determine if insect electroreceptors respond to changes in magnetic fields.

MAGNETIC FIELD RECEPTION THROUGH IRON COMPOUNDS

It is known that animal tissues contain iron compounds with a magnetic moment, which are supposed to be detectors of changes in the external magnetic field [Kirschvink, Gould, 1981; Shaw et al., 2015]. Extensive research in this direction has been conducted on birds and fish, in the tissues of which variously shaped and sized magnetite crystals $FeO{\cdot}Fe_2O_3$ have been found [Kirschvink, Gould, 1981; Walker, 2008; Shaw et al., 2015]. Within cells, magnetite crystals form chains comprising several dozen elements or clusters, allowing the collective magnetic moment to interact more effectively with the relatively weak geomagnetic field [Mann et al., 1988]. These chains or clusters are assumed to be attached to mechanically gated ion channels in the cell membrane via filaments. The movement of the chain, influenced by an external magnetic field, stretches the filaments and opens ion channels. The assumption is that the state of the channel complex at a given moment determines the potential of receptor cells [Walker, 2008].

Magnetite crystals possess a magnetic moment that aligns with the direction of the external magnetic field. Therefore, this type of magnetoreception is sensitive to the polarity of the magnetic field and does not require light, unlike the magnetoreception based on radical pairs mentioned below.

MAGNETIC FIELD RECEPTION THROUGH RADICAL PAIR REACTIONS

The premise for investigating magnetoreception using radicals stemmed from experiments showing birds' orientation in the magnetic field depending on the presence of light from the blue-green part of the spectrum [Wiltschko, Wiltschko, 1981; Wiltschko, Wiltschko, 1999; Muheim et al., 2002]. Such dependence suggested the necessity of photostimulation for the magnetoreceptor to function. In the early 2000s, a hypothesis of light-dependent magnetoreception in cryptochromes in the retina of birds based on the known effect of the magnetic field on the spin state of electrons in radicals was proposed [Ritz et al., 2000].

Cryptochromes are a class of blue-light-sensitive flavoproteins [Cashmore et al., 1999]. Cryptochrome contains a light-sensitive chromophore flavin adenine dinucleotide (FAD) as a cofactor [Sancar, 2003]. During the photoactivation, a light-induced oxidative-reductive electron transfer occurs between FAD and three tryptophan residues (Trp400, Trp377, and Trp324). An electron from the excited FAD reversibly moves between the three tryptophan residues. As a result of this transfer, the last tryptophan residue in this chain becomes deprotonated (Trp324), and FADH is reduced. Cryptochrome with reduced FADH is in its active (signaling) state. Three radical pair states are formed during the described process: FADH – Trp400$^+$, FADH – Trp377$^+$, and FADH – Trp324$^+$. It is presumed that the magnetic inclination may influence the spin state of the electrons in these radical pairs. If the spin state of the radical pair changes from singlet to triplet during the electron transfer along the FAD - triplet tryptophan residue chain, then this electron cannot return to FAD, and the cryptochrome molecule transitions into the signaling state. Otherwise, the electron will return to FAD if it remains in a singlet state, and the cryptochrome molecule will not transition into the signaling state [Solov'yov et al., 2007]. It should also be noted that besides the FAD – triplet tryptophan residues chain, other sources of radical-pair states in cryptochromes are under consideration [Solov'yov, Schulten, 2009; Hogben et al., 2009; Muller, Ahmad, 2011; Evans et al., 2016].

Numerous studies have been published to date on the involvement of cryptochromes in biological magnetoreception [Gegear et al., 2008; Biskup et al., 2009; Foley et al., 2011; Zadeh-Haghighi, Simon, 2022; Bradlaugh et al., 2023]. Extensive data leave no doubt that cryptochromes are essential proteins in the evolutionarily established mechanism of animal orientation in the geomagnetic field, known as the "chemical magnetic compass". However, significant magnetic effects in isolated molecules in vitro have been detected only at magnetic fields that exceed the geomagnetic field [Maeda et al., 2012; Xu et al., 2021]. Responses to fields approximately equal to the geomagnetic field have been demonstrated only in a model molecular triad consisting of covalently bound carotenoids, pyrrole, and fullerene molecules [Kerpal et al., 2019]. There are likely evolutionarily developed mechanisms to enhance the magnetic sensitivity of cryptochromes in cells responsible for magnetic perception. The recent discovery of a magnetoreceptor protein [Qin et al., 2016] could be a significant event in elucidating these mechanisms. Conformational rearrangements during magnetic perception and the molecular environment are probably of importance [Galvan et al., 2024]. Several scientific groups are currently addressing this issue.

A distinguishing feature of biradical magnetoreception is its sensitivity to inclination rather than the polarity of the external magnetic field. Furthermore, the described model suggests that electromagnetic fields in the range of about 1-100 MHz may disrupt magnetoreception through cryptochromes through electron paramagnetic resonance [Timmel, Hore, 1996; Leberecht et al., 2023].

