

## Radio frequency magnetic fields disrupt magnetoreception in American cockroach

Martin Vácha\*, Tereza Půžová and Markéta Kvíčalová

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

\*Author for correspondence (vacha@sci.muni.cz)

Accepted 21 July 2009

### SUMMARY

The sense that allows birds to orient themselves by the Earth's magnetic field can be disabled by an oscillating magnetic field whose intensity is just a fraction of the geomagnetic field intensity and whose oscillations fall into the medium or high frequency radio wave bands. This remarkable phenomenon points very clearly at one of two existing alternative magnetoreception mechanisms in terrestrial animals, i.e. the mechanism based on the radical pair reactions of specific photosensitive molecules. As the first such study in invertebrates, our work offers evidence that geomagnetic field reception in American cockroach is sensitive to a weak radio frequency field. Furthermore, we show that the 'deafening' effect at Larmor frequency 1.2 MHz is stronger than at different frequencies. The parameter studied was the rise in locomotor activity of cockroaches induced by periodic changes in the geomagnetic North positions by 60 deg. The onset of the disruptive effect of a 1.2 MHz field was found between 12 nT and 18 nT whereas the threshold of a doubled frequency field 2.4 MHz fell between 18 nT and 44 nT. A 7 MHz field showed no impact even in maximal 44 nT magnetic flux density. The results indicate resonance effects rather than non-specific bias of procedure itself and suggest that insects may be equipped with the same magnetoreception system as the birds.

Key words: magnetoreception, insects, radical pair, radio frequency, cryptochrome.

### INTRODUCTION

Two basic principles have been put forth to explain the reception mechanism used by land animals to sense the geomagnetic field (reviewed by Johnsen and Lohmann, 2008; Wiltschko and Wiltschko, 2006). The so-called magnetite-based mechanism assumes the presence of ferrimagnetic, iron oxide particles in tissues (Fleissner et al., 2003; Fleissner et al., 2007; Kirschvink et al., 2001), and the other principle postulates the radical pair-based mechanism (Ritz et al., 2000). While ferrimagnetic magnetoreception can basically be perceived as a kind of mechanoreception, the radical pair mechanism is a system closely linked with photoreception. Given the current intensive discussions over as the yet unconfirmed molecular basis of the magnetoreception sense, it is only natural that the interest of both experimentalists and theoreticians turns to neuroethological experiments that could point at one or the other type of receptive mechanism as selectively and unambiguously as possible. An experimental intervention that would cause a loss of the magnetoreceptive behaviour by inactivating only one of the two possible mechanisms while leaving the other intact would ideally meet that condition.

A short and strong magnetic pulse intended to reverse or disrupt compass orientation is considered the kind of experimental interference that may affect the magnetite-based transduction mechanism but should have no long-term effects on photosensitive processes of radical pair reactions [Kalmijn–Blakemore pulse remagnetization experiment (Kalmijn and Blakemore, 1978)]. Effects of such experimental treatment on the magnetic orientation in animals, albeit in various modalities, have really been reported in a number of animals (Holland et al., 2008; Irwin and Lohmann, 2005; Wiltschko et al., 2002).

However, several different types of experiments could be designed that would have no effect on the function of iron oxide-based receptive structures but would interfere with the

photosensitive, radical pair, magnetoreception mechanism. They include experiments investigating the effects of colour and light intensity on magnetic orientation (Wiltschko et al., 2008). The drawback of such experiments is that they involve procedures that, in theory, might affect not only magnetoreception itself but also the motivation of the animals to use the compass.

A much more promising experimental design that will generate no response from ferrimagnetic structures and will be imperceptible for the 'basic' five senses involves the use of a weak radio frequency (RF) field that interferes with natural oscillations between radical pair spin states. Such a field within approximately 0.1–100 MHz range applied against the background of particular static geomagnetic field will have the greatest effect if its frequency matches exactly the radical pair resonance frequency (Larmor frequency, see also Discussion). In that case, the RF field may be only a fraction of the geomagnetic field background (Ritz et al., 2009). Initially predicted only in theory, this effect was eventually discovered to really exist in birds (Thalau et al., 2005; Ritz et al., 2009). This test meets selectivity requirements so well that it has been named the diagnostic test for the radical pair mechanism (Ritz et al., 2004).

