The Journal of Experimental Biology 211, 3682-3690
Published by The Company of Biologists 2008
doi:10.1242/jeb.019901

Static electric field detection and behavioural avoidance in cockroaches

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Accepted 23 September 2008

SUMMARY

Electric fields are pervasively present in the environment and occur both as a result of man-made activities and through natural occurrence. We have analysed the behaviour of cockroaches to static electric fields and determined the physiological mechanisms that underlie their behavioural responses. The behaviour of animals in response to electric fields was tested using a Y-choice chamber with an electric field generated in one arm of the chamber. Locomotory behaviour and avoidance were affected by the magnitude of the electric fields with up to 85% of individuals avoiding the charged arm when the static electric field at the entrance to the arm was above 8–10 kV m^{-1}. Electric fields were found to cause a deflection of the antennae but when the antennae were surgically ablated, the ability of cockroaches to avoid electric fields was abolished. Fixation of various joints of the antennae indicated that hair plate sensory receptors at the base of the scape were primarily responsible for the detection of electric fields, and when antennal movements about the head–scape joint were prevented cockroaches failed to avoid electric fields. To overcome the technical problem of not being able to carry out electrophysiological analysis in the presence of electric fields, we developed a procedure using magnetic fields combined with the application of iron particles to the antennae to deflect the antennae and analyse the role of thoracic interneurones in signalling this deflection. The avoidance of electric fields in the context of high voltage power lines is discussed.

Key words: electric fields, high voltage, sensory, mechanoreception, behaviour, cockroach.

INTRODUCTION

Animals show a variety of behavioural responses to electrical fields that are dependent upon the type of electric field and species involved. For example, Gymnotiform fish have the unique ability to produce and exploit low strength pulsating electric fields for finding prey and for communication (Bullock, 1982; Heiligenberg and Bastian, 1984; Kalmijn, 1988). The nematode, *Caenorhabditis elegans*, orientates to electric fields, which appear to activate amphid sensory neurones (Gabel et al., 2007) whereas electrostatic forces from frictionally charged surfaces alter insect locomotory behaviour (Edwards, 1960b; Maw, 1961; Maw, 1962; Watson et al., 1997).

Changes in an insect's behaviour occur in response to a variety of electric field types, including charged surfaces, static or fluctuating electric fields generated by high voltage power supplies and very low frequency (VLF) electric fields produced by high voltage power lines. Insects respond to charged surfaces by avoiding, or being repelled by, the charged region (Hunt et al., 2005; Maw, 1964). The movements of parasitoids decrease when walking across charged surfaces (Maw, 1961), suggesting that such surfaces could be exploited as a non-toxic pest control method (Jackson and McGonigle, 2005; Maw, 1962; McGonigle et al., 2002).

Electric fields of strengths that occur under high voltage power cables have led to studies of the possible adverse effects of electric fields on insects, including chromosome aberrations and paralysis (McCann et al., 1993; McCann et al., 1998; Watson, 1984), and changes in locomotion and movement (Edwards, 1960a; Edwards, 1961; Perumpral et al., 1978). However, despite these reports, there have been few systematic analyses of the behavioural responses of insects to static and VLF electric fields. Little is known, for example, of the interactions between an insect's body and the electrical forces acting on it, and how electric fields are actually detected. Insect appendages are thought to be influenced by both static and VLF electric fields. For example, the wings of *Drosophila* and bees vibrate when exposed to both static and VLF electric fields (Bindokas et al., 1988; Watson et al., 1997) whereas the antennae of bees and parasitoids appear to be deflected by electric fields (Maw, 1961; Yes'Kov and Sapozhnikov, 1976). It is possible, therefore, that insect appendages are involved in the detection of electric fields, much in the same way that body hairs are believed to contribute to the perception of electric fields by humans (Chapman et al., 2005). Body hairs are deflected by electric fields with the angle of displacement being proportional to the field strength (Shimizu and Shimizu, 2003; Shimizu and Shimizu, 2004) and removal of hairs abolishes our ability to detect such fields (Chapman et al., 2005).

In the present study we have systematically analysed cockroach behaviour in response to static electric fields and utilising a number of different approaches we have asked if insects have an electrosensory sense, how they detect static electric fields and how that information is used to drive adaptive behaviour.

