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How do honeybees use their magnetic compass? Can they see the North?

T. Válková and M. Vácha*

Department of Animal Physiology and Immunology, Faculty of Science,
Masaryk University, Kotlarska 2, 611 37, Brno, Czech Republic

Abstract

While seeking food sources and routes back to their hive, bees make use of their advanced nervous and sensory capacities, which underlie a diverse behavioral repertoire. One of several honeybee senses that is both exceptional and intriguing is magnetoreception – the ability to perceive the omnipresent magnetic field (MF) of the Earth. The mechanism by which animals sense MFs has remained fascinating as well as elusive because of the intricacies involved, which makes it one of the grand challenges for neural and sensory biology. However, investigations in recent years have brought substantial progress to our understanding of how such magneto-receptor(s) may work. Some terrestrial animals (birds) are reported to be equipped even with a dual perception system: one based on diminutive magnetic particles – in line with the original model which has also always been hypothesized for bees – and the other one, as the more recent model describes, based on a sensitivity of some photochemical reactions to MF (radical-pair or chemical mechanism). The latter model postulates a close link to vision and supposes that the animals can see the position of the geomagnetic North as a visible pattern superimposed on the picture of the environment. In recent years, a growing body of evidence has shown that radical-pair magnetoreception might also be used by insects. It is realistic to expect that such evidence will inspire a re-examination and extension or confirmation of established views on the honeybee magnetic-compass mechanism. However, the problem of bee magnetoreception will not be solved at the moment that a receptor is discovered. On the contrary, the meaning of magnetoreception in insect life and its involvement in the orchestration of other senses is yet to be fully understood. The crucial question to be addressed in the near future is whether the compass abilities of the honeybee could suffer from radio frequency (RF) smog accompanying modern civilization and whether the fitness of this dominant pollinator might be affected by RF fields. The goal of this review is to provide an overview of the path that the behavioral research on honeybee magnetoreception has taken and to discuss it in the context of contemporary data obtained on other insects.

Keywords: honeybee, magnetoreception, compass, radical-pair, magnetite, radio-smog

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*Author for correspondence
Fax: +420 549491420
E-mail: vacha@sci.muni.cz

Honeybees – an extraordinary model for research on neural principles of senses and behavior

The honeybee (*Apis mellifera L.*) is an animal rich in behavioral repertoire possessing a highly developed social network, navigation and communication system. It uses learned patterns of colors (Horridge, 2009), shapes (Srinivasan *et al.*, 2006; Srinivasan, 2010), smells and other navigational cues (Menzel & Giurfa, 2006). The typical waggle dance, which provides information on the direction and distance from the hive to a food source, is an example of an advanced communication system in invertebrates. These impressive skills are attributed to a brain weighing less than a milligram, containing only several million neurons, which makes the study of its neural substrate much easier (Srinivasan, 2010). Logically, the honeybee has been attracting the attention of neuroethologists since the beginning of behavioral research (von Frisch, 1967) to the present (Menzel & Giurfa, 2006; Srinivasan *et al.*, 2006).

For their navigational purposes, honeybees use the position of the sun and other celestial cues, a polarized light compass (Rossel & Wehner, 1984, 1986), landmarks on cloudy days (Dyer & Gould, 1981) and, the still somewhat enigmatic, information of geomagnetic field (for a review, see Wiltschko & Wiltschko, 2005).

Magnetoreception in bees

Apart from birds, it was the honeybee that began research on the animal magnetic compass decades ago. A series of works by Lindauer & Martin (1968, 1972) and later Walker & Bittermann (1985, 1989a,b) represented the ceased pioneering era of the honeybee as probably the most thoroughly investigated organism regarding magnetoreception (for a review, see Wajnberg *et al.*, 2010). In recent magnetoreception research, honeybees have been substituted by birds (Wiltschko & Wiltschko, 2006), fish or laboratory insects like the fruit fly *Drosophila* (Dommer *et al.*, 2008; Gegear *et al.*, 2008, 2010) and the cockroach (Vácha *et al.*, 2009). Traditional laboratory species are likely to dominate in the process of answering the cardinal question about the molecular machinery of insect magnetoreception. However, honeybees may become the powerful model organism to reveal how magnetic information is processed and how it is used in orientation.

