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Extremely Low-Frequency Electromagnetic Fields Entrain Locust Wingbeats

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Extremely low-frequency electromagnetic fields (ELF EMFs) have been shown to impact the behavior and physiology of insects. Recent studies have highlighted the need for more research to determine more specifically how they affect flying insects. Here, we ask how locust flight is affected by acute exposure to 50 Hz EMFs. We analyzed the flights of individual locusts tethered between a pair of copper wire coils generating EMFs of various frequency using high-speed video recording. The mean wingbeat frequency of tethered locusts was 18.92 ± 0.27 Hz. We found that acute exposure to 50 Hz EMFs significantly increased absolute change in wingbeat frequency in a field strength-dependent manner, with greater field strengths causing greater changes in wingbeat frequency. The effect of EMFs on wingbeat frequency depended on the initial wingbeat frequency of a locust, with locusts flying at a frequency lower than 20 Hz increasing their wingbeat frequency, while locusts flying with a wingbeat frequency higher than 20 Hz decreasing their wingbeat frequency. During the application of 50 Hz EMF, the wingbeat frequency was entrained to a 2:5 ratio (two wingbeat cycles to five EMF cycles) of the applied EMF. We then applied a range of ELF EMFs that were close to normal wingbeat frequency and found that locusts entrained to the exact frequency of the applied EMF. These results show that exposure to ELF EMFs lead to small but significant changes in wingbeat frequency in locusts. We discuss the biological implications of the coordination of insect flight in response to electromagnetic stimuli. © 2021 Bioelectromagnetics Society.

Keywords: entrainment; flight; wingbeat; ELF electromagnetic fields; grasshopper

INTRODUCTION

Exposure to extremely low-frequency electromagnetic fields (ELF EMFs) has increased dramatically in the last half-century [Belpomme et al., 2018]. There is growing evidence to show that ELF EMFs emitted from anthropogenic sources can have biological effects on organisms with ecological implications. Pellacani and Costa [2018] describe the range of biological effects that ELF EMF pollution causes, including neurological effects that underpin behavioral processes in a variety of organisms. In addition, ELF EMFs can have profound effects on the behavior and cognition of insects [Maliszewska et al., 2018; Shepherd et al., 2018, 2019]. Important pollinator species, such as honeybees, use low-strength magnetic fields as cues for foraging [Chicas-Mosier et al., 2020]. Exposure to 50 Hz EMFs, at levels honeybees may encounter from overhead powerlines in the environment, reduces learning, aggression, and foraging flight [Shepherd et al., 2018, 2019]. Fifty-hertz electric fields (EFs) have

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Conflicts of interest: None.

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also been shown to increase the activities of antioxidant systems in honeybees, including proteolytic and superoxide dismutase (SOD) systems [Migdał et al., 2020]. Moreover, in locusts, walking behavior and motor neuron signaling are also compromised during exposure to 50 Hz EMFs [Wyszkowska et al., 2016]. Taken together, these effects have led to calls for more studies on anthropogenic electromagnetic radiation and its effects on insects (including pollinators and insect models), as well as the identification of key knowledge gaps in this field to improve our understanding of the effects of EMFs in the environment [Vanbergen et al., 2019].

For many insects, flight is a key component of their behavioral repertoire and underlies not only their foraging activity but also the remarkable large-scale migrations shown by some insects such as the monarch butterfly (see review by Reppert and de Roode [2018]), and swarming activity shown in locusts [Kennedy, 1951]. In addition to the effects of anthropogenic EMFs, Bergh [1979] suggested that low-frequency EMFs caused by storms increased the take-off rate of locusts that initiate flights. Ramchandra Rao [1942] found that locusts became active and increased their flying behavior in the time leading up to a dust storm, and Clark [1969] observed increased flight activity in locusts during storm activity. Thunderstorms are known to generate ELF EMFs [WHO, 2007]; however, the fields from these storms, known as Schumann Resonances, are relatively weak in comparison to the fields generated by high-voltage transmission lines (HVTLs) [WHO, 2007]. Nevertheless, these ELF EMFs give rise to signals that can be detected thousands of kilometers away [Reiter, 1960]. Bergh [1979] suggested that locust responses to ELF EMFs from storms could be advantageous by increasing dispersal and convergence in habitats with moist sand for successful egg-laying, leading to improved reproductive success.

Flight behavior has been intensively studied in many insects, and in locusts in particular, making the locust an ideal model system in which to analyze the effects of low-frequency EMF exposure on flight. The flight motor pattern in locusts was one of the first to be identified as being mediated by a central pattern generator [Wilson, 1968]. We know, in exquisite detail, the different components of the neural networks that form the flight motor pattern, from the sensory neurons that detect wing movements [Pearson et al., 1983; Pearson and Wolf, 1988], to the interneurons responsible for generating the flight rhythm [Robertson and Pearson, 1984], through to the motor neurons responsible for activating the multitude of muscles responsible for generating the oscillatory movements of the two pairs of wings [Robertson and Pearson, 1984].

The entrainment of oscillatory motor activity by external inputs is found throughout the animal kingdom [Wilson and Cook, 2016], including the flight motor pattern of locusts [Schmelling et al., 2010]. In fireflies, for example, flashing by males can be synchronized to the flashing of other males [Buck, 1988], while the swimmeret rhythm of crayfish can be entrained to a rhythmical mechanical movement of a number of other swimmerets [Deller and MacMillan, 1989]. In many bird species, there is a coordination between wingbeats and respiration, which is thought to confer an energetic advantage [Funk et al., 1997]. A number of studies have also shown that the wing movements of locusts can synchronize to repetitive visual inputs (light flashes, [Waldron, 1968; Schmelling et al., 2010]) and also to the wing movements of other locusts in a swarm [Kutsch et al., 1994; Camhi et al., 1995]. The latter had been shown to be due to a wake of turbulent air produced by other locusts, which again is thought to provide an aerodynamic advantage.

We know from recent studies on the effects of ELF EMF pollution on honeybees that their foraging activity is affected by ELF EMFs [Shepherd et al., 2018], but it is not clear whether the EMF affects flight activity per se, or whether it led to avoidance behavior by the bees. Understanding the effects of EMF pollution on free-flying insects represents many technical challenges, so here we ask how the oscillatory wing movements of tethered locusts are affected by ELF EMFs and what the consequences are of changes in wingbeat frequency.

MATERIALS AND METHODS

Experiments were performed on adult desert locusts, *Schistocerca gregaria* (Forskål), aged from 4 days to approximately 9 days postmolt and of both sexes, taken from a crowded colony at the University of Southampton. Locusts were fed on seedling wheat and oats and housed under a 12:12 light/dark cycle at 32 °C.