MATERIALS AND METHODS

The cockroach *Periplaneta americana* (L.) was used for all experiments. For behavioural choice assays, third- and fourth-instars were used (there were no significant differences in the results for the different instars) and for physiological experiments, adult cockroaches were used (see below).

Y-tube behavioural bioassay

Three cylindrical, 2 mm thick, silicon glass chambers, 150×30 mm (length×diameter), were fused together in a 'Y' configuration 120 deg. apart (Fig. 1A). A small hole (7 mm diameter) was cut out of the upper surface near the entrance to each anterior chamber into which a copper loop electrode, 5×28 mm (width×diameter), was fixed. Aluminium earth bands were fixed 35 mm from the end of each chamber and a high voltage power supply (Brandendurg Alpha III, Brandenburg, UK) supplied the electrodes. Two capture chambers (85×35 mm) (length×diameter) covered the ends of each anterior chamber to catch the cockroach after every trial, and a release chamber (85×35 mm) (length×diameter) was placed at the base of the Y-tube. The power supply was adjusted to produce electric fields at applied potentials of 0 V, 0.5 kV, 0.75 kV, 1 kV, 2 kV, 3 kV or 4 kV in one pathway, before a cockroach entered the central chamber and the pathway taken by the cockroach determined. Control trials without electric fields were carried out to test for natural preferences within the Y-tube. Cockroaches that spent longer than 5 min in the apparatus, or returned back down the central chamber, were discounted from the analyses. The decision time was defined as the time taken for an animal to pass from the release chamber to a position of one body length past an electrode. Statistical analyses were carried out using a Bionomial Tests of Proportions (S-Plus, v. 6.1 for Windows) and χ^2 tests.

The treated (charged) chamber was alternated after each trial to control for natural bias and was also washed and soaked in 5% Decon90 solution using hot water (55°C) for 10 min after every five trials to remove possible pheromone deposits. After rinsing with distilled water and washing with acetone, the apparatus was dried (110°C) for a minimum of 10 min to remove solvent trace. Experiments were carried out in a room illuminated by a 40 W 1.2 m tube light covered with a far-red filter (Campbell Environmental Products, Preston, UK) between 10:00 and 18:00 h at 21.5±1.5°C and 35.7±3.7% humidity.

Electric field stimulation of antennae

To investigate the effect of static electric fields on antennal deflection, the head of an adult cockroach (*N*=5) was positioned 50 mm from a circular copper electrode (30 mm diameter×7 mm width) after anaesthetisation with CO_2 and restrained in Plasticine™. Another electrode was positioned at the posterior of the cockroach and connected to earth whereas the anterior electrode was connected to the high voltage power supply. Antennal deflection was analysed at stimulus outputs of 3 kV, 4 kV, 5 kV and 6 kV with five trials of 5 s exposure for each individual with 15 s between each trial. All trials were recorded using a digital camera (Sanyo VCB-3372P, Tokyo, Japan) onto DVD (Panasonic DMR-E55EB, Osaka, Japan) for subsequent analysis.

Magnetic field stimulation of antennae

Preliminary studies showed that the application of fine iron powder (spherical, <10 μm diameter, Alpha Aesar, Karlstruhe, Germany) to the antennae was sufficient to deflect the antennae under magnetic fields. Cockroaches exposed to magnetic fields were positioned opposite an electromagnet at the same height and distance to the source as individuals tested under electric fields. After anaesthetisation the distal two-thirds of one antenna was coated in a pre-weighed quantity of iron powder ($0.0153\pm4\times10^{-4}$ g, *N*=5) using a fine paintbrush and any excess gently removed. The effects of four magnetic field strengths on antennal deflection were investigated. It was not possible to measure the magnetic field strengths within the chamber and, thus, the displacements caused by magnetic stimulation were therefore calibrated against displacements caused by electric fields at electromagnet potentials of 20 V, 25 V, 30 V and 35 V (Nihon-Kohden SEN-3301) (see Fig. 2 and Fig. 3C). Control experiments were also carried out to determine if magnetic fields affected the movement of antennae not coated with iron particles. The antennae of each individual was deflected five times (5 s duration) at each electromagnetic coil voltage with 15 s between trials. All experiments were recorded (Sony DCR-TRV9) and video digitised (Apple PowerBook G5, CA, USA) for further analysis.