To utilise the potential of the test maximally, it seems to be vital to map the frequency spectrum and frequency and intensity limits of this extraordinary phenomenon to exclude lingering doubts about the diagnostic quality of the test (Kavokin, 2009), e.g. to eliminate a certain possibility of biasing non-specific inductive effects of the high-frequency field (Johnsen and Lohman, 2008). An analysis of the effects of different combinations of intensity and frequency of the RF field on magnetoreceptive behaviour could, at the same time, help to better identify the photopigments involved in the primary processes of magnetoreception (Ritz et al., 2009; Solov'yov and Schulten, 2009; Thalau et al., 2005).

While RF effects on magnetoreception in vertebrates have already been tested and research into them still continues (Ritz et al., 2009),

there is no information on RF effects on magnetoreception in the invertebrates equipped with the magnetic sense.

In our study, we used an assay of magnetic susceptibility in American cockroach (*Periplaneta americana* L.) based on the monitoring of an increase in locomotor activity of insects located in a periodically rotated geomagnetic field (Vácha, 2006). The basic objective was to determine whether a weak RF field was able to deactivate the insect sensing the geomagnetic field. If it was, the following goal was to identify whether and how thresholds of effective intensities vary at different frequencies.

## MATERIALS AND METHODS

The assay testing magnetic susceptibility of cockroaches (for details, see Vácha, 2006) is based on comparing activity (the number of body position changes larger than 15 deg.) in (and 45 min after) the interval in which the position of the magnetic North is rotated by 60 deg. to and from (periods CDE, 11.30–13.45 h) and the interval before and after the magnetic treatment (periods ABF, 10.00–11.30 h and 13.45–14.30 h).

### Animals

American cockroaches were kept in translucent buckets in a 12h:12h light:dark regime and at temperatures between 27°C and 30°C. Water and cat food pellets were provided *ad libitum*. Before the test, the bucket with cockroaches was placed into a refrigerator for about 30 min to immobilise them and facilitate handling. One cockroach was placed into each of the 11 Petri dishes 15 cm in diameter. Between 14.30 h and 16.00 h, the Petri dishes were brought to the testing room, where the animals stayed until the end of sampling the next day without any interference.

### Testing setup

The Petri dishes were placed on a glass desktop and images of the positions of the animals were taken every minute by a common web camera (Genius, Comp. Tech., Dubai, UAE) situated 1 m below on the floor and hidden behind black cloth. A strip of paper wrapped around each of the dishes prevented the animals from seeing one another. In addition, the set of 11 Petri dishes was covered with a circular arena of white plastic (56 cm in diameter and 42 cm in height). The arena rim was divided into 48 sectors (visible only on the PC monitor), making it possible to determine the positions of the animals.

To diffuse the light, the arena was covered with a lid of transparent white Perspex. A frosted white light bulb (40 W, soft tone, Philips, Hamburg, Germany) placed 50 cm above the lid illuminated the experimental space. The cockroaches could see only the white lid, the white walls around them and the black cloth below. The table with the arena was placed inside a Merritt coil. The temperature in the testing room was 23°C ( $\pm 1^\circ\text{C}$ ).

### Magnetic conditions

The natural geomagnetic background in the laboratory was as follows: horizontal component  $18.3 \pm 0.2 \mu\text{T}$ , total vector  $42.9 \pm 0.2 \mu\text{T}$ , inclination  $64 \pm 1 \text{ deg. } \mu\text{T}^{-1}$ ; spatial variation in the arena region was  $< 2\%$  (measured by HMR 2300 magnetometer Honeywell, NJ, USA).

Only the horizontal component was experimentally rotated by 60 deg. clockwise (CW) by means of a horizontal four-element Merritt coil (2 m  $\times$  2 m  $\times$  2 m in size) (Merritt et al., 1983). The coil system was fed and permanently grounded by means of a DC power supplier [DF1730SB, Ougen Electronics (Ningbo) Co. Ltd, China], which was permanently switched on. The magnetic treatment consisted of nine 5-min automatically set trapezoid pulses that rotated the geomagnetic North by 60 deg. in interval CDE.