Acute Exposure

EMFs were generated using a pair of custom-made 250 mm (inner diameter) Helmholtz coils. Each coil had a bifilar winding, i.e., a pair of wires wound together (350 turns). When connected with the current in the two wires in the same direction, the EMFs summed to produce the desired field strengths used in experiments. When the wires were connected with the

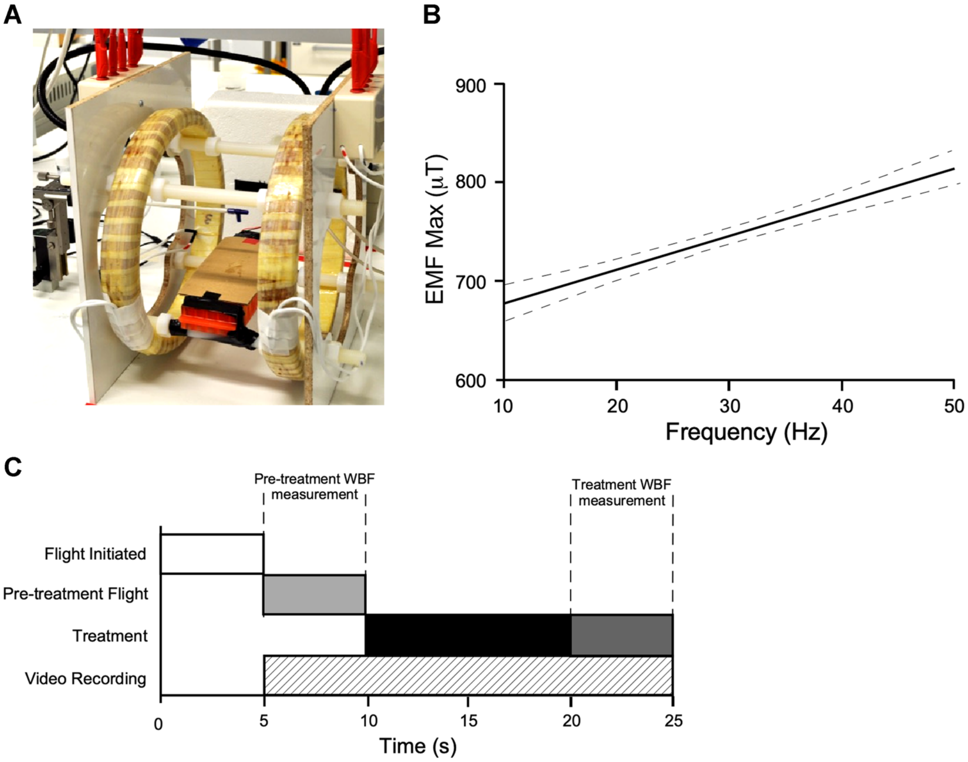

Fig. 1. (**A**) Custom-made Helmholtz coil used for generating homogenous sinusoidal AC electromagnetic fields. (**B**) Maximum EMF strength for each tested frequency using a power amplifier and function generator to power the Helmholtz coil. (**C**) Experimental timetable for analysis of the effect of ELF EMFs on wingbeat frequency. Five seconds were allowed for the initiation of consistent flight followed by 5 s of pretreatment flight to determine the baseline wingbeat frequency levels. EMF was then switched on (or control treatment initiated) for 15 s. The wingbeat frequency over the time period 10–15 s after initiation was used to determine treatment wingbeat frequency. High-speed video was triggered to record 20 s of flight data. ELF EMF = extremely low-frequency electromagnetic field.

current in the two wires in opposite directions, the fields canceled out and no net EMFs were generated to provide control exposures (0 μT). The coils, however, retained the same properties as when connected in the same direction to provide experimental fields. The coils were paired on the same axis, using an adjustable custom stand (Fig. 1A) 125 mm apart. Coils were powered with 240 V 50 Hz AC electricity through an RS Pro 1 Phase 1.2 kVA 1 Output 240 V Variac (890-2806; RS Components, Corby, UK) to generate 50 Hz sinusoidal ELF EMFs with a total range of field strength from 10 to 10,000 μT at the center. Fields were generated in an environmentally controlled insectary at 25 ± 1°C. With less than 15 s exposure, no heat was produced in the center of the coils during field generation. Field strength was also measured with a Model GM2 Magnetometer and high stability probe with a resolution of 1 μT (Alphalab, South Salt Lake, UT). The meter was calibrated to National Institute of Standards and Technology (NIST) standards with an accuracy of 1% at room temperature. Maps of the EMF produced by the coils at different applied voltages have been published elsewhere [Shepherd et al., 2018].

HVTLs operate at different voltages up to a maximum of 1150 kV. In the United Kingdom, the largest powerlines operate at 400 kV using Larger L6 pylons with ratings up to 4 kA per circuit and a minimum ground clearance of 7.6 m. In theory, this produces EMFs up to 100 μT at ground level directly beneath the conductor [WHO, 2007], depending on current loading and ground clearance. Using Ansys Electronic Desktop MAXWELL software, Shepherd et al. [2018] modeled the magnitude of the ELF EMFs around Larger L6 Pylon conductors using a current rating of 3.4 kA, and found the field at 1 cm from the conductor to be 3,000 μT, while at 10 cm to be 2,700 μT, and at 1 m below the lowest conductor to be

1,200 μT. For a 400 kV T-Pylon, the EMFs are higher. For reference, the average magnetic field 1 m above ground under a Pylon is 5–10 μT, and the maximum is 100 μT [WHO, 2007]. We, therefore, chose to use a range of EMFs that reflected those found in the environment of 0; 100; 700; 1,000; and 7,000 μT.

EMF Frequency Range

To analyze the effect of ELF EMF frequency on wingbeats, different EMF frequencies were generated using a custom-made sinusoidal function generator and a TPA power amplifier (HH Electronics, Cambridge, UK), allowing the frequency to be changed from 10 to 50 Hz. As field strength is dependent upon voltage and frequency, we selected test frequencies of 17, 20, and 22 Hz, at which we could vary the voltage to generate the same field strength of 700 μT at each test frequency (Fig. 1B).

Flight Responses

Male locusts were individually removed from the colony and fixed at the pronotum to a custom-made tether using resin-wax, made from a 50:50 w/w mixture of natural resin (Sigma-Aldrich, Dorset, UK) and beeswax (Sigma-Aldrich). Once harnessed, locusts were suspended in the center of the coils (Fig. 1A) and given a small paper ball (3 cm^3) to hold at rest. The flight was initiated by applying a constant warm airflow over the locust, stimulating hair sensilla on the head [Arbas, 1986], and removal of the ball [Wilson, 1961]. The airflow source (D5015 hairdryer; Remington, Middleton, WI) was placed 1.12 m in front of the Helmholtz coil, at a distance where EMFs generated by the hairdryer could not be detected using the magnetometer. The flight was recorded using a high-speed video camera (MotionScope 1000S; Redlake Imaging, CA) at 125 fps. After 15 s of consistent flight, EMF treatment was activated and high-speed video triggered (Fig. 1C) to store 5 s before EMF initiation (pretreatment) and 15 s after EMF initiation (treatment).