To test for the effect of magnetic field exposure on ventral nerve cord (VNC) activity, extracellular recordings from the VNC of each individual were made (see below) prior to applying iron powder to the antennae. Five stimuli of each magnetic potential were applied, 5 s in duration with a 15 s rest period between each stimulus for a given potential as controls. The antenna contralateral to the isolated neck connective was then coated in iron powder ($0.0197\pm4\times10^{-4}$ g, *N*=5) using a fine paintbrush and any excess gently removed.

Differences in mean antennal deflection between field types were analysed using Student's *t*-tests (SPSS for Windows, v. 14, Chicago, IL, USA) after assumptions of normal distributions and homogeneity of variances were met. Regression analysis was carried out to test for the effect of potential on antennal deflection for each field type (Minitab for Windows, v. 12, PA, USA). A Student's *t*-test was also performed to compare regression coefficients and highlight any differences in the effect of voltage potential on antennal deflection between the field types.

Physiological recording

The interneurons that receive input from mechanosensory neurones from the antennae are bundled within the interganglionic neck connective region of the VNC (Burdohan and Comer, 1996) and have axons on the side contralateral to their input side. These interneurones were recorded extracellularly from their axons between the subesophageal ganglion and the prothoracic ganglion (Burdohan and Comer, 1996; Comer et al., 2003). To expose the neck connectives, a small incision was made along the ventral edge of the neck and the remaining soft cuticle removed with fine iridectomy scissors. The connective contralateral to the antenna to be deflected was isolated from surrounding muscle and tissue and placed on a bipolar hook electrode (125 μm silver, Teflon® coated except at the tips), insulated with petroleum jelly and the signals amplified and stored on a computer.

Action potentials, spikes, were amplified (Nihon Kohden MEG-1100), displayed on an oscilloscope (Tektronix 5111A, Beaverton, OR, USA) and digitally recorded using a PowerLab digital acquisition system (ADInstruments, Colorado Springs, CO, USA) running Chart v. 4.01 software. Spike threshold levels were determined using Chart software and the number of large amplitude spikes were compared in a time window 320 ms before stimulus onset (control) with one 320 ms after stimulus onset (test).

Ablation of sensory structures

Mechanoreceptor activation was prevented at various regions of the antennae (the scape, pedicel or flagellum) of third- and fourth-instar cockroaches (abdomen to head length, *N*=263, 8.06±0.56 mm) to determine which mechanoreceptors contribute to the detection and avoidance of electric fields. This was done by applying a non-toxic cyanoacrylate adhesive, VetBond® (WPI, Stevenage, UK), to parts of the head and antennae to prevent movement about specific joints of the antennae using a fine microcapillary held in a micropipette holder. Adhesion was subsequently aided by applying cyanoacrylate adhesive accelerator (RS Components, Corby, UK). This procedure was carried out on the head capsule–scape joint and the scape–pedicel joint. Ablation of the flagellae was carried out using a pair of fine iridectomy scissors after anaesthetising and restricting the movements of animals, which were then allowed to recover for 18–20 h before testing. Exteroceptive input from hair plate hairs was prevented by applying cyanoacrylate adhesive to the hair plates only. The effect of field strength on avoidance behaviour was analysed using χ^2 tests of association for each type of antennal sensory input modification carried out.

High-speed video observation of antennae

The influence of electric fields on cockroach antennae approaching the copper electrodes was filmed in the horizontal plane through the Y-tube apparatus using high-speed video equipment (MotionScope 1000S, Redlake Imaging, CA, USA). Video images were taken of cockroaches, at 250 frames s^{-1} (N=4), exposed to electric fields at 1 kV and 4 kV potentials, in addition to controls.