INSECT ORIENTATION IN THE GEOMAGNETIC FIELD

Compelling experiments demonstrating the use of the geomagnetic field for orientation have been conducted with desert ants *Cataglyphis noda*. Novices of these ants take short learning walks. During the learning walks *C. noda* gather information about the nest surroundings and calibrate their compass systems to successfully find the entrance to the nest in the future [Grob et al., 2019]. Scientists manipulated the magnetic field during the ants' learning walks to prove that ants utilize the geomagnetic field as a compass cue. Initially, experiments disarrayed the geomagnetic field around the nest entrance using an electromagnetic spiral. When the spiral was powered, the ants failed to gaze at the nest entrance and oriented themself randomly, contrasting with their accurate orientation when the spiral was unpowered [Fleischmann et al., 2018]. Subsequent experiments demonstrated that the ants adjusted their gaze directions in response to rotations of the horizontal component of the Earth's magnetic field (either by 180° or ± 90°). Thus, the geomagnetic field is a sufficient and necessary reference system for ants [Fleischmann et al., 2018]. Studies with ants of other species have also shown behavioral responses to changes in the magnetic environment [Anderson, Vander Meer, 1993; Camlitepe, Stradling, 1995; Banks, Srygley, 2003; Camlitepe et al., 2005; Riveros, Srygley, 2008].

The rotation of the horizontal component of the geomagnetic field implies a shift in magnetic polarity. It suggests that ants most likely utilize magnetite for orientation within the geomagnetic field. Indeed, crystals of iron compounds, which may underlie the magnetic sense of ants, were discovered in the antennae of *Pachycondyla marginata* worker ants [Oliveira et al., 2010].

Honeybees (*Apis* sp.) also exhibit behavioral responses to changes in the geomagnetic field. It is known that honeybees can communicate through waggle dances. The character and direction of the waggle dance axis depend on the magnetic environment [Lindauer, Martin, 1972]. Research has revealed that honeybees use the direction of the magnetic field as a reference point during the initial stages of comb construction in a new hive [DeJong, 1982]. Collett and Baron [1994] reported that honeybees consistently orient themselves in one compass direction when learning about or searching for a goal, aided by the Earth's magnetic field. The sensitivity of bees to changes in the magnetic environment is confirmed by other behavioral experiments [Walker, Bitterman, 1985; Walker, Bitterman, 1989a; Walker, Bitterman, 1989b; Kirschvink et al., 1997].

It is known that tissues in the abdomen of the honeybee contain granules of iron compounds, which are presumed to serve as magnetodetectors

[Kuterbach et al., 1982; Hsu, Li, 1993; El-Jaick et al., 2001]. Experiments have shown that the attachment of external magnets to the abdomen interferes with the magnetic sense in bees [Walker, Bitterman, 1989a]. Furthermore, reactions to magnetic fields occur in complete darkness, and pulse-remagnetization affects magnetosensitive behavior in bees [Kirschvink, Kobayashi-Kirschvink, 1991]. The above suggests that bees, like desert ants, most probably utilize magnetodetection based on iron compounds in sensitive cells.

However, other insect species convincingly demonstrate magnetoreception based on radical-pair reactions. An example of this can be seen in experiments conducted by Vacha and colleagues with the mealworm *Tenebrio molitor* [Vacha et al., 2008]. These animals exhibit positive phototaxis. In the experiment, before exposure to magnetic influence, beetles were trained to move towards light from the east, south, west, or north in a plus-maze. Subsequently, they were placed into an open space with uniform upper lighting. Under normal geomagnetic conditions, the beetles moved towards the light they had been trained with. However, when the inclination of the geomagnetic field was reversed while the polarity of the geomagnetic field remained unchanged, the beetles in the arena moved in the direction opposite to the light source, responding to magnetic stimuli [Vacha et al., 2008]. This response to the change in magnetic inclination suggests that magnetic field perception likely occurs due to radical-pair reactions. In another study, a weak radiofrequency magnetic field (with a maximum effect on the Larmor frequency of 1.2 MHz) disrupted the orientation of cockroaches in the geomagnetic field, further indicating the use of radical-pair reactions as a magneto-detector [Vacha et al., 2009].

The utilization of the geomagnetic field appears most advantageous during migrations. Among insects, as well as among birds, some species migrate over long distances. David Dreyer, Eric Warrant, and their colleagues [2018] delved into the migratory behavior of Bogong moths (*Agrotis infusa*) in Australia. These moths undertake highly directed nocturnal migrations spanning over 1,000 km from breeding areas in southeast Australia to specific mountain caves in the Australian Alps. Subsequently, they enter a period of dormancy in the mountains before returning to their breeding grounds in autumn to reproduce and complete their life cycle. The researchers conducted experiments aiming to understand the moths' navigation using visual landmarks and the Earth's magnetic field. They conducted two sets of experiments, each consisting of five phases, manipulating these cues to be either aligned or conflicting.