The 20 s high-speed video was analyzed frame-by-frame to determine wingbeat frequencies. To ensure analyses were conducted on a steady flight, we determined wingbeat frequency in the 5 s period before the initiation of EMF (pretreatment) and the 5 s period from 10 to 15 s following exposure (treatment). The effect of acute EMF exposure on the flight was determined by calculating the change in wingbeat frequency from pretreatment to treatment. The difference in locust wingbeat frequency from the applied magnetic field frequency was calculated and compared to pretreatment frequencies. One hundred and sixty-two locusts were used in all experiments analyzing wingbeat frequency, including 20 locusts per treatment (control, 100 μT; 1,000; and 7,000 μT) in the initial effects of EMF intensity on wingbeat frequency, 22 locusts in the 700 μT 50 Hz treatment as the TPA power amplifier positive control, and 21, 20, and 19 locusts in the 17, 20, and 22 Hz EMF frequency experiments, respectively.

Statistical Analysis

Statistical analyses were performed using SPSS (v.26; IBM, Endicott, NY) and GraphPad Prism (v.8.3.0; Graphpad Software, San Diego, CA). The acute effects of ELF EMF exposure at different treatment levels (control, 100 μT; 1,000 μT; and 7,000 μT) on the change in wingbeat frequency were analyzed using a Kruskall–Wallis test as the data failed the Brown–Forsythe test for equal variance ($P = 0.018$). To test the effects of these same ELF EMF levels on the absolute change in locust wingbeat frequency from pretreatment levels, a one-way analysis of variance (ANOVA) was used. Absolute change in wingbeat frequency was determined as the magnitude of the change in wingbeat frequency between the 5 s “pre-treatment” and 10–15 s “treatment” timepoints, regardless of the sign (positive or negative) of the change. To determine whether locusts synchronized to 20 Hz, the difference in locust wingbeat frequency from 20 Hz before and after treatment was calculated and analyzed in a two-way repeated-measures (RM) ANOVA, with timepoints as a repeated measure and EMF treatments as the main factor. An unpaired *t* test was used to compare the absolute change in wingbeat frequency between the control locusts and the TPA power amplifier control (700 μT 50 Hz). To determine whether locusts synchronized wingbeat frequency to different EMF frequencies, a two-way RM ANOVA was used to compare the difference in locust wingbeat frequency from the applied EMF frequency between pretreatment and 700 μT treatment, for each of the different EMF frequencies tested, with time point as a repeated measure.

EF Modeling

EMFs are composed of both electrical and magnetic components that form fields of force. The fields produced by HVTLs are dynamic and vary in intensity at 50 Hz [WHO, 2007]. In previous studies [Shepherd et al., 2018, 2019], we mapped the EMF generated by the coils and modeled the EMF generated around HVTLs [Shepherd et al., 2018]. Due to the small physical dimensions of the coils, using a meter to map the EF strength was inaccurate. We, therefore, chose to model the 50 Hz EFs generated by the coils using ANSYS Maxwell modeling software (ANSYS, Canonsburg, PA) to determine their potential contribution to the observed responses of locusts. ANSYS Maxwell modeling software is an industry-leading EMF simulation software for electromagnetic and electromechanical devices. With Maxwell, we used the electrostatic solver to precisely characterize the low-frequency EFs in three dimensions around the coils using finite element methods. Using the solver, the alternating electrical fields could be modeled as "quasi-static" fields to estimate their contribution to the effects on locust wingbeats.

Models were based on the physical properties and sizes of material in the coils that were 250 mm diameter and fixed 125 mm apart. The cross-section of a coil was 35 × 35 mm and the coils had two copper wires running in parallel (bifilar winding), each with 350 turns. The models were based on the voltages from the variac used to generate each EMF intensity and were 200 V for 7,000 µT; 43 V for 1,000 µT; 34 V for 700 µT; and 8 V for 100 µT.

RESULTS

Effects of EMF Strength on Wingbeat Frequency

The wingbeat frequencies of locusts tethered between the coils but not exposed to EMF were calculated from captured video images and ranged from 11 to 26 Hz. The mean wingbeat frequency of locusts in all control experiments was 18.92 ± 0.27 Hz ($n = 162$, mean ± standard error of the mean [SEM]) (Fig. 2A).

The effect of acute exposure of 50 Hz EMF on wingbeat frequency was determined for field strengths ranging from 0 (control); 100; 1,000; and 7,000 µT ($n = 20$ locusts for each treatment). Analysis of the change in wingbeat frequency revealed an effect of 50 Hz EMFs on wingbeat frequency compared to control (Fig. 2B), but the amount of change was not consistent across treatment levels (Kruskal–Wallis test: $H = 11.56$, $P = 0.009$). Locusts that were not exposed to 50 Hz EMFs exhibited a small median change in wingbeat frequency of -0.15 Hz (interquartile range: −0.88–1.15 Hz), which did not differ significantly from the −1.25 Hz (interquartile range: −3.35–0.23 Hz) change in wingbeat frequency of locusts exposed to 100 µT ELF EMFs (post hoc Dunn's Test: $P = 0.56$) or the 1.15 Hz (interquartile range: −2.83–2.80 Hz) change in wingbeat frequency of locusts exposed to 7,000 µT ELF EMFs (post hoc

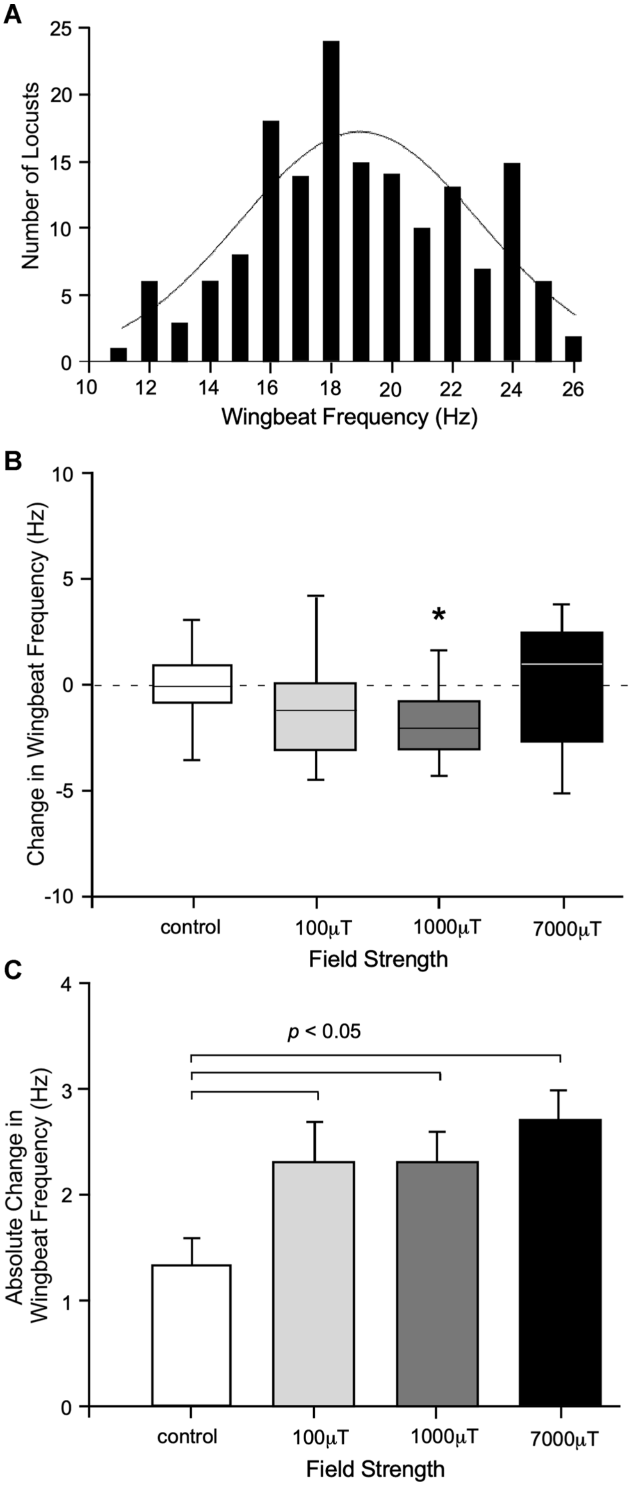

FIGURE 2 Continued.