RESULTS

Cockroaches avoid static electric fields

Static electric fields of various strengths were applied to the electrode of one pathway of the Y-tube to analyse the avoidance behaviour of cockroaches encountering a static electric field (Fig. 1A). Modelling the static electric field within the Y-tube using Maxell SV software showed that the highest static electric field strengths were distributed immediately around the copper ring

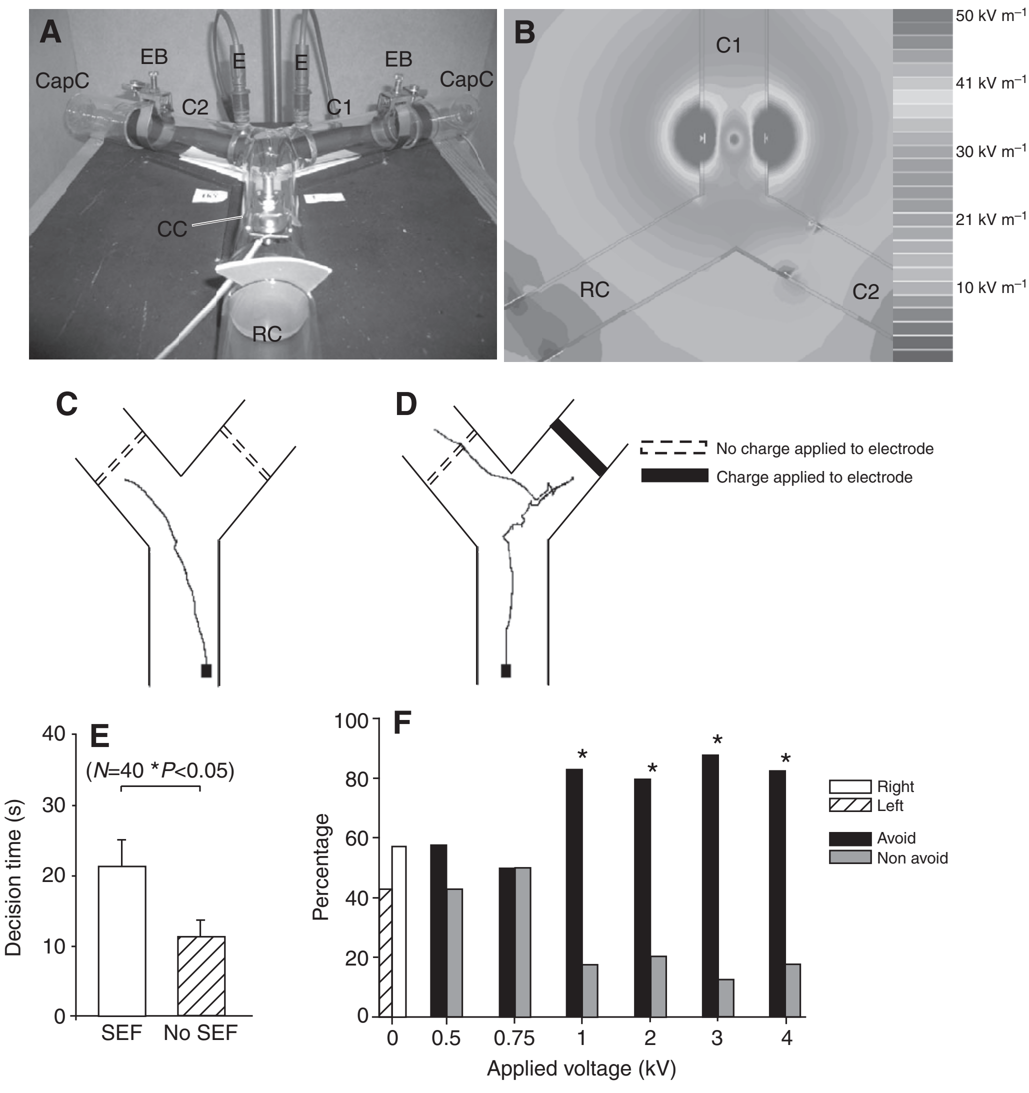

Fig. 1. The Y-tube choice chamber and the avoidance of static electric fields. (A) Photograph of the Y-tube apparatus showing the release chamber (RC) connected to the central chamber (CC). Copper loop electrodes (E), localised the field to one chamber (C1 or C2). At the end of each tube a capture chamber (CapC) was attached to hold tested individuals. Aluminium earth bands (EB) were used to localise the field within the treated chamber. The electrodes (E) were connected to a Brandenburg Alpha III power source. (B) Vector plot of the electric field generated by an electrode in one arm of the Y-tube at 1 kV using Maxwell SV modelling software. (C) The walking path of a control cockroach tracked using Ethovision software when no electric filed was present. (D) The walking path of a cockroach when an electric field was applied to the electrode on the right arm. Note that the cockroach moved toward the electrode, stopped, and walked back to the left arm to avoid the electric field. (E) The time taken by cockroaches encountering static electric fields (SEF) to make a decision within the Y-tube apparatus. The time within the decision zone was greater when cockroaches were exposed to electric fields (means ± s.e.m., standard error of the mean), N=40, P<0.05). (F) The avoidance of static electric fields at different electrode voltages from 0.5 kV to 4 kV. Cockroaches exhibited no natural bias for the left or right pathway (N=40, P>0.05) within the Y-tube apparatus in the absence of electric fields (0 V). Voltage of 0.5 kV and 0.75 kV did not evoke significant avoidance (N=40, P>0.05 in both cases). Voltages of 1 kV and above elicited significant avoidance of the treated pathway (N=40, P<0.05 in all cases, indicated by the asterisks).