RF magnetic field: the maximum RF field interference with radical pair oscillations is expected in the region of the so-called Larmor frequency (LF) (Ritz et al., 2009). Larmor frequency is directly proportional to geomagnetic field intensity according to the equation  $LF = 0.028 \times B$ , where  $B$  is the magnetic flux density of the geomagnetic field. Calculated for our laboratory conditions, the result used was 1.2 MHz.

The RF field was generated, as described by Ritz et al. (Ritz et al., 2004), by the RF generator Stanford Research System DS 34 and amplified with the RF amplifier Research AF Model 25 W 1000 (Stanford Research Systems, Sunnyvale, VA, USA). Generator and amplifier (both permanently switched on) were located in a neighbouring room at a distance of 6 m. Field was measured with the spectrum analyser HP89410A with a calibrated probe (Rohde and Schwarz, Munich, Germany) in steps of 0.25 Hz. The flux densities were then integrated and converted into nT. The bandwidth was 2.25 Hz. The RF field-generating loop was constructed as a single horizontal winding of coaxial cable around the Merritt coil in the plane of the testing table (i.e. square 2 m  $\times$  2 m). A 2 cm piece of the screening was removed in the centre of the loop. The RF field vector and the geomagnetic vector therefore formed a 26 deg. angle.

In the first step, the vertical 1.2 MHz RF field flux density was set at 44 nT, i.e. a level corresponding to 0.1% of the natural field value, which we believed was high enough to interfere with the magnetoreception mechanism as it does in birds. Later we used lower levels (18 nT and 12 nT) in search of the lower limit of RF interference effect. Having localised the intensity threshold zone for Larmor frequency we proceeded with double frequency (2.4 MHz), and previously efficient flux densities (18 and 44 nT) were tested again. Finally, the impact of the most intensive field of 44 nT was tested once again at frequency of 7 MHz.

### Photoc conditions

A white light bulb (40 W, Philips) illuminated the arena through a lid diffusing the light so that its intensity at the bottom was  $0.68 \text{ Wm}^{-2}$  in the centre of the arena and  $0.64 \text{ Wm}^{-2}$  along the wall line (International Light IL700, SHD 033 probe, Peabody, MA, USA).

### Sampling

The web camera started automatic image taking at a rate of 1 image  $\text{min}^{-1}$  when the Petri dishes were put in their positions and finished the next day at the end of the test at 14.30 h. Frames from 10.00 h to 14.30 h were divided into six 45 min intervals: the first two (A,B) prior to North rotation, the middle two intervals (C,D) when the field was rotated back and forth by 60 deg. CW with a frequency of 1 per 5 min and the last two intervals (E,F) after the magnetic treatment.

Body axis changes were determined visually on the monitor using the Screen Protractor software (Iconico.com Software, New York, NY, USA). The double-blind design was applied: the persons preparing the dishes or determining the angles and scoring the activity were not aware which set of images (i.e. what kind of RF field or control) they were evaluating. No persons assisted the experiment except loading the dishes.

### Statistical processing

As described in Vácha (Vácha, 2006), Wilcoxon dependent test was used to compare the frequency of body orientation changes in CDE interval (the North position rotations and 45 min after) *versus* the ABF interval (the North position is stable).

## RESULTS

In the basic control series in the natural field and no kind of magnetic stimulation (Fig. 1B) there were no differences in locomotor activity between the CDE and the ABF intervals (Fig. 1A) ( $N=73$ , Wilcoxon test,  $P=0.73$ ). In the following experiment with no RF field application but with periodically rotated horizontal geomagnetic vector (Fig. 1C), activity in the critical CDE interval of the periodically rotated North was significantly higher than in the ABF interval, when the geomagnetic field was unperturbed (Fig. 1A) ( $N=70$ , Wilcoxon test,  $P=0.003$ ). The functionality of the basic magnetoreception test was thus successfully verified and we were able to proceed to RF field application.