Dunn's Test: $P > 0.99$). Locusts exposed to a 1,000 μT ELF EMF exhibited a change in wingbeat frequency of −2.20 Hz (interquartile range: −3.25–0.75 Hz), which was a small but significant decrease from the changes in wingbeat frequency exhibited by both control (post hoc Dunn's Test: $P = 0.02$) and 7,000 μT (post hoc Dunn's Test: $P = 0.03$) treated locusts.

Given the variation in responses at different EMF levels, the absolute change in wingbeat frequency from pretreatment levels was also analyzed. For all 50 Hz EMF exposures, there were changes in wingbeat frequency 15 s after treatment from pretreatment frequencies (Fig. 2C). For control locusts, the wingbeat frequency increased slightly by 1.3 ± 0.3 Hz (mean ± SEM) from pretreatment levels, and by 2.3 ± 0.4 Hz at 100 μT, 2.3 ± 0.3 Hz at 1000 μT, and 2.7 ± 0.3 Hz at 7,000 μT ($n = 20$ locusts per treatment) (Fig. 2C). A one-way ANOVA showed that 50 Hz EMFs significantly increased the absolute change in wingbeat frequency (ANOVA, $F_{3,76} = 3.857$, $P = 0.013$), and a Bonferroni post-hoc analysis revealed 7,000 μT exposure caused a significantly greater absolute change in wingbeat frequency from pretreatment than control levels (Bonferroni adjusted $P = 0.01$).

To understand why the effects of 50 Hz EMFs were evident when absolute changes in wingbeat frequency were examined, we plotted the changes that occurred in response to the exposure of the same individual locusts (Fig. 3A). For individuals exposed to 0 μT (control), there was no change in the mean wingbeat frequency following exposure and it remained the same at 19.3 ± 0.84 Hz ($n = 20$). For individuals exposed to 100 μT, however, the mean wingbeat frequency changed from 22.1 ± 0.78 Hz to 20.9 ± 0.50 Hz ($n = 20$). For individuals exposed to 1,000 μT, the mean wingbeat frequency changed from 21.8 ± 0.68 Hz to 19.9 ± 0.50 Hz ($n = 20$); while for individuals exposed to 7,000 μT, the mean wingbeat frequency changed from 19.1 ± 0.61 Hz to 19.3 ± 0.40 Hz ($n = 20$). The results suggest that when exposed to a 50 Hz EMF, there is a shift in wingbeat frequency toward 20 Hz.

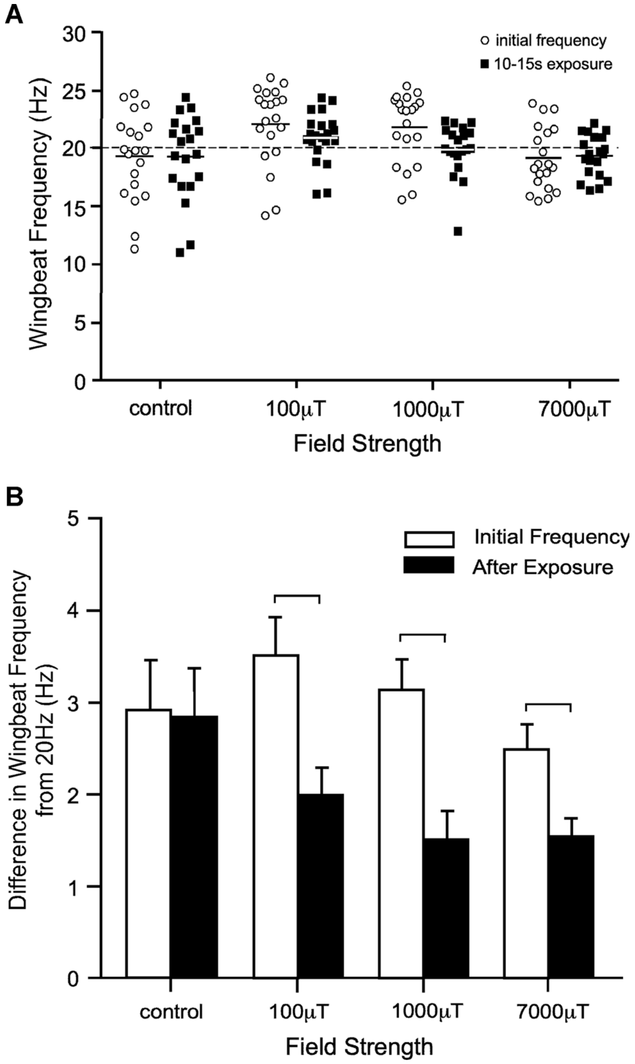

Fig. 3. Exposure to ELF EMF leads to shifts in wingbeat frequency. (**A**) Wingbeat frequencies of individuals before and after exposure to EMFs. Lines show the means for each exposure. For all EMF treatments, wingbeat frequency shifts toward 20 Hz. (**B**) Difference in wingbeat frequency of locusts from 20 Hz for all treatments. Mean and SEM are plotted. Exposure to EMF at all field strengths significantly reduces the difference in wingbeat frequency from 20 Hz, as indicated by horizontal lines above bars. ELF EMF = extremely low-frequency electromagnetic field; SEM = standard error of the mean.

Fig. 2. Effects of 50 Hz EMF on wingbeat frequency. (**A**) Distribution of wingbeat frequency of locusts under control conditions. The gray curve shows the Gaussian distribution with the same mean and standard deviation as the data. (**B**) Change in wingbeat frequency after 10–15 s of ELF EMF exposure. Centerlines of box plots show the median for each treatment. Boxes show interquartile range and whiskers show maximum and minimum values. There was no consistent effect of EMF strength on wingbeat frequency, although exposure to 1,000 μT showed a significant decrease compared with control (indicated by *). (**C**) Effects of acute exposure on the absolute change in wingbeat frequency from pretreatment levels. Mean and SEM change in wingbeat frequency are plotted for each field strength. Exposure to EMF leads to consistent significant increases in the absolute change in wingbeat frequency at all field strengths. ELF EMF = extremely low-frequency electromagnetic field; SEM = standard error of the mean.