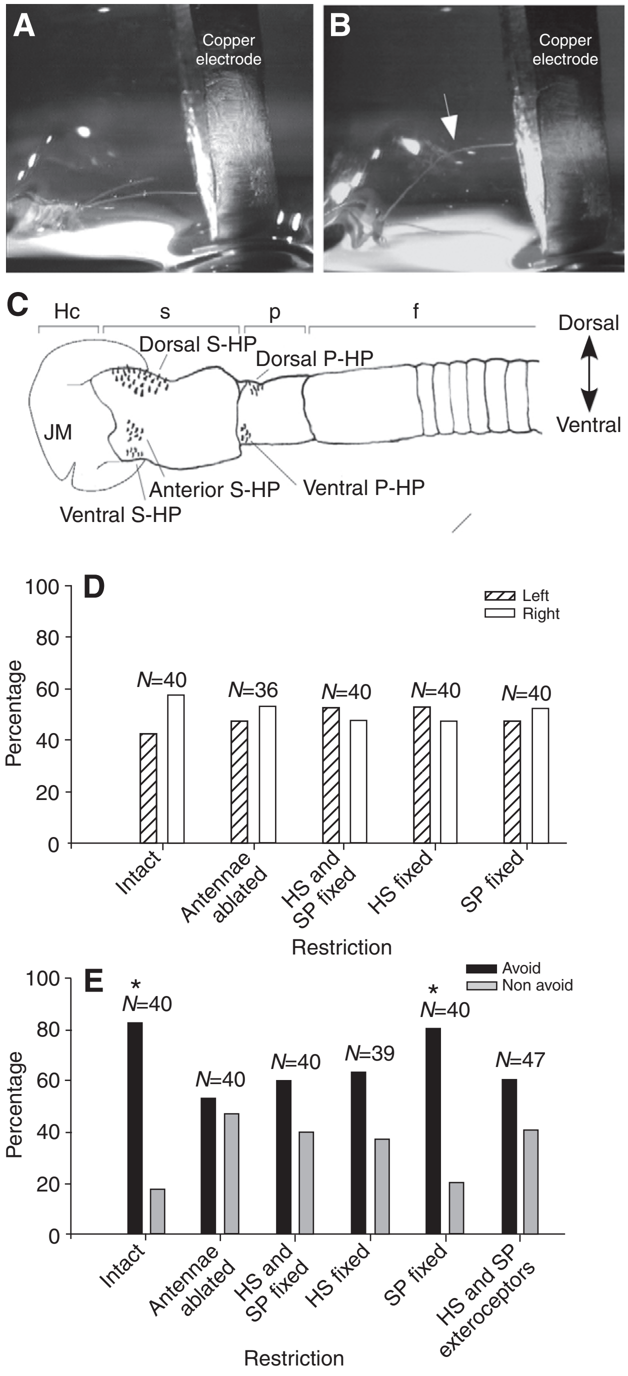

Fig. 2. The antennae are involved in static electric field detection. (A) High-speed video images of an animal approaching an untreated electrode within the Y-tube apparatus. (B) With a 1 kV potential applied to the copper electrode a bending of the antennae was evident (arrow). (C) Antennal mechanoreceptor hair plates located on the scape (s), and pedicel (p) of the dorsal, ventral anterior and posterior locations of a third-instar cockroach nymph antenna viewed from above. f, flagellum, Hc, head capsule; JM, joint membrane; P-HP, pedicel hair plate; S-HP, scape hair plate. (D) The effect of modifying mechanoreceptor input on the preference behaviour of cockroaches within an untreated Y-tube apparatus. No significant preference for either the left or right chamber occurred after surgery or restriction of mechanoreceptor input was performed in the absence of electric fields. HS, Head–Scape joint; SP, Scape–Pedicel joint. (E) The effect of modifying mechanoreceptor input on the avoidance of electric fields at 1 kV. Intact individuals and those with the SP joint fixed exhibited significant avoidance (N=40, P<0.05, represented by the asterisks). Avoidance significantly decreased when the antennae were removed, when both the HS- and SP joint, and when the SP joint alone were restricted in comparison to intact cockroaches (P<0.05 in all cases). Preventing exteroceptor stimulation but allowing proprioceptor input did not result in avoidance (HS and SP exteroceptor) (N=47, P>0.05).

electrode within the treated arm (Fig. 1B). A 0.5 kV potential applied to the electrode generated an electric field at the entrance to the pathway of approximately 4–6 kV m^{-1} that increased to approximately 8–10 kV m^{-1} when a 1 kV potential was applied and 30 kV m^{-1} at 4 kV. There was no difference in the field strength at the entrances to both the treated and untreated chambers when a 0.5 kV potential was used.