When a vertical RF field at magnetic flux density of 44 nT (0.1% natural geomagnetic background) was used, no noticeable response to the magnetic North rotation was observed (Fig. 1D) and the CDE/ABF test parameter was not significant (Fig. 1A) ( $N=69$ , Wilcoxon test,  $P=0.78$ ). No significant response to magnetic treatment was found even when the RF field flux density was reduced to 18 nT (Fig. 1E) (Fig. 1A;  $N=71$ , Wilcoxon test,  $P=0.88$ ). It was only when the RF field flux density was further decreased to 12 nT (Fig. 1A,F) that the pattern of increased locomotor activity reappeared during the critical period CDE ( $N=70$ , Wilcoxon test,  $P=0.01$ ).

The results indicated that the onset of disruptive effects of 1.2 MHz vertical RF field on the magnetosensitive response was between 12 nT and 18 nT of magnetic flux density, which corresponds to approximately 0.03% of the geomagnetic background. Reaching this stage, we wanted to know whether the effect will show frequency dependence and so we doubled frequency to 2.4 MHz.

Under 2.4 MHz, 44 nT field (Fig. 1G), no response to magnetic treatment was apparent (Fig. 1A;  $N=79$ , Wilcoxon test,  $P=0.74$ ). When reduced to 18 nT, RF did not disrupt magnetosensitive reaction (Fig. 1H) (Fig. 1A;  $N=88$ , Wilcoxon test,  $P=0.03$ ). Thus, the threshold of disruptive effects of 2.4 MHz RF field was found between 18 nT and 44 nT.

Even the most intensive field of flux density 44 nT (Fig. 1I) did not affect magnetic susceptibility when 7.0 MHz frequency was used (Fig. 1A;  $N=82$ , Wilcoxon test,  $P=0.03$ ).

## DISCUSSION

### RF: from birds to insects

Birds have become the most thoroughly investigated group with respect to RF effects (Ritz et al., 2004; Ritz et al., 2009; Stapput et al., 2008; Thalau et al., 2005; Wiltshcko, W. et al., 2007; Wiltshcko, R. et al., 2007). They lose compass orientation at low RF intensity of 5–15 nT, which corresponds to about 0.01% of the static background geomagnetic field (Ritz et al., 2009). Besides birds, only rodents were tested, but no effects were found, and it seems that underground mammals use a different reception mechanism (Thalau et al., 2006; Wegner et al., 2006). The effect is not absolutely universal in birds either. The experiments with specific light regimes and local anaesthesia of the upper beak where magnetite is found (Wiltshcko et al., 2005) suggest that birds are probably equipped with both of the alternative mechanisms, i.e. the radical pair-based and the magnetite-based ones, for different types of orientation behaviour. The magnetite model [may be older from the evolutionary point of view (Wiltshcko, R. et al., 2007)] would seem to be the most likely for very precise sensing of the intensity and inclination of the Earth's field, i.e. for the so-called map sense, whereas the radical pair-based model would be the most likely for the so-called compass mechanism.

The results of our study demonstrate the sensitivity of the insect reception system that monitors the geomagnetic vector position to a weak high-frequency magnetic field. This result suggests that the insects use radical pair-based processes for at least some types of magnetosensitive behaviour. The lower limit of sensitivity to the RF field (12–18 nT) found in our study is close to the values found in European robins (5–15 nT). This similarity between taxa with such different demands on orientation as land-running insects and migrating birds indicates that the RF field probably affects their common peripheral mechanism rather than higher brain centres that integrate different sensory inputs. A critique of the role of Cryptochromes in magnetoreception, according to which they are not primary field sensors and only serve to calibrate the magnetite-based compass against the Sun, therefore, seems rather unlikely.

In view of the low sensitivity thresholds found, we cannot rule out that the almost omnipresent electromagnetic smog will have to be taken more seriously in animal magnetoreception experiments than it has been generally assumed to date.

Furthermore, our findings show that the intensity threshold of the 'deafening' RF impact is frequency-dependent with its lowest value found in the vicinity of Larmor frequency 1.2 MHz. Magnetic field at Larmor frequency (value changes with geomagnetic background) is expected to interfere most effectively with such kind of radical pair where one of the radical partners is devoid of any magnetic interactions other than with the geomagnetic field (Ritz et al., 2009). A molecule fulfilling such a prerequisite seems to be the superoxide radical. This radical (joined with cryptochrome photoreceptors as a reaction partner) is supposed to link the bird's photo- and magnetoreception (Solov'yov and Schulten, 2009).

