



Sensitivity threshold of avian magnetic compass to oscillating magnetic field is species-specific

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Abstract

One of the most unusual features of the avian magnetic compass is its sensitivity to weak oscillating magnetic fields (OMF) in the radiofrequency range. This effect, observed earlier in numerous experiments in European robins *Erithacus rubecula* and garden warblers *Sylvia borin*, is usually associated with the radical-pair magnetoreception in the eye, which is the mainstream biophysical model of the avian magnetic compass. We studied the effect of OMF on the orientation behavior of a long-distance migrant, the pied flycatcher *Ficedula hypoleuca*. The OMF with an amplitude of 190 nT disoriented pied flycatchers, similarly to the species studied earlier. However, the application of OMF with an amplitude of 17 nT did not lead to disorientation in pied flycatchers when tested in round arenas: the birds showed their correct season-specific migratory direction. This finding is in stark contrast with previous results, obtained in garden warblers at exactly the same place and under the same conditions: garden warblers were disoriented by OMF which was an order of magnitude weaker. Moreover, the threshold of sensitivity to OMF amplitude in pied flycatchers is found to be higher than that in both species previously studied, the European robin and the garden warbler. We discuss the variable sensitivity of avian compass to OMF in the context of migration ecology of two long-distance African migrants, the pied flycatcher and garden warbler, and the short-distance migrant, the European robin.

Significance statement

Birds are known to use a magnetic compass to determine the proper direction of their flight during seasonal migrations. Many previous experiments demonstrated that operation of this compass is disrupted by weak oscillating magnetic fields (OMF) in the radiofrequency range. Among the two bird species studied so far, a long-distance migrant, garden warbler, is more sensitive to OMF than a short-distance migrant, European robin. This might be a result of finer tuning of the magnetic compass of long-distance migrants, making it less robust to perturbations. In our experiments, however, the magnetic compass of another long-distance migrant, pied flycatcher, remained operational under OMF even stronger than that which disrupted magnetic orientation of European robins. This unexpected result demonstrates high variability of navigational systems of birds and raises questions about their adaptation to behavioral patterns of birds on their migration routes.

Keywords Magnetic compass · Migratory orientation · Oscillating magnetic fields · Pied flycatcher *Ficedula hypoleuca*

Introduction

The magnetic sense, present in many species of animals (Wiltschko and Wiltschko 1972; Quinn et al. 1981; Burda et al. 1990; Lohmann 1991; Lohmann and Lohmann 1993; Deutschlander et al. 1999, 2003; Holland et al. 2006; Diego-Rasilla et al. 2010, 2013; Shakhparonov and Ogurtsov 2017), but apparently absent in humans (Chernetsov et al. 2021; but see Wang et al. 2019), remains most mysterious, since its biophysical and neurophysiological mechanisms are

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still not known with certainty. The most studied aspects of magnetoreception are those related to the magnetic compass systems of migratory animals, notably birds (Wiltschko and Wiltschko 2015, 2019). In particular, the magnetic compass of migratory birds is shown to be light-dependent (Wiltschko and Wiltschko 2001; Muheim et al. 2002) and is believed to be placed in eyes (Ritz et al. 2000). This hypothesis is corroborated by electrophysiological (Astakhova et al. 2020; Rotov et al. 2022) and neurophysiological (Heyers et al. 2007) data. Radical pair photochemical reactions in a photosensitive protein cryptochrome were proposed as the biophysical basis of the light-dependent compass (Ritz et al. 2000). A recent study demonstrated *in vitro* that the modification of the cryptochrome Cry4a expressed in birds' eyes is sensitive to magnetic fields, and that this sensitivity varies among studied bird species, being the highest for the migratory bird, the European robin (Xu et al. 2021).

A most unusual feature of avian magnetic compass is its sensitivity to weak oscillating magnetic fields (OMFs) in the radiofrequency range (the effect of OMF with frequencies from 0.4 to 85 MHz has been reported so far) (Ritz et al. 2004, 2009; Thalau et al. 2005; Engels et al. 2014; Pakhomov et al. 2017; Kobylkov et al. 2019; Leberecht et al. 2022). OMFs with amplitudes more than three orders of magnitude weaker than the static geomagnetic field disrupt the bird's compass. The compass sensitivity to both monochromatic, single-frequency OMF (Ritz et al. 2004, 2009; Thalau et al. 2005; Pakhomov et al. 2017) and broadband magnetic noise (Ritz et al. 2004; Engels et al. 2014; Leberecht et al. 2022) has been demonstrated.