To summarize available behavioral data, we know that (i) bees forced to dance on a horizontal comb, in place of a vertical, switch to the cardinal magnetic axes instead of the vertical line of gravity (Martin & Lindauer, 1977). (ii) Orientation of typical waggle dances may be affected by changes in MF (Lindauer & Martin, 1972). (iii) When dancing, bees commit a certain number of errors – variances up to 20° left or right around the correct direction of the waggle dance axis. This misdirection is dependent on variations of the Earth's MF and disappears 30–45 min after zeroing the field (Lindauer & Martin, 1968). (iv) Furthermore, when learning about or searching for a goal, bees orient consistently in one compass direction, aided by magnetic power lines (Collet & Baron, 1994). (v) Honey bees were also reported to use MF direction as a reference at the beginning of comb construction in a new hive (DeJong, 1982). The most impressive and elegant series of experiments was performed by means of a conditioning paradigm developed by Walker & Bitterman (1985, 1989a). The magnetic sensory system of bees has turned out to be surprisingly sensitive and could (vi) discriminate a local weak magnetic anomaly against the earth-strength magnetic background (Walker & Bitterman, 1989c; Walker, 1997; Kirschvink *et al.*, 1997). In all behavioral studies where the sensory mechanism was discussed, only ferrimagnetic particles (magnetite or maghemite) were considered as a plausible transducer between MF energy and the nervous system of the honeybee.

Mechanisms of animal magnetoreception

Both in birds and insects uncertainty persists about the manner in which the energy of the MF is transformed into neural signaling and, particularly in insects, where exactly in the body the receptor is located. The last decade, however, has brought a number of important discoveries concerning the molecular definition of the receptor(s) (reviewed in Wiltschko & Wiltschko, 2006 and Johnsen & Lohman, 2008). For honeybees as well as for other terrestrial animals, two main models can aspire to explain the puzzle of compass orientation since the 1980s when a chemical-radical pair compass mechanism was put forward as a conceivable alternative to the existing ferrimagnetic light-independent model.

A light-independent mechanism using magnetic particles could detect even minute changes in the intensity and polarity of the MF (reviewed in Johnsen & Lohmann, 2005). The principle is based on the existence of iron oxide (magnetite/maghemite) crystals in tissues, which behave as small compass needles transforming magnetic energy into mechanical force if the position of the animal changes with respect to the MF of the Earth. Clusters or chains of such magnetite particles anchored to the receptor cell membrane near mechanically activated ion channels (Davila *et al.*, 2003; Walker, 2008; Cadiou & McNaughton, 2010) may cause a respective electric change and elicit nervous activity.

The great virtue of the magnetite theory is its simplicity and the fact that iron oxide particles are widespread in animal tissues. Magnetite particles were first found in bacteria in the 1970s and, subsequently, in a number of other species, including ants (Wajnberg *et al.*, 2004; Abraçado *et al.*, 2005), termites (Alves *et al.*, 2004) and bees (Hsu & Li, 1993; Takagi, 1995; Esquivel *et al.*, 2002; Oliveira *et al.*, 2005; Lucano *et al.*, 2006), inspiring the idea of their involvement in magnetic detection.

As researchers have been seeking for selective discrimination tests that would point to one mechanism leaving the other intact, a diagnostic test for this mechanism was designed (Kirschvink & Kobayashi-Kirschvink, 1991): a brief and properly configured magnetic pulse applied to the whole animal. Such a pulse could change the direction of magnetization or disrupt the alignment of magnetite in tissues. In such an experiment, north-seeking organisms could be converted into south-seeking ones or disoriented in the long term. When applied, it really caused disorientation in birds, sea turtles and rodents (Wiltschko *et al.*, 2006) and changed the orientation in bees (see below and Kirschvink & Kobayashi-Kirschvink, 1991).

In the case of the light-dependent chemical (radical-pair) mechanism, the underpinning theory is based on interactions between MF and the excited state of some biochemical molecules. According to theory and concerning the role of light, in some photochemical reactions, the absorption of photon energy triggers an electron transfer from a donor to an acceptor molecule creating a donor-acceptor pair with one unpaired electron each, a so-called radical pair (RP) (Ritz *et al.*, 2010b). Spinning electrons of each radical possess magnetic moments and orient their movements according to the Earth-strength MF. The Earth's field may affect subsequent reaction pathways of RP and, depending on electrons spin states, different reaction products will be formed (Ritz *et al.*, 2009, 2010b). In this manner, the MF may act as a switch between two alternative reaction pathways.