To further analyze whether wingbeat frequency was entrained to 20 Hz, a subharmonic of 50 Hz EMF was applied to expose the locusts, and the difference in

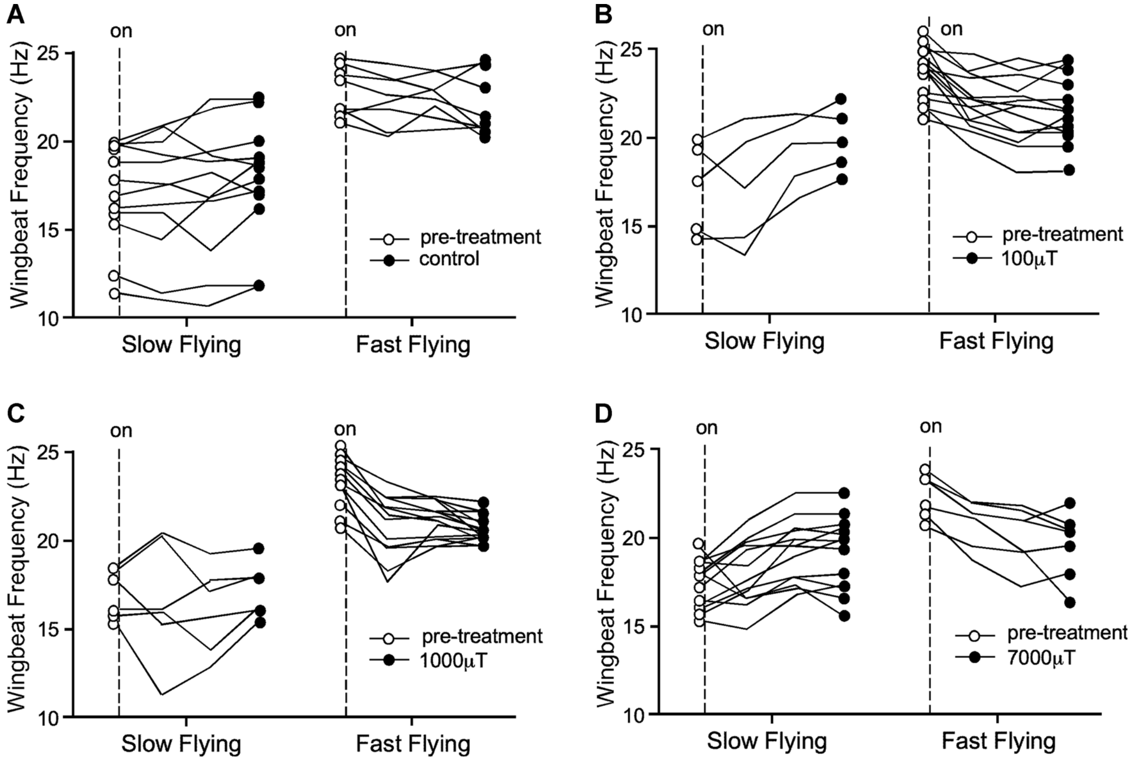

Fig. 4. Effects of 50 Hz EMF on the wingbeat frequencies of individual "slow-flying" (flying < 20 Hz before treatment) and "fast-flying" (flying > 20 Hz before treatment) locusts. Pretreatment (open circles) and treatment wingbeat frequencies (black circles) are shown. (**A**) exposure to 0 μT (control); (**B**) exposure to 100 μT; (**C**) exposure to 1,000 μT; and (**D**) exposure to 7,000 μT. EMF = electromagnetic field.

wingbeat frequency from 20 Hz was calculated (Fig. 3B). If wingbeat frequency entrains to 20 Hz, then locusts with wingbeat frequencies higher than 20 Hz would decrease their wingbeat frequency, while locusts with wingbeat frequencies lower than 20 Hz would increase their wingbeat frequency. For all EMF exposures, wingbeat frequency shifted toward 20 Hz (Fig. 3B) as the difference in wingbeat frequency from 20 Hz decreased (100 μT: from 3.5 ± 0.4 Hz to 2.0 ± 0.3 Hz; 1,000 μT: from 3.2 ± 0.3 Hz to 1.5 ± 0.4 Hz; 7,000 μT: from 2.5 ± 0.3 Hz to 1.5 ± 0.3 Hz). There was a significant interaction between treatment (EMF or control) and time (before or after exposure) on wingbeat frequency (two-way RM ANOVA: $F_{3,76} = 4.97$, $P = 0.003$), as all EMF exposures caused a significant shift of wingbeat frequency toward 20 Hz (Bonferroni adjusted P: 100 μT, $P < 0.0001$; 1,000 μT, $P < 0.0001$; 7,000 μT, $P = 0.015$), whereas control did not (Bonferroni adjusted $P > 0.9999$).

To further show that the effects of ELF EMF were dependent on initial wingbeat frequency, locusts were grouped based on their initial wingbeat frequencies. Locusts that were initially "slow-flying" (wingbeats below 20 Hz before treatment) increased their wingbeat frequency when the 50 Hz ELF EMF was applied, while locusts that were "fast-flying" (wingbeats above 20 Hz before treatment) decreased their wingbeat frequency when the 50 Hz ELF EMF was applied (Fig. 4). For control animals (0 μT), there was no interaction between the treatment and the initial flight speed of locusts (two-way RM ANOVA; $F_{1,18} = 6.05$, $P = 0.05$). Overall locust wingbeat frequency did not change over time (two-way RM ANOVA; $F_{1,18} = 0.02$, $P = 0.91$). Over the course of the experiment flight, speed was higher in locusts that were initially fast-flying than in locusts that were initially slow-flying (two-way RM ANOVA; $F_{1,18} = 19.26$, $P = 0.0004$). On exposure to 100 μT (Fig. 4B) there was an interaction effect on wingbeat frequency of the treatment and initial flight speed of locusts (two-way RM ANOVA; $F_{1,18} = 35.38$, $P < 0.0001$). Exposure to 100 μT increased wingbeat frequency of slow-flying locusts from 17.10 ± 1.15 Hz to 19.84 ± 0.82 Hz (Bonferroni adjusted $P = 0.0026$), whereas exposure to 100 μT ELF EMF significantly reduced wingbeat frequency of fast-flying locusts from 23.73 ± 0.39 Hz to 21.53 ± 0.45 Hz (Bonferroni adjusted $P < 0.0001$). For 1,000 μT (Fig. 4C), there was an interaction effect on wingbeat frequency of the treatment and initial flight speed of locusts (two-way RM ANOVA; $F_{1,18} = 19.61$, $P = 0.0003$). The wingbeat frequency of slow-flying locusts did not change markedly as a result of exposure, changing from 17.22 ± 0.59 Hz to 17.32 ± 0.75 Hz (Bonferroni adjusted $P > 0.99$), whereas exposure to 1,000 μT ELF EMF significantly reduced wingbeat frequency of fast-flying locusts from 23.30 ± 0.37 Hz to 20.55 ± 0.20 Hz (Bonferroni adjusted $P < 0.0001$). For 7,000 μT (Fig. 4D), there was again an interaction effect on wingbeat frequency of the treatment and the initial flight speed of locusts (two-way RM ANOVA; $F_{1,18} = 19.29$, $P = 0.0004$). Exposure to 7,000 μT increased wingbeat frequency of slow-flying locusts from 17.40 ± 0.37 Hz to 19.20 ± 0.57 Hz (Bonferroni adjusted $P = 0.016$), whereas 7,000 μT ELF EMF treatment significantly reduced wingbeat frequency of fast-flying locusts from 22.33 ± 0.45 Hz to 19.66 ± 0.71 Hz (Bonferroni adjusted $P < 0.0088$).