The OMF effect finds its qualitative explanation within the radical-pair model of avian compass, as a result of spin resonance of electrons forming the radical pair (Hiscock et al. 2017). It should be noted, however, that the radical pair model did not so far succeed in reproducing the outstanding sensitivity of the bird compass to OMF (Kavokin 2009; Hiscock et al. 2017); in experiments, magnetic orientation of birds is disrupted by OMFs two orders of magnitude weaker than the theoretical estimations suggest. An unknown amplification mechanism might be involved (Hiscock et al. 2017), but so far no plausible model of such an internal amplifier has been proposed (see Kavokin 2017). Moreover, OMF applied locally to the eyes of garden warblers did not disrupt their magnetic orientation, while OMF of similar amplitude applied to the whole bodies of the birds did (Bojarinova et al. 2020). This latter result might hint to the existence of a separate receptor of OMF, aimed at detection of magnetic perturbations of solar or atmospheric origin (Kirschvink 2014; Granger et al. 2022).

Assuming nevertheless, for lack of better explanation, that the OMF effect is related to radical pair reaction in cryptochrome, one can suggest that sensitivity of an avian species to the OMF is determined by the species-specific

form of the cryptochrome. If this is the case, it is likely that the sensitivity of the cryptochrome to the OMF is positively correlated with its sensitivity to static fields. Indeed, both values are largely determined by the coherence conservation time in the radical pair, as well as by the structure of hyperfine interactions of the electrons involved. If the parameters of the cryptochrome molecule are fine-tuned so that the electron spins are easily affected by static fields, one can expect that they will be also easily perturbed by oscillating fields. According to Xu et al. (2021), the cryptochrome of the European robin demonstrates higher sensitivity to static magnetic fields than cryptochromes of non-migratory birds, namely chicken and pigeons.

If now we look at the available data on OMF effects, we find that most of the results were obtained in European robins, with no data on non-migratory birds suitable for comparison. However, single-frequency OMF effect in another songbird migrant, the garden warbler, was studied in detail (Kavokin et al. 2014; Pakhomov et al. 2017). Garden warblers failed to show the seasonally appropriate orientation if subjected to the 1.4 MHz OMF (the Larmor frequency of the free electron spin in the geomagnetic field at the experimental location in Rybachy, Eastern Baltic) as weak as 1 nT (Pakhomov et al. 2017). The sensitivity threshold, obtained from the value of average length of orientation vector, is somewhat higher, between 2 and 3 nT. To compare, European robins were disoriented by 15 nT OMF at 1.315 MHz (the Larmor frequency of the free electron spin in the geomagnetic field at the experimental location in Frankfurt), while 5 nT at the same frequency showed no effect (Ritz et al. 2009). Having in mind that garden warblers are long-distance migrants, migrating from Europe and West Siberia to equatorial Africa, while European robins migrate within Europe, one could conclude that higher sensitivity of garden warblers to OMF correlates with supposedly finer tuning of its magnetic compass, needed for long-distance navigation (Pakhomov et al. 2017).

In this work, we study the OMF effect on the magnetic orientation of another long-distance migrant, the pied flycatcher. The experiments were performed at the same location and conditions as for the garden warbler, which makes possible a direct comparison of the OMF effect for these two species. Unexpectedly, we find that the sensitivity threshold of the pied flycatcher to the 1.4 MHz OMF is not only much higher than in the garden warbler, but exceeds also the corresponding threshold in the short-distance migrant, the European robin. This finding confirms high variability of the OMF sensitivity among migratory bird species, and puts into question its correlation with the performance of the magnetic compass in different birds.