The most promising candidate molecule forming RP is the Cryptochrome (Cry), a photopigment sensitive maximally to blue-green light. Cry exists in both animals and plants (Cashmore *et al.*, 1999) where it controls biological clocks. It has been found in insects (Yuan *et al.*, 2007; Yoshii *et al.*, 2009), amphibians (van der Schalie *et al.*, 2007), birds and mammals (reviewed by Wiltschko & Wiltschko, 2005). Some of the RP reaction products are believed to affect the efficiency of light conversion into membrane potential in animal photoreceptors (reviewed by Liedvogel & Mouritsen, 2010). Since the effect depends on the angle between magnetic vector and the axis of photoreceptors in the eye (Solov'yov *et al.*, 2010), some photoreceptors (rods and cones in vertebrates or ommatidia in insects) may be more impacted than others, causing brighter or darker regions in the visual field. Hence, the animals could perceive different visual patterns superimposed on the picture of the environment in different magnetic directions (Ritz *et al.*, 2000, 2010a). Overlapping the visual and magnetic patterns would incorporate magnetic landmarks into an animal's visual surrounding (Phillips *et al.*, 2010). In insects, landmarks of both origins might together become a part of the retinotopic memories used for orientation.

This model provides a more plausible explanation than the magnetite-based hypothesis on the sensitivity of some animals' compasses to the wavelength and intensity of light as observed in newts (Phillips & Borland, 1992), birds (Wiltschko *et al.*, 2004, 2007), fruitflies (Phillips & Sayeed, 1993) and mealworm beetles (Vácha *et al.*, 2008b). However, within the realm of wavelength and intensity of light, the impact of magnetite particles might still be worth considering. Instead of the magnetoreceptor being directly dependent on light activation (RP model), an alternative hypothesis put forward by Jensen (2010) explains the impacts of diverse colors on magnetic orientation on the basis of a magnetite receptor. His model postulates the integration between a light-independent magnetite compass and a distinct skylight color gradient compass reported from both vertebrates and insects (see Jensen, 2010, also Kirschvink *et al.*, 2010). The idea is definitely worth experimental verification.

Seeking diagnostic experiments to verify possible involvement of an RP mechanism selectively, researchers came up with the application of weak RF electromagnetic waves, which could affect the ratio between relative spin states and 'jam' the compass orientation (Ritz *et al.*, 2004). The magnetite particles should not be impacted or, at least, not in such a narrow frequency window as RP processes are. Radio waves of discrete resonance frequencies rendered the magnetic compass of birds useless (Ritz *et al.*, 2004, 2009) but left subterranean rodents unaffected (Thalau *et al.*, 2006).

Chemical magnetoreception also in honeybees?

Since the beginning of the study of magnetoreception in honeybees, the magnetite hypothesis has predominated over the light-dependent chemical magnetoreception. In fact, the RP model in bees seems to have no recent advocates (see Hsu *et al.*, 2007; Hsu & Chan, 2011). Let us first list what major arguments have been raised in favor of a light-independent compass and then compare them with light-dependent evidence:

(i) The existence of magnetite particles in close proximity to innervated structures: it was shown that the anteriodorsal abdomen in bees is a site of magnetite biomineralization (Gould *et al.*, 1978; Kirschvink, 1982). In subsequent studies, all the other body parts were reported to host magnetite particles of diverse size and properties (for details, see the review by Wajnberg *et al.*, 2010).
(ii) The attachment of magnets to the abdomen near the region of anteriordorsal magnetite concentration interfered with magnetic discrimination (Walker & Bitterman 1989b).
(iii) Pulse-remagnetisation experiments affected magnetosensitive behavior (Kirschvink & Kobayashi-Kirschvink, 1991).
(iv) Bees were able to perceive MF even in darkness (Kirschvink & Kobayashi-Kirschvink, 1991).

Alternative evidence of the impact of light, which first referred to the link between magneto- and photoreception, have been reported both in vertebrates and in insects (see the recent review by Phillips *et al.*, 2010). Following the work of Phillips & Sayeed (1993), who showed a shift of magnetic orientation in *Drosophila* after a change of light color, a similar phenomenon was also discovered in the mealworm beetle (Vácha *et al.*, 2008b, but see Jensen, 2010). This species was originally reported to orient magnetically in darkness (Arendse, 1978) but later attempts at replication failed (Vácha & Soukopová, 2004), showing light-dependence only. Also, restlessness of the American cockroach elicited by periodical North shifts took place under light of sufficient intensity in contrast to complete darkness (Kvicalova & Vacha, unpublished data).