In the initial experiments, the moths exhibited a preference for visual cues over the magnetic field. When these cues contradicted each other, the moths initially followed visual landmarks but eventually became disoriented. Upon restoring the cues to their initial conditions, the moths resumed their orientation toward the visual landmarks. Similar results were obtained in the second set of experiments, confirming that changes in the magnetic field direction led to disorientation among the moths [Dreyer et al., 2018].

These findings suggest that Bogong moths likely rely on a combination of visual and magnetic cues for navigation. The researchers propose that the moths utilize a magnetic compass to establish their migratory direction, aligning it with a celestial or terrestrial landmark in the same direction. They then use this landmark as a visual reference point, periodically calibrating their fidelity to these landmarks with their magnetic sense, which may check the landmark direction fidelity every few minutes [Dreyer et al., 2018].

It's challenging to determine the exact type of magnetoreception used by Australian Bogong moths in the described above experiment because both polarity and magnetic inclination were manipulated. However, lepidopterans such as *Urania fulgens, Aphrissa statira, Heliconius ethilla, Anartia amathea, An. fatima,* and *Actinote thalia*, have been found to possess magnetic material that could potentially be used for orientation in the Earth's magnetic field [Alves et al., 2020].

The monarch butterfly (*Danaus plexippus*), another representative of migrating Lepidoptera, relies on radical-pair reactions for navigation. Experiments have shown that these insects react to changes in magnetic inclination. Moreover, magnetoreception in monarch butterflies is influenced by light [Guerra et al., 2014]. Other experiments have investigated a phenomenon termed "magnetic hyperactivity," where monarchs exhibited increased wingbeat frequency when the magnetic inclination was reversed. Using the CRISPR/Cas9 technique, Guijun Wan and his colleagues (2021) developed monarch butterflies with knocked-out CRY genes. The findings indicated that Cry1 is crucial for this magnetic sense, while dpCry2 does not play a significant role. Furthermore, the study illustrated that both antennae and compound eyes are necessary for monarch magnetosensing [Wan et al., 2021].

Therefore, different insect species appear to employ distinct mechanisms of magnetodetection. Depending on the evolutionary process of magnetodetection development, whether the ability to perceive magnetic fields was lost or regained, it is conceivable that the utilization of a particular magnetoreception mechanism may not be exclusive to a specific species but perhaps even to a genus or family. Moreover, it is plausible that various insect species utilize both types of magnetoreception to different extents.

THE IMPACT OF GEOMAGNETIC ACTIVITY ON INSECTS

Initial studies suggesting that geomagnetic fluctuations could influence animal orientation pertained to birds and emerged approximately 50 years ago [Keeton et al., 1974; Larkin, Keeton, 1976; Kowalski et al., 1988]. Subsequently, there were many years of limited research in this area due to a lack of understanding of how such weak influences could impact directional choices. However, recent work has revitalized this field of study. Researchers utilized extensive, long-term datasets from magnetometers to investigate a potential connection between geomagnetic disturbances and disruptions in nocturnal bird migration. They observed a 9%-17% reduction in the number of migrating birds, both in spring and fall, during geomagnetic storms. Moreover, birds that opted to migrate during such events seemed to experience more difficulty navigating, especially under overcast conditions in autumn [Gulson-Castillo et al., 2023].

What do we know about this phenomenon among insects? Research on this topic was conducted in the 1960s-1970s in the Soviet Union by Vladimir Chernyshev. He examined the attraction of insects to light in various regions of the USSR and evaluated the correlation with geomagnetic indices reflecting disturbances in the geomagnetic field and magnetic storms. In Turkmenistan, significant associations were observed at different times between the number of beetles attracted to light and intense geomagnetic storms. During geomagnetic storms, there was a notable increase in the number of beetles attracted to light [Chernyshev, 1966]. However, in the central region of Russia, where mainly certain species of butterflies and dipterans are attracted to light, such a connection did not appear [Chernyshev, 1994].

Chernyshev draws the following conclusions: Insects react differently to geomagnetic storms. The attraction to light noticeably increases during these days for many beetle species, such as darkling beetles, ground beetles, lamellicorn beetles, rove beetles, and representatives of several other families. However, some species of insects do not respond to magnetic storms. Butterflies react differently. Flights to the light of the Siberian silk moth, moths of the Yponomeutidae family, and the American white butterfly intensify during geomagnetic storms, while flights of the garden tiger moth (*Spilarctia lutea*) and the grass moth (*Syllepta ruralis*) weaken. The flights of dipterans are unaffected by geomagnetic activity [Chernyshev, 1996].

Similar studies were conducted later. Chinese scientists showed that changes in the population of rice planthoppers and beet webworm, *Loxostege sticticalis*, correlate with the 11-year solar activity cycle, which directly affects the quantity and intensity of geomagnetic disturbances [Chen et al., 1994; Huang et al., 2008].