Materials and methods

Study site and bird keeping

We performed orientation tests in autumn 2021 and 2022 with pied flycatchers (*Ficedula hypoleuca*) captured during their first migration on the Courish Spit (Kaliningrad region, Russia; 55°09'N, 20°52'E). Experimental birds ($n=20$ in 2021, captured on August 18–September 2 and $n=17$ in 2022, captured on August 8–18) were kept in an outdoor aviary in individual cages; they experienced natural photoperiod, natural geomagnetic field and had access to astronomic orientation cues (sun, sunset polarization patterns and stars) during their time in captivity. They were provided with food (mealworms *Tenebrio molitor*, a homemade mix of mashed boiled eggs with grated carrots, Padovan complete feed for insect-eating birds) and water ad libitum. The aviary was equipped with online infrared video cameras, and only those birds which exhibited migratory restlessness in a given night were selected for experiments.

Experimental conditions and setup

All experiments in the natural magnetic field (NMF) and radiofrequency OMF were performed outdoors on wooden tables placed in the clearing of reeds on the coast of the Courish Lagoon. In 2021, we performed two series of experiment. In the first series of tests, migratory orientation of pied flycatchers was studied in NMF in aluminium Emlen funnels (Emlen and Emlen 1966) (top diameter 350 mm, bottom diameter 100 mm, slope 45°) under simulated total overcast. On top of Emlen funnels, we put lids made of milk glass which completely obscured stars and any other patterns. Thus, the only orientation cue available to experimental birds during the test was the geomagnetic field. This experimental arrangement was used previously to study magnetic orientation of birds (e.g. Kavokin et al. 2014; Pakhomov et al. 2017).

In the second series of tests, the same birds were tested in radiofrequency OMF with the amplitude 17 nT and frequency 1.41 MHz (matching the Larmor frequency of a freestanding electrons spin in the local NMF of 50,400 nT). The birds were tested in the OMF in similar Emlen funnels but made of plastic (a dielectric material, which does not screen the OMF (Pakhomov et al. 2017)). For this experiment, we used the equipment employed in our previous studies of the orientation of other species, the garden warblers, in the OMF (Kavokin et al. 2014; Pakhomov et al. 2017). The field was created by single-loop coils 0.75 m in diameter, fed from a commercial stabilized

high-frequency generator Rigol DG4162 (Rigol Technologies Inc., Beaverton, USA) through a 50 Ohm coaxial cable. The generator was placed in a wooden cabin in 15 m along the straight line from the centre of a clearing in reeds, where three wooden tables were build. This ensured that the acoustic noise from the generator was not discernible over the background of natural noises. Four coils were installed on each table. Coils on each table were connected in parallel by small lengths of coaxial cable to a resistive voltage divider that impedance-matched the coils to the main radiofrequency cable. This assembly could provide the OMF with the amplitude up to 17 nT at the centre of each coil at the frequency of 1.41 MHz. The details of the OMF frequency spectrum are given in (Pakhomov et al. 2017). One side of the coil was raised above the table top to increase the angle between OMF and NMF, which as a result was approximately 30°. Emlen funnels were placed on tables, one in the centre of each coil. The parameters of the OMF were controlled before and after each test. To this end, we used a 25 cm loop antenna, connected to a digital storage oscilloscope Tektronix TPS 2012B (Tektronix Inc., USA). The tests were performed under milky glass, so that experimental birds had no access to astronomic orientation cues.

In 2022, we performed three series of experiment: in the NMF, radiofrequency OMF with the amplitude 190 nT and frequency 1.41 MHz, and in NMF with reverse vertical component of the magnetic field.

The birds were tested in the OMF in Emlen plastic funnels similar to those used in 2021. To apply higher amplitudes of OMF, we used 16 two-loop coils 75 cm in diameter, fed by radiofrequency current from 16 custom-made broadband amplifiers. There were 4 coils on each table, each fed from its own amplifier. The amplifiers were mounted in aluminium boxes (4 in each box), placed under each of the 4 experimental tables and received 1.41 MHz sinusoidal input signals through coaxial cables from 4 output channels of 2 function generators placed in the cabin 15 m apart. The 18 V DC power to the amplifiers was delivered through a cable from a power supply placed in the same cabin as the generators. Other details of testing in NMF and OMF were the same as in 2021.