The behaviour of cockroaches was first analysed within an untreated Y-tube apparatus to determine if a natural bias for one pathway existed, however, no natural preference for either the left or right untreated pathway was exhibited (N=40, P>0.05) (Fig. 1C,F). The effects of electric field strength on cockroach avoidance were then tested at applied voltage potentials of 0.5 kV, 0.75 kV, 1 kV, 2 kV, 3 kV and 4 kV and the preference of cockroaches for the treated or untreated pathway determined. Potentials applied at 0.5 kV and 0.75 kV caused no clear effects on the walking behaviour of cockroaches nor any significant preference for cockroaches to take either the treated or untreated pathway (Fig. 1E) (N=40, P>0.05 for both cases, Mann–Whitney U-test). Increasing the voltage to 1 kV and above resulted in cockroaches spending significantly more time in the decision zone around the intersection of the tubes, as their walking speed declined on approaching a field and a different path eventually taken (Fig. 1E). Moreover, a significantly greater number of animals avoided the treated pathway of the Y-tube (N=40, P<0.01, Mann–Whitney U-test) (Fig. 1F). A preference for the untreated (not charged) pathway continued to be exhibited when the electrode was charged at 2 kV, 3 kV and 4 kV (N=40, P<0.01 in all cases, Mann–Whitney U-test) (Fig. 1F).

Thus, cockroaches exhibit a clear avoidance of electric fields at applied electrode voltages over 1 kV, equivalent to a modelled electric field strength of 8–10 kV m^{-1}.

The antennae are responsible for the detection of static electric fields

Previous studies have shown that activation of mechanoreceptors on and in the antennae mediate escape behaviour and avoidance in response to predator attack or tactile stimulation (Comer et al., 2003; Ye and Comer, 1996). Given previous reports of electric fields influencing insect antennae (Maw, 1961; Yes'Kov and Sapozhnikov, 1976), we investigated whether static electrical fields could cause antennal movement, thereby activating mechanoreceptors that could in turn elicit avoidance behaviour.

Single frames from high-speed video showed the influence of static electric fields on cockroach antennal deflection within the Y-tube apparatus. While the antennae of cockroaches within an untreated pathway were not affected when the copper electrode was approached (Fig. 2A) (N=4), applying a 1 kV potential resulted in a clear attraction of the flagellae towards the electrode (Fig. 2B) (N=4) (Fig. 3C,D).