As for evidence concerning the role of light in magnetoreception in honeybees, unfortunately, older reports do not provide details about intensity, wavelength and bandwidth of light necessary for comparative analysis. Gould *et al.* (1980) successfully tested magnetoreception on a horizontal plane under red light (without details). Schmitt & Esch (1993) published magnetic orientation from complete darkness (infra-red illumination). Taken together, the existing results imply that honeybees would not need the light, at least for some kind of magnetic orientation. However, the orientation of waggle dances was sensitive to changes in light wavelengths (Lindauer & Martin, 1972; Leucht, 1984). Thus, honeybee compass behavior is likely to be light-sensitive but not dependent (Wajnberg *et al.*, 2010). Light-independence seems to be an obvious requisite for an animal using compass orientation in darkness inside a hive. Nevertheless, the European honeybee *Apis mellifera carnica*, foraging only during the day, still retains achromatic vision down to moonlight intensities (Theobald *et al.*, 2006). Since light-dependent magnetoreception in night-migrating birds seems to function even in very dim light (Muheim *et al.*, 2002; Wiltschko *et al.*, 2007), in theory, twilight inside a hive may still provide a sufficient amount of light energy necessary for photochemical magnetoreception.

In terms of other features of the RP mechanism, Cryptochrome should be considered. Cry has turned out to be essential to the fruit fly's ability to recognize the presence of MF in the arms of a T-maze in the compelling experiments of Gegear *et al.* (2008, 2010). Similarly, the magnetosensitive reaction of cockroaches was confined to the unsuppressed expression of Cry (Bazalova *et al.*, unpublished data). The honeybee possesses Cryptochrome 2 (Yuan *et al.*, 2007), but its role in its magnetosensitivity has not yet been tested.

Furthermore, a distinguishing feature to be discussed here is the impact of a weak RF electromagnetic field. An RF field resembling that which confused bird's compasses (see above) obstructed the magnetosensitivity of cockroaches as well (Vácha *et al.*, 2009). As for bees, no specific experiments targeting the RF impact on magnetoreception have been performed yet. Nevertheless, the sensitivity of animals to radio waves has raised discussion due to suspicions that cell phone or wifi radiation may contribute to declines in bee populations (see below).

The impact of demagnetizing pulses which were employed in a series of diagnostic tests on vertebrates (Irwin & Lohmann, 2005; Wiltschko *et al.*, 2006; Holland *et al.*, 2008; Holland, 2010) demands further consideration and discussion. The original work dealing with the impact of strong pulses on honeybees reports a change of behavior but admits incompleteness (Kirschvink & Kobayashi-Kirschvink, 1991, p. 183) due to very few (three) specimens tested. The authors suggested using combinations of one strong pulse field and another weak background field so that the properties and structure of the putatively involved magnetic material may be unveiled in future experiments. Although not using honeybee as an insect model, the experimental paradigm meeting the demands of a diagnostic experiment according to Kirschvink & Kobayashi-Kirschvink (1991) was published quite recently by Riveros & Srygley (2008). Rather than change their bearings, leafcutter ants (*Atta colombica*) lost orientation after having been exposed to a magnetic pulse. Such a complete disruption of orientation is not in line with the involvement of particles having a single magnetic domain but rather with other types of magnetic particles: multidomain or superparamagnetic ones. There have been no attempts at replicating pulse experiments, and no extensive study on honeybee has yet been published since the pilot experiment in 1991; it would be of great importance to extend and complete existing data.

Since the principle of the RP model cannot distinguish the polarity of MF, the insects were tested as to what kind of compass, whether polarity or inclination, they use. For the mealworm beetle, an inclination reaction was reported (Vácha *et al.*, 2008a). Such a finding is in line with an RP compass but doesn't exclude magnetite as a receptor (Kirschvink, 1982). In the realm of honeybee research, a distinguishing test of orientation using reversed inclination has not been performed yet. However, it was reported from the stingless bee, *Tetragonisca angustula*, that a reversed vertical field affected flight trajectory, indicating that these bees can sense whether the MF is pointed up or down, a sign of inclination reaction (see Wajnberg *et al.*, 2010).

As another important argument in favor of magnetite-based reception in bees, experiments involving tiny magnets glued on the honeybee body should be mentioned. Small magnetic wires fixed to the anteriodorsal abdomen were shown to interfere with magnetic discrimination abilities in a series of choice experiments by Walker & Bitterman (1989a,b). Control animals carrying small pieces of nonmagnetic wire succeeded in tests, whereas those with magnetic ones did not. Since the anteriodorsal abdomen was reported to be the region of major magnetite concentration (Gould *et al.*, 1978), results pointed to its involvement in reception. However, it was estimated (Walker & Bitterman, 1989b) that the biasing field around the magnetic wires reached distances up to about 5 mm at well detectable intensities (10 uT). As only preliminary experiments (two bees with wire attached to the thorax; Walker & Bitterman 1989c, p. 493) were done to localize the effect, there is still a possibility, yet to be verified on a larger dataset, that other potentially sensitive sites, like the head, were affected by magnetic wire.