Iso-Ivari and Koponen [1997] explored the impact of geomagnetism on the catch of insects in light traps in the northernmost part of Finland. They discovered a weak but significant correlation between the geomagnetic parameters and the number of specimens from various insect orders caught.

Another paper reports on a correlation between the summarized values of change in the horizontal component of the geomagnetic field measured at night and the number of light-trap catches of the fall webworm moth (*Hyphantria cunea*) [Kiss et al., 1981].

Recently, Hungarian researchers correlated the quantity of light-trapped caddisfly (Trichoptera) species and pheromone-trapped fruit pest moths with the global geomagnetic *Dst*-index [Nowinszky et al., 2021; Nowinszky et al., 2023]. Different species exhibited varying trends of increased or decreased catch rates in response to changes in the index. Another study deals with long-term observation data from the Hungarian forestry light-trap network and the local geomagnetic M-index. It revealed a dependency of moth catch rates on the presence of geomagnetic disturbances, as reflected in the M-index value. Furthermore, the nature of this dependency was species-specific [Nowinszky et al., 2020].

In the previous section, we emphasized the distinction between two types of magnetoreception in insects. Perhaps it is also the reason for the differences in the reactions of different species to geomagnetic disturbances described in this section.

Magnetic storms are relatively weak low-frequency magnetic fluctuations that may not affect iron-based receptor systems. However, it is conceivable that these fluctuations could alter the complex oscillations associated with the local magnetic environment experienced by radical pairs in cryptochromes or other biomolecules involved in radical pair magnetoreception.

In essence, the effects of magnetic storms are unlikely to be associated with changes in “magnetic coordinates” because they are too weak to cause any significant change in the inclination or direction of the geomagnetic field vector. Therefore, the effects of geomagnetic storms are not the choice of an incorrect direction through a normally functioning magneto-navigation system. Fluctuations during magnetic storms are most likely temporarily "switching off" magnetoreception based on radical pairs, and perhaps they do not affect magnetite-based magnetoreception.

The impact of geomagnetic storms on the number of light-trapped insects, for instance, could be as follows. Specimens near the light source fly towards it, while those farther away use the geomagnetic field for navigation under a quiet geomagnetic field. Geomagnetic navigation approves that the weak light source in the distance should be disregarded. However, when magnetoreception is switched off during a geomagnetic storm, insects from a wider area are drawn toward the light source. Therefore, if geomagnetic storms can temporarily deactivate radical pair magnetoreception, there may be potential for utilizing this phenomenon in pest management. However, further investigation is needed to validate this hypothesis.

The study was supported by the Ministry of Science and Higher Education of the Russian Federation (121051100109-1), the National Key Research and Development Program of China (2021YFD1401100), the Natural Science Foundation of Jiangsu Province (BK20221510), and National Natural Science Foundation of China (32172414).

REFERENCES

Akasofu S.I., Chapman S. Solar-Terrestrial Physics. Oxford, Clarendon Press, 1972. 901 p.

Albert J.S., Crampton W.G.R. Electroreception and electrogenesis. *The Physiology of Fishes.* Boca Raton, CRC Press, 2006, pp. 429–470.

Alken P., Thebault E., Beggan C.D., et al. International geomagnetic reference field: the thirteenth generation. *Earth Planets Space*, 2021, vol. 73, id 49. doi:10.1186/s40623-020-01288-x.

Alves O.C., Wajnberg E., Esquivel D.M.S., Srygley R.B. Magnetic material in migratory and non-migratory neotropical Lepidoptera: A magnetic resonance study. *J. Magn. Magn. Mater.,* 2020, vol. 513, id 167053.

Anderson J.B., Vander Meer R.K. Magnetic orientation in the fire ant, *Solenopsis invicta*. *Naturwissenschaften*, 1993, vol. 80, pp. 568–570.

Andrianov G.N., Brown H.R., Ilyinsky O.B. Responses of central neurons to electrical and magnetic stimuli of the ampullae of Lorenzini in the Black Sea skate. *J. Comp. Physiol.*, A. 1974, vol. 93, pp. 287–299.

Banks A.N., Srygley R.B. Orientation by magnetic field in leaf-cutter ants, *Atta colombica* (Hymenoptera: Formicidae). *Ethology*, 2003, vol. 109, pp. 835–846.

Bartels J. The standardized index Ks and the planetary index Kp. *IATME Bull.*, 1949, vol. 12b, pp. 97–120.

Bartels J., Heck N.H., Johnston H.F. The three-hour-range index measuring geomagnetic activity. *Terr. Mag. Atmos. Electr.*, 1939, vol. 44, pp. 411–454.

Berthelier A. The geomagnetic indices: derivation, meaning and use in solar-terrestrial physics. *Solar-Terrestr. Predict.*, 1994, vol. 4, pp. 3–20.