The experiments with reversed vertical component of NMF were performed in a set of Merritt magnetic coils described in detail in (Kirschvink 1992). The coils were installed at the same location in the clearing of reeds and fed from a current-stabilized DC power supply. Up to 8 Emlen funnels were placed on a table in the inner space of the set of magnetic coils. The components of the static magnetic field inside the magnetic coils were measured with a fluxgate magnetometer (FVM-400, Meda, Dulles, VA, US) before and after each test.

Orientation tests and data analysis

Orientation tests were carried out within a period of 8 days in 2021 (September 15–September 21) and within the period of 25 days in 2022 (August 24–September 17). The tests started at the beginning of astronomical twilight. Experimental birds were transferred from their cages to the Emlen funnels in individual opaque textile bags. The directionality of the birds' activity was recorded as scratches left by their claws as they hopped in the funnels on a print film covered with a dried mixture of whiting and glue. Every test day consisted of two rounds of the same experimental condition with only the position of the funnel on the experimental table changed between rounds for each bird. After the second test, the birds were brought back to their housing cages. After every experimental round, the scratch papers were collected; then, if necessary, new pieces of scratch paper were put in funnels, for another round. Each test lasted for 25–30 min, two tests with one bird per night. After 2 nights of tests, the birds had a rest for 1–3 days. Each bird was tested in every trial at least twice (except one bird that escaped after the first test in OMF in 2021; Tables S1, S2, S3, S4).

From three to four researchers (JB, DS, AF, A. Prokshina and AP) independently determined each bird's mean direction from the distribution of scratches. The mean of the directions determined by observers was recorded as the orientation result. In most cases, the mean direction could be very precisely identified using the simple visual estimation method (Mouritsen and Larsen 1998). If at least two observers considered the scratches to be randomly distributed or if the two mean directions deviated by more than 30°, then the bird was considered to be not oriented in the given test. If a pattern of scratches was not clear, the number of scratches in each of $36 \times 10^\circ$ sectors were counted. Then we used circular statistics software to assess the directionality based on the numbers of scratches. If the number of scratches was fewer than 40 scratches, the bird was considered to be inactive

in a given test. The total number of tests in a trial was 76 and 77 in 2021 and from 98 to 108 in 2022. The percent of tests eliminated as non oriented varied from 30 to 43% in different trials (Table S5). To minimize observers bias, blinded method was used when the data were analysed: the final decision was made by AP who was not aware which experimental condition was realized in each specific test. For group direction analysis, to avoid pseudoreplication, we used mean direction of each bird obtained during all days. If bird showed two directions in one night, we also averaged these two angles.

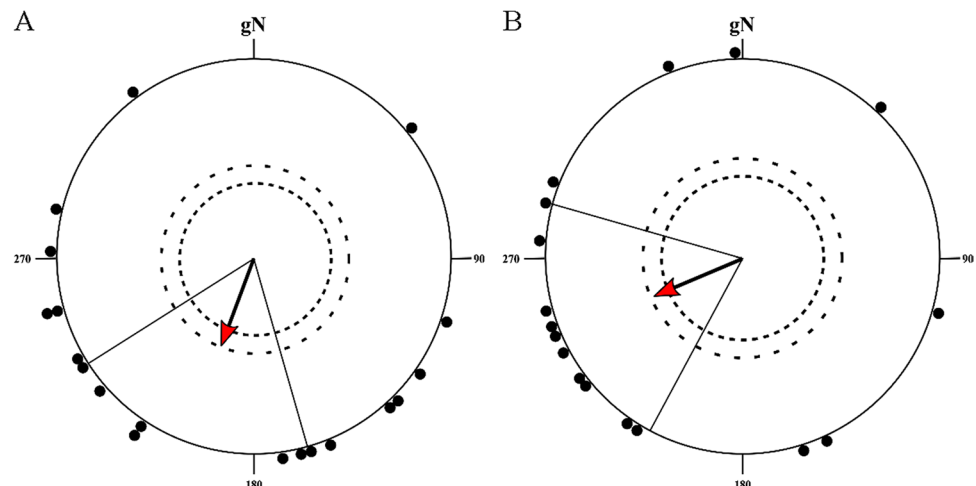
Statistical tests were performed with ORIANA (Kovach Computing Services, v. 4.0). The differences in mean orientation direction between experimental groups were tested by the nonparametric Mardia-Watson-Wheeler (MWW) test.