### Non-specific bias of RF?

The phenomenon of RF sensitivity of biologically relevant magnetosensitive radical pair reactions faces the criticism concerning the risks of possible biasing non-specific impacts. Physiological systems other than magnetoreceptors might theoretically be affected by RF or RF-producing systems, e.g. effects of electromagnetic induction or vibrations inhibiting the natural behaviour and motivation of animals. Following this argument, it would be reasonable to assume that cockroaches will perceive arbitrary non-specific RF effects as disturbing signals with impact comparable with that of geomagnetic field treatment. Periodical 60 deg. rotations of geomagnetic field evoke restlessness of cockroaches (grey bars in Fig. 1A). Then growing intensity of RF fields should also enhance movement activity in periods when only RF is applied. Our results, however, show that ABF periods (white bars in Fig. 1A) did not differ among experiments. If motivation state was changed in stronger RF fields, the baseline of body turns of resting animals should also be affected. Our results do not show signs of non-specific RF-induced alert.

### Insects: demagnetisation versus RF effects?

The evolution and the importance of magnetoreception in insects remains a great challenge to sensory physiology. If we summarise behavioural data obtained in insects, we will see that magnetoreceptive orientation depends on the colour of light (Phillips and Sayeed, 1993; Vácha et al., 2008a), that the magnetic compass is inclination-type (Vácha et al., 2008b), that it depends on the presence of a functional gene for Cryptochrome (Gegear et al., 2008), and our new data show that RF effects play a role, either of which all point to the radical pair mechanism involvement. Just like in the case of birds, we thus have a number of arguments in favour of the hypothesis that insects employ radical pair reactions of precisely