Biskup T., Schleicher E., Okafuji A. Link G., Hitomi K., Getzoff E.D., Weber S. Direct observation of a photoinduced radical pair in a cryptochrome blue-light photoreceptor. *Angew. Chem. Int. Ed. Engl.*, 2009, vol. 48, pp. 404–447.

Bradlaugh A.A., Fedele G., Munro A.L., Hansen C.N., Hares J.M., Patel S., Kyriacou C.P., Jones A.R., Rosato E., Baines R.A. Essential elements of radical pair magnetosensitivity in *Drosophila*. *Nature*, 2023, vol. 615, pp. 111–116. doi: 10.1038/s41586-023-05735-z.

Brown H.R., Ilyinsky O.B. The ampullae of Lorenzini in the magnetic field. *J. Comp. Physiol. A.,* 1978, vol. 126, pp. 333–341.

Camlitepe Y., Aksoy V., Uren N., Yilmaz A., Becenen I. An experimental analysis on the magnetic field sensitivity of the black-meadow ant *Formica pratensis* Retzius (Hymenoptera: Formicidae). *Acta Biol. Hung.*, 2005, vol. 56, pp. 215–224. doi: 10.1556/ABiol.56.2005.3-4.5.

Camlitepe Y., Stradling D.J. Wood ants orient to magnetic fields. *Proc. R. Soc. Lond. B.,* 1995, vol. 261, pp. 37–41.

Cashmore A., Jarillo J., Wu Y.J., Liu D. Cryptochromes: blue light receptors for plants and animals. *Science*, 1999, vol. 284, pp. 760–765.

Chen L. Ouyang X., Yang Z., Tong Z. The study on the relationship between solar activity and the fluctuation of rice planthopper population. *Jiangxi Plant Protection*, 1994, vol. 17, pp. 1–3. (in Chinese)

Chernyshev V.B. Influence of disturbed magnetic field on the activity of insects. *Soveschsanie po Izucheniyu Vliyaniya Magnetikh Poley na Biologicheskie Obyekti* [Meeting on the Study of the Influence of Magnetic Fields on Biological Objects]. Moscow, 1966, pp. 80–83. (in Russian)

Chernyshev V.B. Anomalies in insect behavior and geomagnetic storms. *Priroda*, 1994, no. 9, pp. 20–25. (in Russian)

Chernyshev V.B. Ecology of insects. Moscow, Izd. Mosk. Univ., 1996. 304 p. (in Russian)

Clarke D., Whitney H., Sutton G., Robert D. Detection and learning of floral electric fields by bumblebees. *Science*, 2013, vol. 340, pp. 66–69.

Collett T.S., Baron J. Biological compasses and the coordinate frame of landmark memories in honeybees. *Nature*, 1994, vol. 368, pp. 137–140.

Davis T.N., Sugiura M. Auroral electrojet activity index AE and its universal time variations. *J. Geophys. Res.*, 1966, vol. 71, pp. 785–801.

DeJong D. The orientation of comb-building by honeybees. *J. Comp. Physiol. A.*, 1982, vol. 147, pp. 495–501.

Dreyer D., Frost B., Mouritsen H., Gunther A., Green K., Whitehouse M., Johnsen S., Heinze S., Warrant E. The Earth's magnetic field and visual landmarks steer migratory flight behavior in the nocturnal Australian Bogong moth. *Curr. Biol.*, 2018, vol. 28, pp. 2160–2166.e5.

El-Jaick L.J., Acosta-Avalos D., Motta de Souza Esquivel D., Wajnberg E., Linhares P.M. Electron paramagnetic resonance study of honeybee *Apis mellifera* abdomens. *Eur. Biophys. J.*, 2001, vol. 29, pp. 579–586.

Evans E.W., Kattnig D.R., Henbest K.B., Hore P.J., Mackenzie S.R., Timmel C.R. Sub-millitesla magnetic field effects on the recombination reaction of flavin and ascorbic acid radicals. *J. Chem. Phys.*, 2016, vol. 145, id 085101.

Fleischmann P.N., Grob R., Muller V.L., Wehner R., Rossler W. The geomagnetic field is a compass cue in *Cataglyphis* ant navigation. *Curr. Biol.*, 2018, vol. 28, pp. 1440–1444.e2. doi: 10.1016/j.cub.2018.03.043.

Foley L.E., Gegear R.J., Reppert S.M. Human cryptochrome exhibits light-dependent magnetosensitivity. *Nat. Commun.,* 2011, vol. 2, id e356.

Galvan I., Hassasfar A., Adams B., Petruccione F. Isotope effects on radical pair performance in cryptochrome: A new hypothesis for the evolution of animal migration: The quantum biology of migration. *Bioessays*, 2024, vol. 46, id e2300152. doi: 10.1002/bies.202300152.

Gegear R.J., Casselman A., Waddell S., Reppert S.M. Cryptochrome mediates light-dependent magnetosensitivity in *Drosophila*. *Nature*, 2008, vol. 454, pp. 1014–1018.