Results

Pied flycatchers tested in the NMF in 2021 were oriented in the seasonally appropriate migratory direction ($\alpha = 201^\circ$, $r = 0.47$, $n = 19$, $P = 0.014$, 95% CI = 164° – 238° , Fig. 1A). The mean direction of birds obtained in the control tests was similar to the mean autumn migratory direction of the same species ($\alpha = 211^\circ$, $r = 0.82$, $n = 10$, $P < < 0.001$, 95% CI = 185° – 238°), according to recoveries of birds ringed on the Courish Spit (Bolshakov et al. 2001) and unpublished data of the Biological Station Rybachy. This result was also similar to the data obtained in previous experiments in pied flycatchers outdoors, with full access to celestial cues (Kishkinev et al. 2006; Pakhomov et al. 2022), as well as indoors (Zolotareva et al. 2021).

The same birds, subjected to 17 nT OMF created by stationary coils, were also significantly oriented ($\alpha = 248^\circ$, $r = 0.47$, $n = 17$, $P = 0.022$, 95% CI = 209° – 286° , Fig. 1B). This direction was not significantly different from the one

Fig. 1 Orientation of pied flycatchers in 2021: **A** in the natural geomagnetic field (NMF); **B** in 17 nT OMF. Dots show mean directions of individual birds in each experimental condition. Arrows show the second-order mean of the group of birds in each condition. The inner and outer dashed circles indicate 5% and 1% significance level of the Rayleigh test, respectively. Radial lines indicate 95% CI



that the same birds showed in the control experiments (MWW test: $W = 1.83$, $P = 0.4$).

Both in NMF and OMF tests, there were birds that showed opposite direction in two sequential tests in one night or in two nights (the difference between two directions was $175\text{--}180^\circ$) (Table S1). When we omitted such cases from the analysis, the result did not change: in both trials birds showed the seasonally appropriate migratory directions (NMF: $\alpha = 213^\circ$, $r = 0.48$, $n = 16$, $P = 0.024$, 95% CI = $174^\circ\text{--}252^\circ$; OMF: $\alpha = 240^\circ$, $r = 0.51$, $n = 15$, $P = 0.017$, 95% CI = $200^\circ\text{--}279^\circ$). No statistically significant difference was found between these directions (MWW test: $W = 0.12$, $P = 0.94$) (see Supplementary Materials Fig. S1).