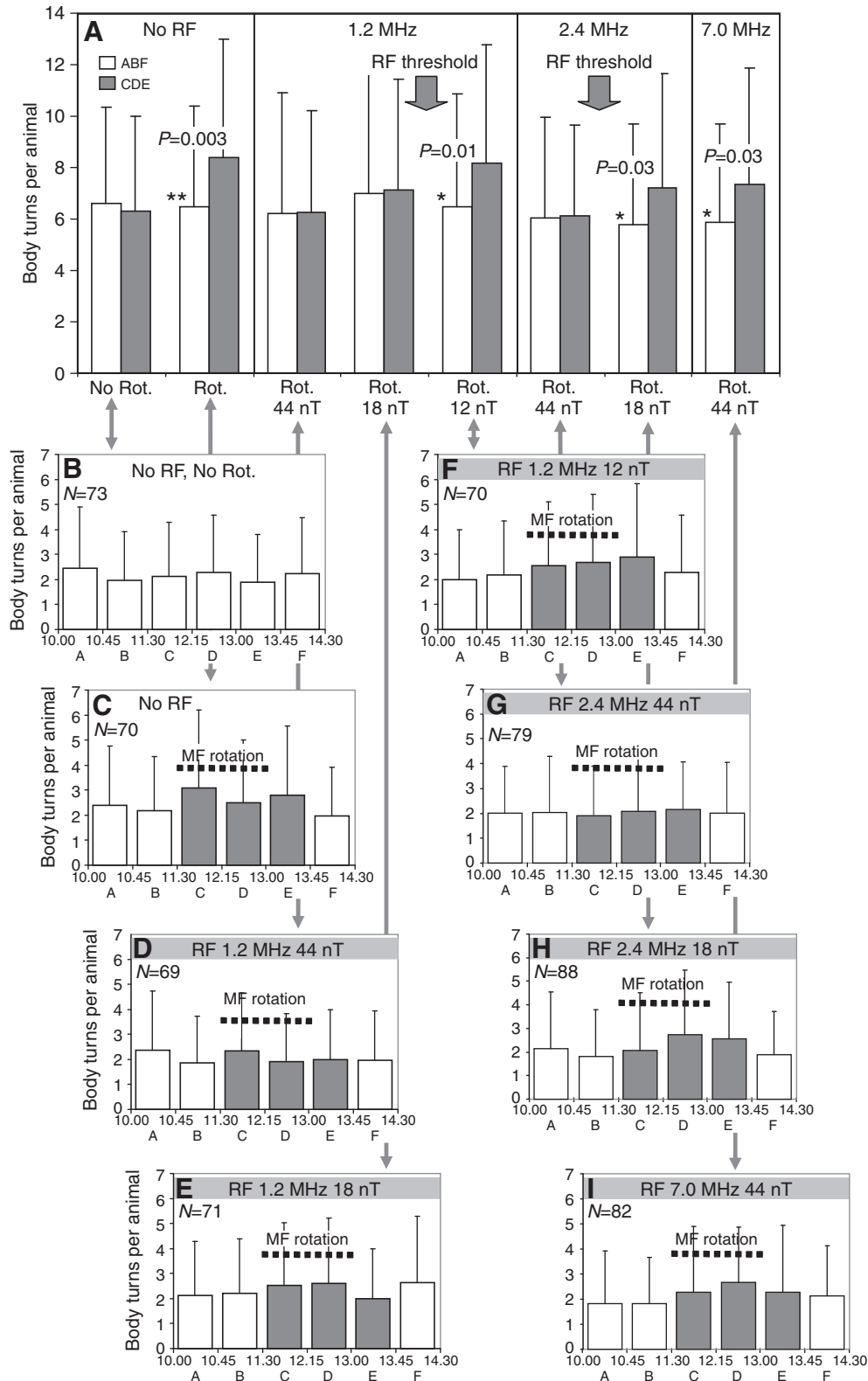


Fig. 1. Reaction of cockroaches to periodically rotated geomagnetic field and the impact of radio frequency (RF) magnetic fields – based on methods by Vácha (Vácha, 2006). On the upper summary graph (A), comparisons between periods CDE (critical period corresponding to rotations of geomagnetic North by 60deg. in 5 min intervals) and ABF (period of stable field) are given for all particular variants of the test. (B) Basic distribution of activity between 10.00 h and 14.30 h when no magnetic treatment is applied; (C) when horizontal geomagnetic vector is periodically rotated, activity rises in CDE period compared with ABF; however, both 44 nT (D) and 18 nT (E) vertical RF fields disrupts the pattern of increased activity in CDE period and CDE/ABF parameter is not significant. When a weaker 12 nT RF field is applied (F), the pattern of growing activity in CDE is restored. The threshold of 1.2 MHz RF impact falls in the region of 12–18 nT (left closed arrow). When 2.4 MHz RF field is applied, the threshold (right closed arrow) of its disrupting impact shifts up between 44 nT (G) and 18 nT (H). Finally, even though 44 nT flux density is used 7 MHz RF field does not disrupt magnetosensitive reaction (I).



defined properties for magnetoreception purposes, and that these reactions most probably are linked to Cryptochromes.

The effect of a strong and short demagnetising pulse that blocked magnetic orientation in ants (Riveros and Srygley, 2008) nevertheless speaks in favour of magnetic particle involvement in the orientation of some insect species. An experiment involving an attempt at demagnetisation with a permanent magnet affected the migration direction of butterflies (Perez et al., 1999; Srygley et al., 2006). In line with this, a compass sense detecting field polarity was described in spiny lobsters from a group Crustacea related to insects, which is a characteristic that, on principle, cannot exist in a radical pair-based compass (Lohmann et al., 1995).

Consequently, insects may be equipped with both reception systems, just like birds are supposed to be, i.e. by both the high-sensitivity magnetite-based sense of the magnetic map and the radical pair-based sense for magnetic compass orientation (Wiltschko, R. et al., 2007). It follows from their biology, however, that the compass sense alone would be sufficient for most insect species. Therefore, a question arises why species with an action radius of several dozen or hundred metres need an extra detector necessary for the magnetic map sense. Or do different insect species use different sensors? Such a problem remains to be addressed.