Greggers U., Koch G., Schmidt V., Durr A., Floriou-Servou A., Piepenbrock D., Gopfert M.C., Menzel R. Reception and learning of electric fields in bees. *Proc. Roy. Soc. B Biol. Sci.*, 2013, vol. 280, id 20130528. doi: 10.1098/rspb.2013.0528.

Grob R., Fleischmann P.N., Rossler W. Learning to navigate – how desert ants calibrate their compass systems. *Neuroforum*, 2019, vol. 25, pp. 109–120. doi: 10.1515/nf-2018-0011.

Guerra P.A. Gegear R.J., Reppert S.M. A magnetic compass aids monarch butterfly migration. *Nat. Commun.*, 2014, vol. 5, id 4164. doi: 10.1038/ncomms5164.

Gulson-Castillo E.R., Van Doren B.M., Bui M.X., Horton K.G., Li J., Moldwin M.B., Shedden K., Welling D.T., Winger B.M. Space weather disrupts nocturnal bird migration. *Proc. Natl. Acad. Sci.*, 2023, vol. 120, id e2306317120. doi: 10.1073/pnas.2306317120.

Hofmann M.H. Physiology of ampullary electrosensory systems. *Encyclopedia of Fish Physiology from Genome to Environment.* San Diego, Acad. Press, 2011, pp. 359–365.

Hogben H.J., Efimova O., Wagner-Rundell N., Timmel C.R., Hore P. Possible involvement of superoxide and dioxygen with cryptochrome in avian magnetoreception: Origin of Zeeman resonances observed by in vivo EPR spectroscopy. *Chem. Phys. Lett.*, 2009, vol. 480, pp. 118–122.

Hsu C.Y., Li C.W. The ultrastructure and formation of iron granules in the honeybee (*Apis mellifera*). *J. Exp. Biol.*, 1993, vol. 180, pp. 1–13.

Huang S., Jiang X., Lei C., Luo L. Correlation analysis between the periodic outbreaks of *Loxostege sticticalis* (Lepidoptera: Pyralidae) and solar activity. *Acta Ecol. Sin.*, 2008, vol. 28, pp. 4823–4829.

Iso-Ivari L., Koponen S. Insect catches by light trap compared with geomagnetic and weather factors in subarctic Lapland. *Rep. Kevo. Subarctic Res. Stat.*, 1976, vol. 13, pp. 33–35.

Jacobs J.A., Kato Y., Matsushita S., Troitskaya V.A. Classification of geomagnetic micropulsations. *J. Geophys. Res.*, 1964, vol. 69, pp. 180–181.

Kalmijn A.J. The detection of electric fields from inanimate and animate sources other than electric organs. *Handbook of Sensory Physiol. vol. 3.* Berlin, Springer, 1974, pp. 147–200.

Kalmijn A.J. Theory of electromagnetic orientation: a further analysis. *Comparative Physiology of Sensory Systems*. Cambridge, Cambridge Univ. Press, 1984, pp. 525–560.

Kane R.P. Geomagnetic field variations. *Space Sci. Rev.*, 1976, vol. 18, pp. 413–540.

Keeton W.T., Larkin T.S., Windsor D.M. Normal fluctuations in the Earth's magnetic field influence pigeon orientation. *J. Comp. Physiol.*, 1974, vol. 95, pp. 95–103.

Kerpal C., Richert S., Storey J.G., Pillai S., Liddell P.A., Gust D., Mackenzie S.R., Hore P.J., Timmel C.R. Chemical compass behaviour at microtesla magnetic fields strengthens the radical pair hypothesis of avian magnetoreception. *Nat. Commun.*, 2019, vol. 10, id 3707.

Kirschvink J.L., Gould J.L. Biogenic magnetite as a basis for magnetic field detection in animals. *Biosystems*, 1981, vol. 13, pp. 181–201.

Kirschvink J.L., Kobayashi-Kirschvink A. Is geomagnetic sensitivity real? Replication of the Walker-Bitterman magnetic conditioning experiment in honey bees. *Am. Zool.*, 1991, vol. 31, pp. 169–185.

Kirschvink J.L., Padmanabha S., Boyce C.K., Oglesby J. Measurement of the threshold sensitivity of honeybees to weak, extremely low-frequency magnetic fields. *J. Exp. Biol.*, 1997, vol. 200, pp. 1363–1368.

Kiss M., Ekk I., Toth G., Szabo S., Nowinszky L. Common effect of geomagnetism and change of moon phases on light-trap catches of fall webworm moth (*Hyphantria cunea* Drury). *Z. Angew. Entomol.*, 1981, vol. 91, pp. 403–411.

Klimley A.P. Highly directional swimming by scalloped hammerhead sharks, *Sphyrna lewini*, and subsurface irradiance, temperature, bathymetry, and geomagnetic field. *Marine Biol.*, 1993, vol. 117, pp. 1–22.