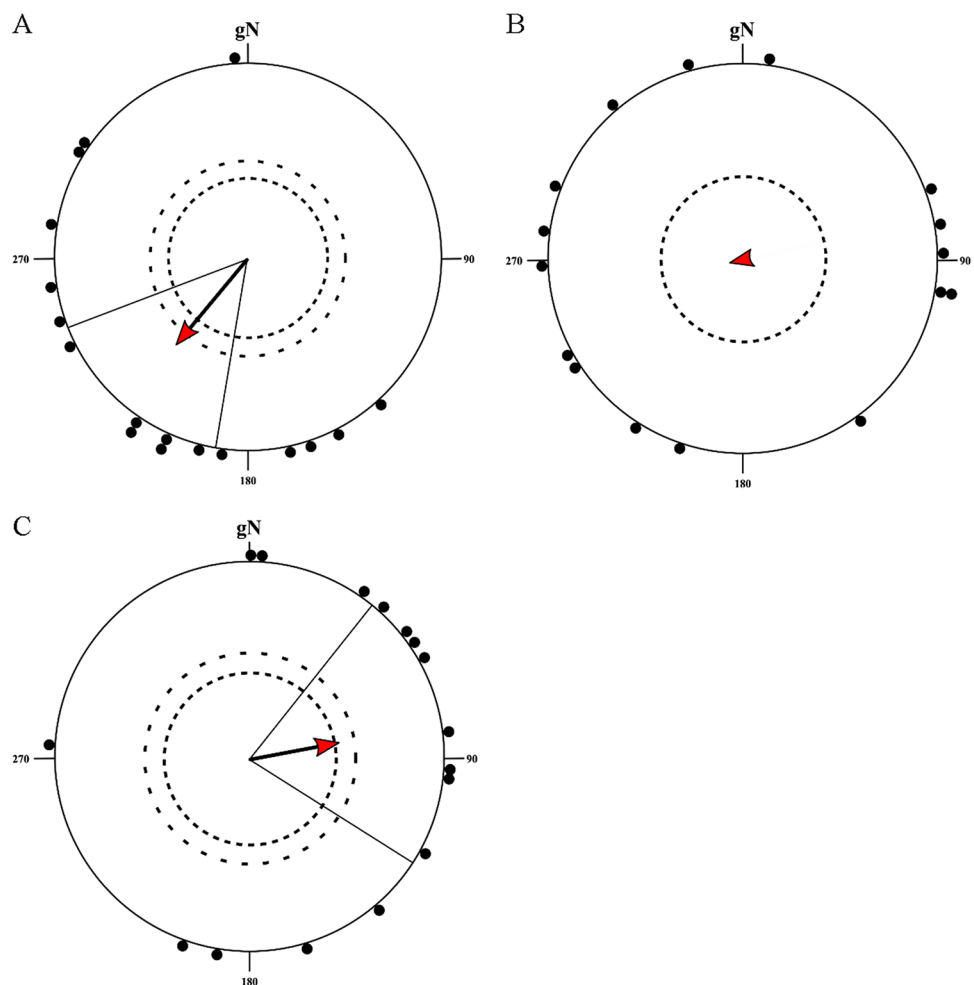
Pied flycatchers tested in NMF in 2022 (as in 2021) were oriented in the seasonally appropriate migratory direction ($\alpha = 220^\circ$, $r = 0.58$, $n = 17$, $P = 0.002$, 95% CI = $189^\circ\text{--}249^\circ$; Fig. 2A). The mean directions of birds obtained in the control tests in different years did not differ significantly (MWW test: $W = 0.63$, $P = 0.73$). The same birds subjected to 190 nT OMF by stationary coils were disoriented ($\alpha = 259^\circ$, $r = 0.05$, $n = 16$, $P = 0.96$; Fig. 2B).

When subjected to magnetic field with the vertical component reversed, the mean direction of this group was changed from SW to the NNE ($\alpha = 80^\circ$, $r = 0.45$, $n = 16$, $P = 0.038$, 95% CI = $38^\circ\text{--}122^\circ$; Fig. 2C). In this trial, one bird showed opposite direction in two nights (the difference between two directions was $175\text{--}180^\circ$; Table S4). With this case omitted, the result did not change ($\alpha = 86^\circ$, $r = 0.43$, $n = 15$, $P = 0.06$). The mean direction in this trial differed significantly from the mean direction they showed in the NMF (MWW test: $W = 12.56$, $P = 0.002$).

Discussion

Migratory orientation of pied flycatchers demonstrates the fundamental features of the light-dependent inclination compass of birds. First, it provides seasonally appropriate orientation in both spring and autumn at our location (Zolotareva et al. 2021; Pakhomov et al. 2022). Second, it is disrupted by OMF (in our case with the amplitude of 190 nT). Third, it can be reversed by reversing the vertical component of the local static field (this was first shown in indoor

Fig. 2 Orientation of pied flycatchers in 2022: **A** in the natural geomagnetic field (NMF); **B** in 190 nT OMF; **C** in trial with the sign of vertical component of the local static field reversed. Dots show mean directions of individual birds in each experimental condition. Arrows show the second-order mean of the group of birds in each condition. The inner and outer dashed circles indicate 5% and 1% significance level of the Rayleigh test, respectively. Radial lines indicate 95% CI



experiments in Frankfurt (Beck and Wiltschko 1982) and confirmed in this study for our location and experimental conditions). These results rule out other potential origins of the observed orientation behaviour, e.g. the fixed direction response observed in the European robin (Wiltschko et al. 2010). However, the OMF with the amplitude of 17 nT was not sufficient to disrupt the magnetic orientation of our pied flycatchers. This is in a stark contrast with garden warblers that were disoriented by OMF with the amplitude of just 1 nT in our earlier experiments (Pakhomov et al. 2017).

We conclude that the effect of OMF on the magnetic compass orientation of pied flycatchers and garden warblers is strongly different. Pied flycatchers turn out to be at least one order of magnitude less sensitive to OMF than garden warblers. Since the experiments with these two species were performed at exactly the same location, under the same conditions (including the OMF frequency spectrum, equipment, time of the year and of the day) and by the same team of researchers, this conclusion indeed seems to be robust.