The magnetic response used in the present study describes a degree of activity rather than orientation. For that reason, it cannot be generalised with certainty that the RF field disrupts insect magnetic orientation – contrary to results in birds. Nevertheless, the threshold sensitivity of the system informing cockroaches about the position of the magnetic North to the RF field was so close to the sensitivity threshold found in birds that a common principle in the two is quite likely.

In the present study, we report original evidence of RF effects on magnetoreception in an invertebrate animal. We show that frequencies different from the Larmor frequency (1.2 Mhz) require much higher fields to ‘deafen’ the magnetoreception sensitivity of the cockroach. We consider the results as an important step forward in insect magnetoreception analysis and as an argument in favour of reproducibility of RF effects on animal magnetoreception and the radical pair hypothesis as such. The next step to be taken may concern more detailed analysis of the frequency spectrum, which might give us a better understanding of properties of the molecules involved in radical pair reactions in animal taxa different from birds.

Our thanks are due particularly to Dr. Petr Thalau for measuring the RF field parameters and for providing us with instruments necessary for our experiments. This research was supported by a grant from the Czech Science Foundation (GACR 206/07/J041) and from the Ministry of Education, Youth and Sports (MSM 0021622416).

## REFERENCES

- Fleissner, G., Holtkamp-Rotzler, E., Hanzlik, M., Winkhofer, M., Fleissner, G., Petersen, N. and Wiltschko, W. (2003). Ultrastructural analysis of a putative magnetoreceptor in the beak of homing pigeons. *J. Comp. Neurol.* **458**, 350-360.
- Fleissner, G., Stahl, B., Thalau, P., Falkenberg, G. and Fleissner, G. (2007). A novel concept of Fe-mineral-based magnetoreception: histological and physicochemical data from the upper beak of homing pigeons. *Naturwissenschaften* **94**, 631-642.
- Gegear, R. J., Casselman, A., Waddell, S. and Reppert, S. M. (2008). Cryptochrome mediates light-dependent magnetosensitivity in *Drosophila*. *Nature* **454**, 1014-1018.
- Holland, R. A., Kirschvink, J. L., Doak, T. G. and Wikelski, M. (2008). Bats use magnetite to detect the earth's magnetic field. *PLOS* **3**, e1676.
- Irwin, W. P. and Lohmann, K. J. (2005). Disruption of magnetic orientation in hatchling loggerhead sea turtles by pulsed magnetic fields. *J. Comp. Physiol. A Sens. Neural Behav. Physiol.* **191**, 475-480.
- Johnsen, S. and Lohmann, K. J. (2008). Magnetoreception in animals. *Phys. Today* **61**, 29-35.
- Kalmijn, A. J. and Blakemore, R. P. (1978). The magnetic behavior of mud bacteria. In *Animal Migration, Navigation and Homing* (ed. K. Schmidt-Koenig and W. T. Keeton), pp. 354. Berlin: Springer-Verlag.
- Kavokin, K. V. (2009). The puzzle of magnetic resonance effect on the magnetic compass of migratory birds. *Bioelectromagnetics* **30**, 402-410.
- Kirschvink, J. L., Walker, M. M. and Diebel, C. E. (2001). Magnetite-based magnetoreception. *Curr. Opin. Neurobiol.* **11**, 462-467.
- Lohmann, K. J., Pentcheff, N. D., Nevitt, G. A., Stetten, G. D., Zimmerfaust, R. K., Jarrard, H. E. and Boles, L. C. (1995). Magnetic orientation of spiny lobsters in the ocean: experiments with undersea coil systems. *J. Exp. Biol.* **198**, 2041-2048.
- Merritt, R., Purcell, C. and Stroink, G. (1983). Uniform magnetic field produced by three, four, and five square coils. *Rev. Sci. Instrum.* **54**, 879-882.