Effects of EMF Frequency on Wingbeat Frequency

The ability of locusts to shift their wingbeat frequency was further analyzed by exposing locusts to different ELF EMF frequencies. EMF strength was kept constant at 700 μT and ELF EMFs were applied at 17, 20, and 22 Hz. The difference between the locust wingbeat frequency and the frequency of the applied ELF EMF was calculated for all timepoints, including pre-EMF exposure and 15 s post-EMF exposure for each individual locust and for each applied ELF EMF frequency (Fig. 5).

For all tested EMF frequencies, the difference between wingbeat frequency and applied EMF frequency was lower during exposure compared to pretreatment levels (Fig. 5B), i.e., wingbeat frequency entrained to all applied EMF frequencies. Locusts flew 2.5 ± 0.3 Hz ($n = 21$) above the test EMF frequency of 17 Hz before exposure but at 1.9 ± 0.4 Hz above during exposure (Bonferroni adjusted $P = 0.38$). At 20 Hz locusts flew 2.1 ± 0.3 Hz ($n = 20$) above test frequency before exposure, and 1.6 ± 0.2 Hz above test frequency during exposure (Bonferroni adjusted $P = 0.37$), while for a 22 Hz EMF locusts flew 5.1 ± 0.5 Hz ($n = 19$) above test frequency before exposure, and 3.8 ± 0.8 Hz after EMF exposure (Bonferroni adjusted $P = 0.003$). A two-way RM-ANOVA showed that the application of a 700 μT EMF significantly increased entrainment of the locust wingbeat toward the frequency of the applied EMF (two-way RM ANOVA, $F_{1,51} = 14.69$, $P = 0.0003$). As the mean wingbeat frequency of locusts was approximately 19 Hz, the difference in locust wingbeat frequency from the frequency of the applied EMF varied significantly (two-way RM ANOVA, $F_{2,57} = 13.58$, $P < 0.0001$). There was no significant interaction effect between the differing test frequencies and the applied EMF (two-way RM ANOVA, $F_{2,57} = 1.334$, $P = 0.272$).

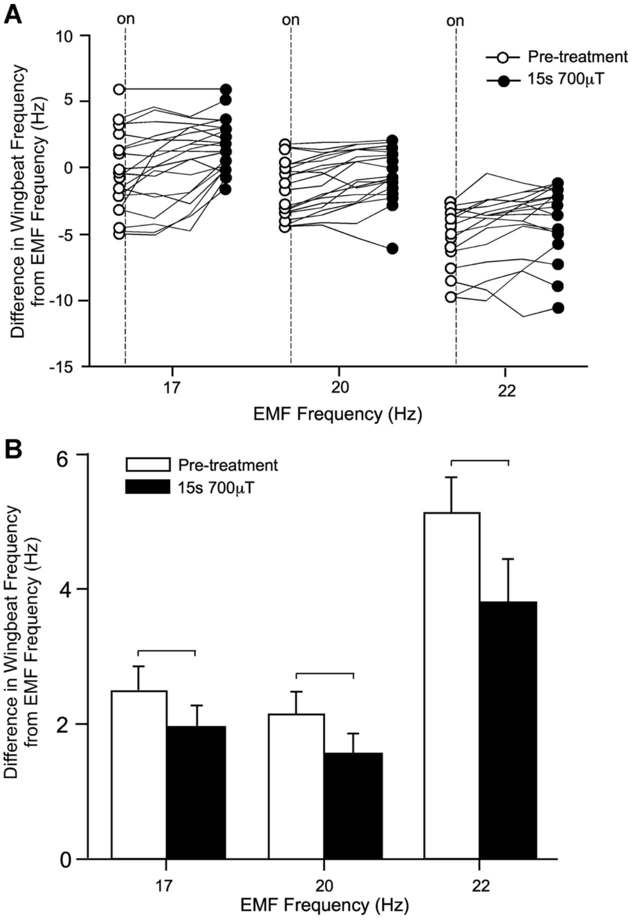

Fig. 5. Effects of ELF EMF frequency on wingbeat frequency. (**A**) Effects of 700 μT EMFs at varying frequencies (17, 20, and 22 Hz) on the difference in wingbeat frequencies from the applied frequency of the ELF EMF. Pretreatment (open circles) and treatment (black circles) wingbeat frequencies are shown. (**B**) Effects of 700 μT EMFs at varying 17, 20, and 22 Hz on the mean difference in wingbeat frequencies of locusts from the applied frequency of the ELF EMF. Mean and SEM are plotted and significant differences indicated by horizontal lines above bars. ELF EMF = extremely low-frequency electromagnetic field; SEM = standard error of the mean.

Modeling EF Levels Around the Coils

To determine whether the EF component of an EMF could contribute to the responses of the locusts, we modeled the 50 Hz EF using Maxwell software as quasi-static EFs around the coils at different applied voltages (Fig. 6). Voltage along a wire is distributed