One can also compare the OMF effect on orientation of pied flycatchers and garden warblers with that observed earlier in European robins, for which the sensitivity to single-frequency OMF was also studied (Thalau et al. 2005; Ritz et al. 2009). This comparison is not that direct, because European robin was studied at a different location (Frankfurt) and different migration season (simulated spring migration in winter) (Thalau et al. 2005). Also, the OMF frequency was slightly different (1.3 MHz vs. 1.4 MHz in our studies), because it was chosen to match the Larmor frequency of a free electron spin in the geomagnetic field in Frankfurt. The question of the so-called Zeeman resonance at the Larmor frequency was hotly debated in the literature on the OMF effect (Ritz et al. 2009; Engels et al. 2014; Hiscock et al. 2017); for the purpose of comparison with our results, it is important that the Larmor frequency was matched for all three species (the European robin, pied flycatcher and garden warbler), while the variation of absorption within broad spectral bands defined by hyperfine interactions is not expected to be large between 1.3 and 1.4 MHz (Hiscock et al. 2017; Leberecht et al. 2022). For this reason, we believe that the OMF effect in European robins can be compared with that in garden warblers and pied flycatchers, but one has to keep in mind that conditions in that case were not exactly identical.

At present, we have no clear explanation of such differences between these species. Below, we discuss several possibilities, based on suggestions expressed in the literature on bird orientation and migration and related to this subject.

As mentioned in the “Introduction” section, the biophysics and sensory physiology of the OMF effect are not yet crystal clear, since the mainstream radical-pair model does not provide a quantitative account for the strength of the effect. Nevertheless, recent results of *in vitro* studies

of cryptochrome modifications from different bird species (Xu et al. 2021) suggest that properties of the cryptochrome molecule related to its role in magnetoreception can vary from species to species. Moreover, cryptochromes from non-migratory birds were found to be less sensitive to static magnetic fields than those of migrants. Assuming that the OMF directly affects cryptochrome molecules involved in compass magnetoreception, one may expect that sensitivity to OMF may be correlated to the migration pattern of a particular species: long-distance migrants should have a different (presumably higher) sensitivity to OMF as compared to non-migratory species and short-distance migrants (Pakhomov et al. 2017). Since the avian magnetic compass is not sensitive to the polarity of the geomagnetic field and relies on its inclination (Wiltschko and Wiltschko 1972), magnetic orientation of migratory birds near the magnetic equator, where the inclination is close to zero, is challenging (Schwarze et al. 2016). One can suppose that using magnetic compass at inclination angles close to zero requires better sensitivity of the compass receptor. Since effects of static and oscillating magnetic fields on radical-pair reactions depend on the same factors (spin decoherence and hyperfine interactions), higher sensitivity of the cryptochrome-based receptor would, hypothetically, also make it more vulnerable to OMF.

An alternative interpretation of the OMF effect (Kirschvink 2014; Bojarinova et al. 2020) invokes an additional sensory system aimed at detection of the environmental magnetic noise. As suggested by Kirschvink (2014), this system blocks the magnetic compass when a magnetic storm may compromise its precision, so that birds might either wait until the magnetic storm is over or use another compass system. European robins were experimentally shown to reduce nocturnal migratory restlessness in response to simulated solar storms (Bianco et al. 2019). At the same time, robins increased their activity during early morning. The authors suggested that robins reduced activity at night when the perception of magnetic information would be strongly disrupted by temporal variations of the magnetic field, to extend their migration during daytime when several visual cues become available for orientation. The other two species studied, chiffchaff *Phylloscopus collybita* and dunnock *Prunella modularis*, showed low or no nocturnal migratory activity and did not respond to solar storms by changing their activity level (Bianco et al. 2019). A recent study (Granger et al. 2022) demonstrated that high-frequency magnetic perturbations, capable of producing the OMF effect in birds, result mainly not from solar flares, but from atmospheric sources, i.e. lightnings. Correspondingly, they are concentrated mainly in the geographic areas where thunderstorms are frequent and powerful, that is, in the tropics (Granger et al. 2022). One can therefore suggest that higher sensitivity of the

specialized OMF receptor (if existing) should be evolutionary favoured in the species whose migration routes cross tropical regions.