Kowalski U., Wiltschko R., Fuller E. Normal fluctuations of the geomagnetic field may affect initial orientation of pigeons. *J. Comp. Physiol. A.*, 1988, vol. 163, pp. 593–600.

Kuterbach D.A., Walcott B., Reeder R.J., Frankel R.B. Iron-containing cells in the honey bee (*Apis mellifera*). *Science*, 1982, vol. 218, pp. 695–697.

Larkin T.S., Keeton W.T. Bar magnets mask the effect of normal magnetic disturbances on pigeon orientation. *J. Comp. Physiol.*, 1976, vol. 110, pp. 227–231.

Leberecht B., Wong S.Y., Satish B., Doge S., Hindman J., Venkatraman L., Apte S., Haase K., Musielak I., Dautaj G., Solov'yov I.A., Winklhofer M., Mouritsen H., Hore P.J. Upper bound for broadband radiofrequency field disruption of magnetic compass orientation in night-migratory songbirds. *Proc. Natl. Acad. Sci.*, 2023, vol. 120, id e2301153120. doi: 10.1073/pnas.2301153120.

Lindauer M., Martin H. Magnetic effects on dancing bees. *Animal Orientation and Navigation*. Washington, US Government Printing Office, 1972, pp. 559–567.

Maeda K., Robinson A.J., Henbest K.B., Hogben H.J., Biskup T., Ahmad M., Schleicher E., Weber S., Timmel C.R., Hore P.J. Magnetically sensitive light-induced reactions in cryptochrome are consistent with its proposed role as a magnetoreceptor. *Proc. Natl. Acad. Sci.*, 2012, vol. 109, pp. 4774–4779.

Mann S., Sparks N.H., Walker M.M., Kirschvink J.L. Ultrastructure morphology and organization of biogenic magnetite from sockeye salmon, *Onchorhynehus nerka*: implications for magnetoreception. *J. Exp. Biol.*, 1988, vol. 140, pp. 35–49.

Muheim R., Backman J., Akesson S. Magnetic compass orientation in European robins is dependent on both wavelength and intensity of light. *J. Exp. Biol.*, 2002, vol. 205, pp. 3845–3856.

Muller P., Ahmad M. Light activated cryptochrome reacts with molecular oxygen to form a flavin-superoxide radical pair consistent with magnetoreception. *J. Biol. Chem.*, 2011, vol. 286, pp. 21033–21040.

Nowinszky L., Puskas J., Hill L., Kiss M., Barczikay G. Pheromone trap catch of fruit pest moths influenced by the geomagnetic disturbance storm time (Dst). *Mathews J. Vet. Sci.*, 2023, vol. 7, id 19. doi:10.30654/MJVS.10019

Nowinszky L., Puskas J., Kiss M. Influence of geomagnetic M-Index on light-trap catch of Macrolepidoptera species selected from different families and subfamilies. *Int. J. Zoo. Animal Biol.*, 2020, vol. 3, id 000246. doi: 10.23880/izab-16000246.

Nowinszky L., Kiss O., Puskas J., Kiss M., Barta V., Szentkiralyi F. Effect of the geomagnetic disturbance storm time (Dst) on light trapped caddisfly (Trichoptera) species. *Acta Sci. Microbiol.*, 2021, vol. 4, pp. 11–16.

Oliveira J.F., Wajnberg E., Esquivel D.M., Weinkauf S., Winklhofer M., Hanzlik M. Ant antennae: are they sites for magnetoreception. *J. R. Soc. Interface*, 2010, vol. 7, pp. 143–152. doi: 10.1098/rsif.2009.0102.

Qin S., Yin H., Yang C., Dou Y., Liu Z., Zhang P., Yu H., Huang Y., Feng J., Hao J., Hao J., Deng L., Yan X., Dong X., Zhao Z., Jiang T., Wang H.W., Luo S.J., Xie C. A magnetic protein biocompass. *Nat. Mater.*, 2016, vol. 15, pp. 217–226. doi: 10.1038/nmat4484.

Ritz T., Adem S., Schulten K. A model for photoreceptor-based magnetoreception in birds. *Biophys. J.*, 2000, vol. 78, pp. 707–718.

Riveros A.J., Srygley R.B. Do leafcutter ants, *Atta colombica*, orient their path-integrated home vector with a magnetic compass. *Anim. Behav.*, 2008, vol. 75, pp. 1273–1281. doi: 10.1016/j.anbehav.2007.09.030.

Sancar A. Structure and function of DNA photolyase and cryptochrome blue-light photoreceptors. *Chem. Rev.*, 2003, vol. 103, pp. 2203–2237.

Shaw J., Boyd A., House M., Woodward R., Mathes F., Cowin G., Saunders M., Baer B. Magnetic particle-mediated magnetoreception. *J. R. Soc. Interface*, 2015, vol. 12, id 20150499. doi: 10.1098/rsif.2015.0499.