- Perez, S. M., Taylor, O. R. and Jander, R. (1999). The effect of a strong magnetic field on monarch butterfly (*Danaus plexippus*) migratory behavior. *Naturwissenschaften* **86**, 140-143.
- Phillips, J. B. and Sayeed, O. (1993). Wavelength-dependent effects of light on magnetic compass orientation in *Drosophila melanogaster*. *J. Comp. Physiol. A* **172**, 303-308.
- Ritz, T., Adem, S. and Schulten, K. (2000). A model for photoreceptor-based magnetoreception in birds. *Biophys. J.* **78**, 707-718.
- Ritz, T., Thalau, P., Phillips, J. B., Wiltschko, R. and Wiltschko, W. (2004). Resonance effects indicate a radical-pair mechanism for avian magnetic compass. *Nature* **429**, 177-180.
- Ritz, T., Wiltschko, R., Hore, P. J., Rodgers, C. T., Stapput, K., Thalau, P., Timmel, C. R. and Wiltschko, W. (2009). Magnetic compass of birds is based on a molecule with optimal directional sensitivity. *Biophys. J.* **96**, 3451-3457.
- Riveros, A. J. and Srygley, R. B. (2008). Do leafcutter ants, *Atta colombica*, orient their path-integrated home vector with a magnetic compass? *Anim. Behav.* **75**, 1273-1281.
- Solov'yov, I. A. and Schulten, K. (2009). Magnetoreception through cryptochrome may involve superoxide. *Biophys. J.* **96**, 4804-4813.
- Srygley, R. B., Dudley, R., Oliveira, E. G. and Riveros, A. J. (2006). Experimental evidence for a magnetic sense in Neotropical migrating butterflies (Lepidoptera: Pieridae). *J. Anim. Behav.* **71**, 183-191.
- Stapput, K., Thalau, P., Wiltschko, R. and Wiltschko, W. (2008). Orientation of birds in total darkness. *Curr. Biol.* **18**, 602-606.
- Thalau, P., Ritz, T., Stapput, K., Wiltschko, R. and Wiltschko, W. (2005). Magnetic compass orientation of migratory birds in the presence of a 1.315 MHz oscillating field. *Naturwissenschaften* **92**, 86-90.
- Thalau, P., Ritz, T., Burda, H., Wegner, R. E. and Wiltschko, R. (2006). The magnetic compass mechanisms of birds and rodents are based on different physical principles. *J. Royal. Soc. Interface* **3**, 583-587.
- Vácha, M. (2006). Laboratory behavioural assay of insect magnetoreception: magnetosensitivity of *Periplaneta americana*. *J. Exp. Biol.* **209**, 3882-3886.
- Vácha, M., Půžová, T. and Dršťková, D. (2008a). Effect of light wavelength spectrum on magnetic compass orientation in *Tenebrio molitor*. *J. Comp. Physiol. A* **194**, 853-859.
- Vácha, M., Dršťková, D. and Půžová, T. (2008b). Tenebrio beetles use magnetic inclination compass. *Naturwissenschaften* **95**, 761-765.
- Wegner, R. E., Begall, S. and Burda, H. (2006). Magnetic compass in the cornea: local anaesthesia impairs orientation in a mammal. *J. Exp. Biol.* **209**, 4747-4750.
- Wiltschko, R. and Wiltschko, W. (2006). Magnetoreception. *BioEssays* **28**, 157-168.
- Wiltschko, R., Ritz, T., Stapput, K., Thalau, P. and Wiltschko, W. (2005). Two different types of light-dependent responses to magnetic fields in birds. *Curr. Biol.* **15**, 1518-1523.
- Wiltschko, R., Stapput, K., Ritz, T., Thalau, P. and Wiltschko, W. (2007). Magnetoreception in birds: different physical processes for two types of directional responses. *Hfsp J.* **1**, 41-48.
- Wiltschko, R., Munro, U., Ford, H., Stapput, K. and Wiltschko, W. (2008). Light-dependent magnetoreception: orientation behaviour of migratory birds under dim red light. *J. Exp. Biol.* **211**, 3344-3350.
- Wiltschko, W., Munro, U., Wiltschko, R. and Kirschvink, J. L. (2002). Magnetite-based magnetoreception in birds: the effect of a biasing field and a pulse on migratory behavior. *J. Exp. Biol.* **205**, 3031-3037.
- Wiltschko, W., Freire, R., Munro, U., Ritz, T., Rogers, L., Thalau, P. and Wiltschko, R. (2007). The magnetic compass of domestic chickens, *Gallus gallus*. *J. Exp. Biol.* **210**, 2300-2310.