Summarising the above considerations, we would expect the following factors to influence the sensitivity of the magnetic compass system of an avian migrant to perturbation by OMF: overall length of the migration route; flying near the magnetic equator or crossing it; crossing tropical regions with frequent thunderstorms.

Looking into the migration ecology of the three species, we see an obvious difference between long-distance migrants, the pied flycatcher and the garden warbler, wintering in Africa around the magnetic equator (Cramp and Brooks 1992; Cramp et al. 1993) or even south of it, and the European robin. The latter species winters mainly in southern Europe, occasionally crossing the Mediterranean, never crosses the Sahara and never enters the tropical regions (Cramp 1988). One can see, however, that among the three species, the difference in the OMF sensitivity is the largest between the two long-distance migrants, the pied flycatcher and garden warbler. The sensitivity of the medium-distance migrant, the European robin, is higher than that of the pied flycatcher but lower than that of the garden warbler. This fact apparently does not support the idea of correlation between the aforementioned factors and the sensitivity to OMF.

Furthermore, different species of avian migrants may rely on different compass systems to a varying degree (Chernetsov 2015; Pakhomov and Chernetsov 2020). Results of some cue-conflict studies indicate that garden warblers and European robins prefer certain compass systems in direct cue-conflict (the 120° clockwise rotated magnetic field with a view of the clear natural night sky) during orientation tests (Wiltschko and Wiltschko 1975a, b). Garden warblers changed their orientation according to the rotation of the magnetic field, despite contradicting information from the stars (Wiltschko and Wiltschko 1975b). European robins, in contrast, did not respond to a deflection of the horizontal component of the magnetic field and used their stellar compass as the main compass system (Wiltschko and Wiltschko 1975a, b). It was shown that astronomical cues (the sun and stars) dominate over the magnetic field in pied flycatchers (Giunchi et al. 2015; but see Pakhomov et al. 2022). To summarize, these studies suggested that in garden warblers, the magnetic compass is of higher priority compared to other two species studied. Having this in mind, we could speculate that the highest sensitivity to OMF in the garden warbler is connected with the fact that this species relies mainly on its magnetic compass and therefore needs to detect high-frequency magnetic perturbations that occur naturally.

We should stress that the above list of possible reasons is by no means exhaustive; moreover, it might happen that neither of the discussed is related to the observed differences. Finally, there remains a possibility that the inter-species

variability of the sensitivity of bird compass systems to OMF does not possess any adaptive significance.

In conclusion, we find that the pied flycatcher has the lowest sensitivity to oscillating magnetic field with respect to its effect on the orientation by geomagnetic field, among all three migratory bird species studied so far. The difference in OMF amplitudes tolerated by magnetic compasses of the pied flycatcher and the garden warbler exceeds an order of magnitude. The reason for such strong a variability is not obvious. It might be related to the biophysics of the magnetic compass, to ecological adaptations, or both. Further research is needed to find the explanation to this unusual feature of the magnetic navigation system of migratory birds.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s00265-022-03282-7>.

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Author contribution JB, KK and NC conceived the research; RC developed the RF system; RC, KK, DS and AP installed the equipment and provided technical support for experiments, JB, KK, DS, AF and AP performed orientation tests and analysed the data; JB, KK, AP and NC wrote the paper. All authors commented on the manuscript. All authors gave final approval for publication and agree to be held accountable for the work performed therein.

Data availability The data analyzed in this study are available in Table S1, S2, S3, S4.

Declarations

Ethics approval All animal procedures (in this case, capture of the birds and simple, non-invasive, behavioural experiments) were approved by the appropriate authorities: Permit 24/2018–06 by Kaliningrad Regional Agency for Protection, Reproduction and Use of Animal World and Forests; and Permit 6–2021 by the Bioethics Committee of Sechenov Institute of Evolutionary Physiology and Biochemistry RAS. All experiments were performed in accordance with relevant guidelines and regulations. The birds were released back into the wild after all experiments had been completed.

Competing interests The authors declare no competing interests.

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