Solov’yov I.A., Chandler D.E., Schulten K. Magnetic field effects in Arabidopsis thaliana cryptochrome-1. *Biophys. J.*, 2007, vol. 92, pp. 2711–2726.

Solov’yov I.A., Schulten K. Magnetoreception through cryptochrome may involve superoxide. *Biophys. J.*, 2009, vol. 96, pp. 4804–4813.

Sugiura M., Kamei T. Equatorial Dst index 1957–1986. *IAGA Bull.*, 1991, vol. 40, pp. 1–246.

Sutton G. P., Clarke D., Morley E.L., Robert D. Mechanosensory hairs in bumblebees (*Bombus terrestris*) detect weak electric fields. *Proc. Natl. Acad. Sci.*, 2016, vol. 113, pp. 7261–7265. doi: 10.1073/pnas.1601624113.

Timmel C.R., Hore P.J. Oscillating magnetic field effects on the yields of radical pair reactions. *Chem. Phys. Lett.*, 1996, vol. 257, pp. 401–408.

Vacha M., Drstkova D., Puzova T. Tenebrio beetles use magnetic inclination compass. *Naturwissenschaften*, 2008, vol. 95, pp. 761–765.

Vacha M., Puzova T., Kvicalova M. Radio-frequency magnetic fields disrupt magnetoreception in American cockroach. *J. Exp. Biol.*, 2009, vol. 212, pp. 3473–3477.

Walker M.M. A model for encoding of magnetic field intensity by magnetite-based magnetoreceptor cells. *J. Theor. Biol.*, 2008, vol. 250, pp. 85–91.

Walker M.M., Bitterman M.E. Conditioned responding to magnetic fields by honeybees. *J. Comp. Physiol. A.*, 1985, vol. 157, pp. 67–71.

Walker M.M., Bitterman M.E. Attached magnets impair magnetic field discrimination by honeybees. *J. Exp. Biol.*, 1989a, vol. 141, pp. 447–451.

Walker M.M., Bitterman M.E. Honeybees can be trained to respond to very small changes in geomagnetic field sensitivity. *J. Exp. Biol.*, 1989b, vol. 145, pp. 489–494.

Wan G., Hayden A.N., Iiams S.E., Merlin C. Cryptochrome-1 mediates light-dependent inclination magnetosensing in monarch butterflies. *Nat Commun.*, 2021, vol. 12, id 771. doi:10.1038/s41467-021-21002-z.

Wiltschko R, Wiltschko W. Magnetoreception in birds. *J. R. Soc. Interface*, 2019, vol. 16, id 20190295. doi: 10.1098/rsif.2019.0295.

Wiltschko W., Wiltschko R. Disorientation of inexperienced young pigeons after transportation in total darkness. *Nature*, 1981, vol. 291, pp. 433–434.

Wiltschko W., Wiltschko R. The effect of yellow and blue light on magnetic compass orientation in European robins, *Erithacus rubecula*. *J. Comp. Physiol. A.*, 1999, vol. 184, pp. 295–299.

Xu J., Jarocha L.E., Zollitsch T., Konowalczyk M., Henbest K.B., Richert S., Golesworthy M.J., Schmidt J., Dejean V., Sowood D.J.C., et al. Magnetic sensitivity of cryptochrome 4 from a migratory songbird. *Nature*, 2021, vol. 594, pp. 535–540. doi: 10.1038/s41586-021-03618-9.

Zadeh-Haghighi H., Simon C. Magnetic field effects in biology from the perspective of the radical pair mechanism. *J. R. Soc. Interface*, 2022, vol. 193, id 20220325. doi: 10.1098/rsif.2022.0325.

ВЛИЯНИЕ ГЕОМАГНИТНОГО ПОЛЯ НА ПОВЕДЕНИЕ НАСЕКОМЫХ

В. В. Крылов[1, *], Гуйджун Ван[2]

[1] *Институт биологии внутренних вод им. Папанина РАН,*
*Борок, Ярославская область 152742, Россия; *e-mail: kryloff@ibiw.ru*
[2] *Кафедра энтомологии, Колледж защиты растений,*
Нанкинский сельскохозяйственный университет, Нанкин 210095, Китай

Поступила в редакцию 26.02.2024

В обзоре представлены современные данные о влиянии геомагнитного поля и его вариаций на поведение насекомых. Обсуждаются наиболее вероятные механизмы магниторецепции у разных видов. Рассмотрены перспективы изучения электрорецепторов насекомых в качестве магнитодетекторов. Особое внимание уделено исследованиям влияния геомагнитных бурь на поведение. Различия в механизмах первичной магниторецепции рассмотрены как вероятная причина расхождений в реакциях разных видов насекомых на геомагнитные возмущения.

Ключевые слова: магнетит; криптохром; геомагнитная активность; геомагнитная буря.