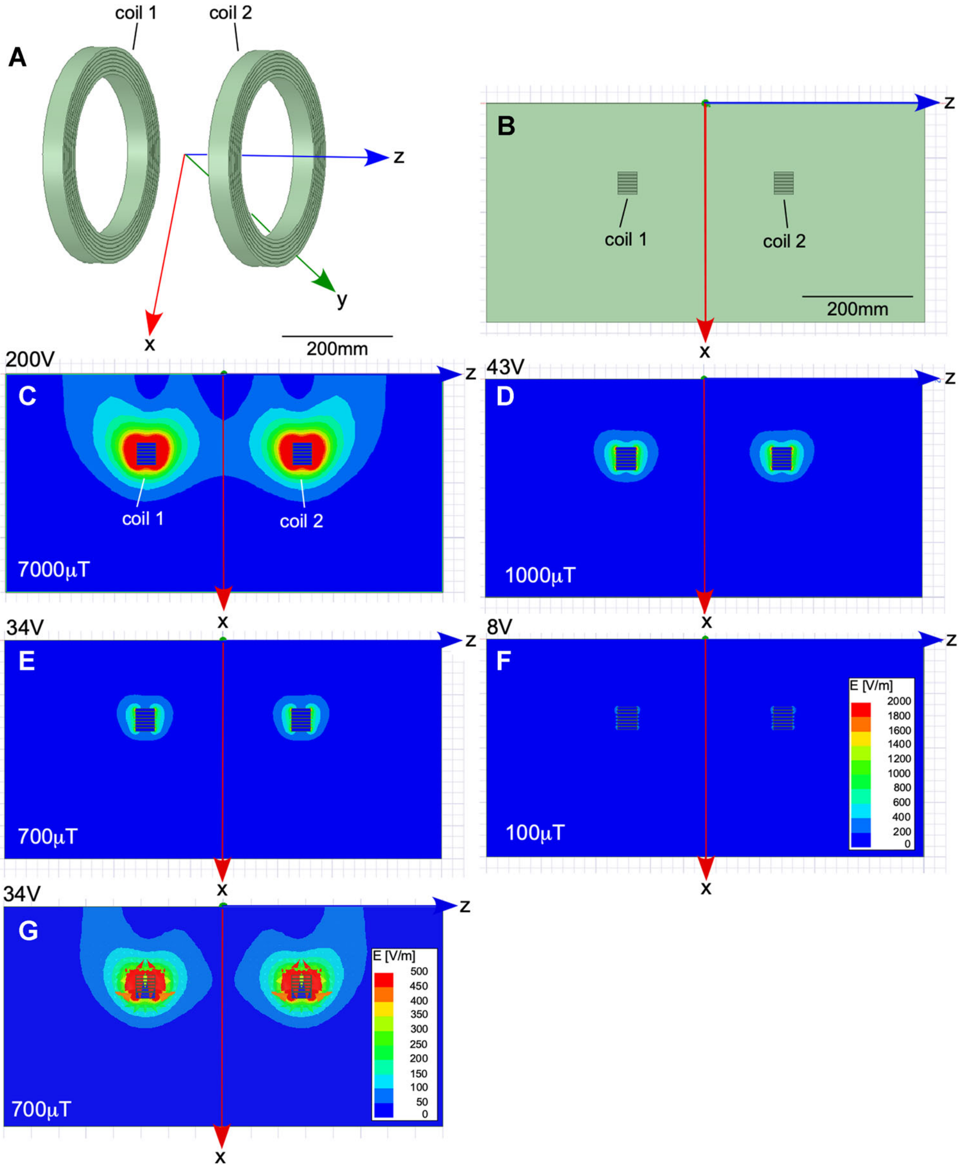

Fig. 6. Maxwell models of electric fields around the coils. (**A**) Diagram of the two coils illustrating the three axes in which the fields were modeled. (**B**) Profiles of the cross-section through the two coils developed in the model. Electric fields generated by (**C**) 200 V, (**D**) 43, (**E**) 34, and (**F**) 8 V. Electric fields at the center of the coils were less than 400 V/m at 200 V, and lower than 200 V/m at 43, 34, and 8 V. (**G**) A higher resolution model at 34 V, the voltage at which most experiments were carried out, showed that the field strength at the center of the coils was less than 50 V/m. The spiky artifacts immediately around the coils in the field map are due to limiting the maximum value of the field in this higher resolution plot.

uniformly. One of the limitations in modeling using Ansys Maxwell software is that it is not possible to model uniform distribution along a wire. We, therefore, made a number of assumptions, the first of which was that the coil was made of several (seven in total) constant voltage layers (Fig. 6A and B), with high voltage on the outside layer and 0 V on the inside layer. We also assumed the coils were connected in parallel and that the distribution of voltage on both coils was identical. Finally, the models were solved using axisymmetric geometry in which the materials and conditions were symmetric with respect to any axis (Fig. 6B). The models revealed that the EF strength at the center of the two coils generated by a 200 V applied voltage (used to generate 7,000 μT EMF) was less than 400 V/m. EFs generated with applied voltages of 43 V (1,000 μT EMF), 34 V (700 μT EMF), and 8 V (100 μT EMF) (Fig. 6D–F) were all lower than 200 V/m at the center of the coils. A higher resolution model with an applied voltage of 34 V (700 μT EMF), the voltage at which most flight experiments were carried out, showed that the field strength at the center of the coils was less than 50 V/m (Fig. 6G).

DISCUSSION

Acute exposure to ELF EMFs caused significant changes in the flight activity of locusts. We found that 50 Hz EMFs caused an increase in the absolute frequency of the wingbeat in tethered flying locusts, with the increase dependent on EMF strength. Moreover, the effects of EMF on wingbeat frequency depended on the initial wingbeat frequency of a locust. Locusts flying at an initial wingbeat frequency greater than 20 Hz reduced wingbeat frequency when the EMF was applied, while locusts flying with a wingbeat frequency lower than 20 Hz increased wingbeat frequency. Finally, locust wingbeat frequencies entrained to different frequencies of applied EMFs when the EMF frequency was modulated in a range close to their normal wingbeat frequency.

Environmental Stimuli and Wingbeat Frequency

Various environmental stimuli can affect wingbeat frequency, as locusts are known to phase lock wingbeat frequency to a variety of oscillatory stimuli, including light flashes [Waldron, 1968; Henningsson et al., 2015], modulated airflow [Horsmann et al., 1983], and even neighboring locusts in flight (i.e., locust flying in the wake of another locust) [Kutsch et al., 1994]. Mathematical analysis of phase-locking in locusts has described the phenomenon as a function of the amplitude of the sinusoidal stimulus and the relative frequencies of the oscillator and the sinusoidal stimulus [Glass and Mackey, 1979]. This would suggest that with increasing EMF intensity, entrainment between wingbeat frequency and EMF may be more likely. Such entrainment to oscillatory stimuli is also more likely if the frequency of the external stimuli is not substantially different to the initial wingbeat frequency [Waldron, 1968], or close to the natural wingbeat frequency of locusts, 20 Hz, or a factor of this [Henningsson et al., 2015].

Our results suggest that when a 50 Hz EMF is applied to locusts, their wingbeat frequency entrains toward a 2:5 subharmonic of the applied EMF (i.e., two wingbeats to every five cycles of EMF). The underlying frequency of the EMF, 50 Hz, was well beyond the wingbeat frequency of any locusts in these experiments (e.g., the fastest locust flight recorded was 26 Hz). Twenty hertz, however, is a 2:5 ratio of the applied 50 Hz EMF, which is much closer to the mean wingbeat frequency of locusts. Wingbeat frequency is a critical parameter of locust flight as a principal determinant of aerodynamic power output, and increases in wingbeat frequency are normally associated with increased force production [Taylor, 2001]. When entraining to applied oscillatory stimuli, insects are unable to decrease wingbeat frequency to any great extent, as they must maintain sufficient force to remain airborne. On the other hand, they may not increase wingbeat frequency by much as energy efficiency and physiological limitations come into play. For example, Horsmann et al. [1983] found that with wind modulation, phase-locking of locusts occurred in a range 3 Hz around their initial wingbeat frequencies, but when the applied oscillatory stimulus was outside of this range, the flight pattern was found only to be weakly coordinated with the oscillatory stimuli. Similarly, we found that convergence of locust flight frequency with the exact frequency of the applied EMF stimulus could occur, but only when the applied frequency was close to the locust's normal wingbeat frequency.