To summarize, the survey through articles dealing with principles of magnetoreception behavior of honeybees and other insects, "diagnostic characteristics of a magnetite-based compass are polarity sensitivity, light independence, long-lasting disruption by strong magnetic pulses (which, properly applied, can serve to reverse the polarity of some or all domains), independence from RF jamming. It is particularly well suited to animals without access to blue/UV light such as hive-dwelling, subterranean, nocturnal, or deep sea creatures" Gould (2010, p. 435). In light of new findings and after a careful reading of the original reports, we speculate that the idea of an exclusively magnetite-based compass for honeybees has been built on some explicitly preliminary experiments and deserves confirmation or extension. Key diagnostic tests still wait for replication on larger samples in more laboratories. Since the same objection may rightly be admitted against the RP-based hypothesis, we reason that no final conclusions concerning the mechanism of honeybee magnetic sense may be drawn at present.

Honeybee compass and radio smog

The sensitivity of bees to magnetic and electromagnetic fields, which are inaccessible to humans, has given birth to an apprehension about the possible detrimental impact of growing electromagnetic smog produced by modern technologies. The question that has also found its way into the media (CNN World, June 30, 2010, available online at http://articles.cnn.com/2010-06-30/world/bee.decline.mobile.phones_1_bee-populations-cell-phone-radiation-ofcom?_s=PM:WORLD) was raised on whether the evolutionary benefit of compass-sense has turned into a pitfall in the environment of a highly technical civilization rich in sources of magnetic and electromagnetic fields. The reports of sensitivity of animal compasses to RF fields even many hundred times weaker than the Earth's field (Ritz *et al.*, 2009) have inspired concern about a link between bee decline and the thickening network of mobile phones (Sharma & Kumar, 2010).

Radio waves are a man-made environmental factor that were introduced in the last century and have essentially different physical properties than the static MF of the Earth. For example, a compass sensitive to a MF is an inappropriate tool for radio broadcast detection. Similarly, the compass of bees has certainly not been 'engineered' to perceive human-made technical fields. Reliable conclusions in terms of whether it is jammed by them or not are too soon to draw. Surprisingly, both dominant models of compasses have been predicted to be sensitive to certain kinds of radio waves since also magnetite seems to be a good absorber of microwave energy (Kirschvink, 1996). However, the problem is that technical fields differ substantially along with their frequencies, and this is even more true considering their biological impacts. The resonance point where an RP compass is most sensitive to RF is 1000 × lower than the basic frequency of mobile phones. Is that too much or is it enough to have a real biological effect? To our knowledge, no satisfactory and consensual reply exists. Moreover, mobile phone networks produce heterogenous and variously modulated radiance, which may interfere with other RF sources. To reach qualified conclusions, necessary cooperation between physicists and biologists should be started.

Concluding remarks

Although its existence has been demonstrated convincingly in behavioral experiments in the last decades of the 20th century, the mechanism underlying the magnetic compass-sense of honeybees has not been satisfactorily explained. Since the beginning of the exploration of a bee's compass, all findings have been interpreted in favor of interactions of magnetic particles of iron oxides with the geomagnetic field. However, these conclusions were made at a time prior to the development and major experimental evidence of the RP mechanism. In recent times, at least in vertebrates, the chemical RP model is taken as a plausible partner of magnetite/maghemite reception mechanism. The research on insects has revealed a growing body of evidence that invertebrates may also use compass mechanisms linked to vision. Thinking of the honeybee as a model species, a series of questions arise: does the honeybee use a different kind of magnetoreceptor than the fruit fly? Could honeybees, like birds, be equipped with more receptors? For what reason? Is its compass system interfered with by technical radio fields? To answer such questions, researchers should return to the honeybee as a model organism and re-examine its magnetoreception skills by means of combinations of established and new behavioral paradigms with contemporary diagnostic tests and methods of molecular biology. Even if the traditional magnetite-based reception mechanism was definitely proven for the honeybee, this remarkable insect species could provide answers to subsequent questions concerning the evolution and meaning of the perception of Earth magnetism in the life of animals.

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