Underlying Mechanisms

EMFs can act directly at the molecular, physiological, and behavioral levels. For example, Li et al. [2013] found in *Drosophila* that acute and chronic exposure to 3 mT 50 Hz EMF caused the different expression of hsp22, hsp68, hsp70bc, hsc70-4, and hsp60d. Other stress-related proteins have been shown to increase after ELF EMF exposure. For example, Todorović et al. [2013] found that stick insects, *Baculum extradentatum*, exposed to a 50 Hz 6 mT EMF during embryonic development increased antioxidative defense activities of SOD and catalase, both enzymes that prevent oxidative damage. A variety of interactions with charged ions could affect physiological processes. For example, the Na^+/K^+ATPase pump is known to be affected by ELF EMFs as the frequency range of ELF EMFs is very close to the turnover rate of the enzyme [Yoda et al., 1984; Blank, 2005]. Short-term exposure to magnetic fields has also been shown to have effects on motor neuron signaling in desert locusts [Wyszkowska et al., 2016]. Transcriptomic molecular effects, and many of the short-term physiological effects described above, cannot occur within the 15 s acute exposure in this experiment. However, the behavioral changes (in response to acute EMF exposure) that we observed may be explained by direct acute effects on insect physiology or behavioral responses to avoid environmental stimuli that cause molecular/physiological stress.

Insects use a variety of environmental stimuli to navigate and migrate over long distances. Earth's static geomagnetic field has been proposed as one of these important stimuli, with evidence in various species of magnetoreception as a sensory process utilized by insects to navigate and orient about their environment [Mouritsen, 2018]. While the physiological mechanisms of magnetoreception in insects are unresolved, there are multiple mechanisms for magnetoreception that are currently considered to be physically viable [Mouritsen, 2018], including cryptochrome-based [Gegear et al., 2010] and magnetite-based [Kirschvink et al., 2001] magnetoreception. Magnetite-based systems detect static fields and not the 50 Hz alternating EMF of the type found under HVTLs, and which do not provide directional information. Kirschvink et al. [1997] found that honeybees are able to discriminate 60 Hz 100 μT EMFs, which is at least an order of magnitude higher than that for static fields [Walker and Bitterman 1989], and also significantly higher than the 20 μT levels, which we found previously to reduce olfactory learning [Shepherd et al., 2018]. In addition, Walker and Bitterman [1989] suggested that the magnetoreceptor system in honeybees fails to function in EMFs greater than 500 μT, well below the 1,000 μT level found near powerlines, which we found here to significantly affect wingbeat frequency. This suggests it is unlikely that a magnetite-based magnetosensitive system underlies the changes in wingbeat frequency.

A cryptochrome-based magnetosensitive system has also been widely reported in insects [Gegear et al., 2010] and is thought to provide geomagnetic information via a quantum effect in a light-initiated radical pair reaction. As with magnetite-based magnetoreception, cryptochrome-based reception is dependent on directional information and can be used to underpin large-scale migration, such as in the monarch butterfly [Kyriacou, 2009]. Again, this would suggest that the activation of the magnetosensitive system alone may not underlie the changes in wingbeat that occur as a result of acute ELF EMF exposure.

The mechanisms by which electrostatic fields act are far better understood and are known to change insect behavior due to physical forces generating mechanical inputs [Newland et al., 2015] that can displace mechanosensory hairs and generate proprioceptive inputs through the displacement of the antennae and wings (cockroach [Newland et al., 2008], honeybees [Greggers et al., 2013], and *Drosophila* [Newland et al., 2015]). Interestingly, Pratt et al. [2017] recently showed that the wings of the hawk moth, *Manduca sexta*, themselves might serve a dual role in generating lift and in a sensory role, as they have similar sensory structures to the halteres, which are known to influence flight. To determine whether the EF component could be of sufficient intensity to cause changes in the flight behavior, we modeled the EFs generated by the EMFs. Our models found that quasi-static EFs were less than 50 V/m, which are small compared to field strengths that modify insect behavior. For example, *Drosophila* avoids static EFs, and exposure to fields of 26 kV/m and above lead to the displacement of the wings, whereas cockroaches avoid EFs of 8–10 kV/m. Edwards [1960] found that blowflies, *Calliphora vicina*, show decreased locomotion when exposed to fields of ~0.5 kV/m. Sutton et al. [2016], however, showed that much lower static EFs of the same magnitude as modeled here could displace hairs on the bumblebee. Clearly, the AC EFs do not provide the same directional information as these static fields; nevertheless, there remains the possibility that they could generate subthreshold or modulatory effects on behavior.

The wingbeat frequency of locusts is generated by a central pattern generator composed of interneurons and motor neurons [Reye and Pearson, 1988; Marder and Bucher, 2001] that generate the wingbeat pattern independently of peripheral input. A cooperative system of central and mechanosensory signals [Horsmann et al., 1983] plays a crucial role in modulating the activity of the central pattern generator by increasing or decreasing the rhythmic activity of the elevator and/or depressor motor neurons [Waldron, 1968; Pearson, 1985]. It is possible, given the current wider understanding of electric and magnetic phenomena and their biological effects that central and sensory processes could be affected by acute ELF EMF exposure, which could then underlie the changes in wingbeat frequency observed here.

Wider Biological Implications

It has been known for a long time that locomotor and ventilatory rhythms are coordinated in many mammals [Funk et al., 1997] and that such coordination confers an energetic advantage for an animal. Bipeds and quadrupeds synchronize their rhythms [Bramble and Carriers, 1983] as do birds [Berger et al., 1970], and often at a ratio other than 1:1. Funk et al. [1997] suggested that even with couplings of 3:1, there remains an energy-saving to an animal. Kutsch et al. [1994] analyzed the coupling of wingbeats of closely tethered flying locusts and suggested that by coupling their wingbeats to a forward neighbor's wake, the turbulence could be utilized to generate an aerodynamic advantage. Further studies by Camhi et al. [1995] found that lift could be increased by 16% depending on the preferred phase. These studies suggest that animals coordinate specific motor tasks to gain energetic advantages. The implication of this is that the convergence of locust wingbeat frequency to EMF frequency may also confer an energetic advantage, as wing movements entrain to the fields of force produced by the EMFs. As most ELF EMFs in the environment occur around 50 or 60 Hz, it is likely that flight pattern will be affected differentially depending on insect species. For example, locusts often fly with a 20 Hz wingbeat frequency [Henningsson et al., 2015]; however, hemipterans often fly at 40–45 Hz, *Ochlodes* butterflies often fly at 50 Hz, and Bumblebee wingbeat frequencies can often be in a range of 100–115 Hz [San Ha et al., 2013]. Recent studies indeed show that ELF EMFs lead to a reduction in wingbeat frequency in honeybees [Shepherd et al., 2018]; however, the relationship with EMF frequency was not studied.

CONCLUSION

Exposure of locusts to 50 Hz ELF EMFs caused the wingbeat frequency of tethered flying locusts to entrain to 20 Hz, a 2:5 subharmonic of the applied EMF. When EMF frequency was modulated within a narrow range of normal flight frequency, the wingbeat frequency shifted toward the exact frequency of the applied EMF instead of a subharmonic. These results have implications for determining how anthropogenic ELF EMF pollution affects insect behavior, as well as how insects respond to environmental electromagnetic stimuli. In future studies, the applied ecological implications of ELF EMFs on insect flight should be considered as well as the mechanisms by which these environmental stimuli bring about these effects.

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