To determine what sensory receptors (Fig. 2C) might be activated by this deflection and could, in turn, contribute to avoidance, the effect of preventing specific antennal sensory inputs on the behaviour of freely moving cockroaches was analysed. Experiments were first carried out to control for any effect of preventing antennal

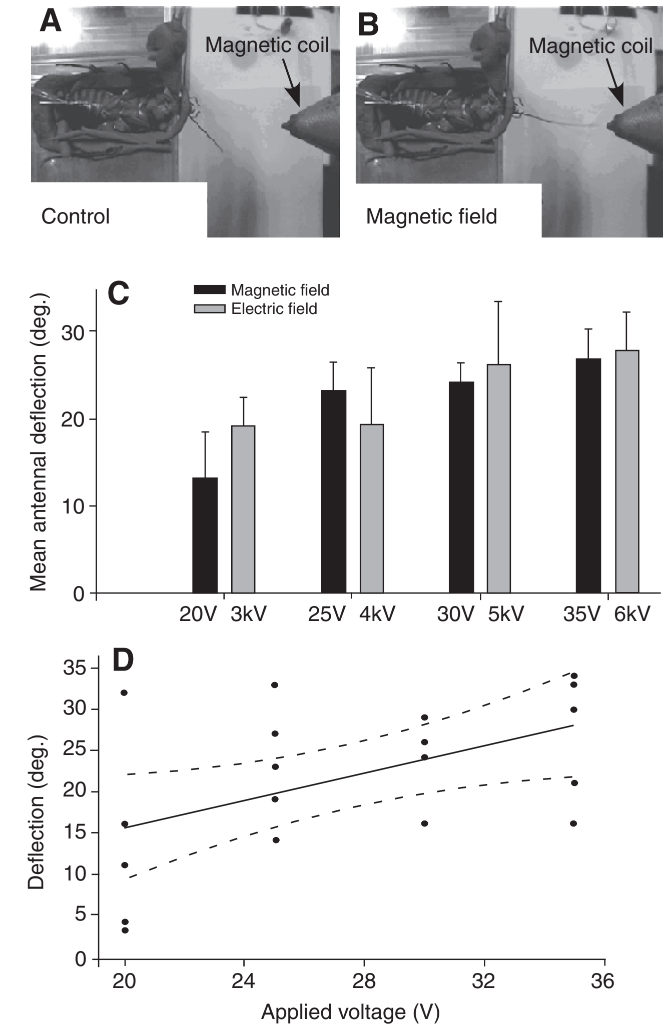

Fig. 3. Magnetic field deflection of the antennae. Antennal deflection caused by magnetic field stimulation did not occur in the absence of iron powder applied to an antenna (A) but did following iron powder application (B) as indicated by the antennae being attracted towards the coil tip. (C) Mean deflection (± s.e.m.) of coated adult antennae exposed to magnetic and electric fields at different potentials. Increasing the electric or magnetic field strength caused greater antennal deflection. Voltages were selected such that no significant differences occurred between each field type for a given pair of potentials (N=5, d.f.=8, P>0.05 in all cases). (D) Fitted line regression plot of the effect of magnetic fields on antennal deflection at varying coil potentials (b=0.84, t=2.55, P<0.05). Dotted lines represent 95% confidence limits.

mechanoreceptor input on natural preference within the Y-tube apparatus (Fig. 2D). Restricting antennal movement or ablating the antennae did not result in a significant preference for the left or right pathway (N=40, P>0.05 in all cases) in the absence of an electric field. In addition, sham experiments demonstrated that VetBond® application had no effect on preference behaviour (N=40, P>0.05).

When a 1 kV potential was applied to the electrode of one arm of the Y-tube, over 80% of intact animals avoided the electric field (Fig. 2E). Preventing all antennal sensory input by ablating the antennae resulted in animals showing no significant preference for the treated or untreated pathways. Preventing the activation of mechanoreceptors on the scape and pedicel by covering the head–scape and scape–pedicel joints with glue also caused significantly less avoidance than in intact control cockroaches (N=40 P<0.05). Preventing movement of the antennae about the head–scape joint alone resulted in significantly less avoidance than intact control cockroaches (N=40, P<0.05) whereas fixing the scape–pedicel joint alone had no significant effect on avoidance compared with control animals, with 80% of individuals avoiding the charged arm of the Y-tube (N=39, P>0.05). Finally, applying glue directly to the hair plates on the scape and pedicel, while still allowing joint movement, also significantly reduced avoidance (N=47, P<0.05). These results suggest that mechanoreceptive hair plates at the base of the scape are important in detecting movements of the antennae caused by electric fields and contributing to avoidance behaviour.

Using magnetic fields to deflect the antennae

To determine whether antennal deflection caused by electric fields evoked changes in neural activity that could underlie the detection of electric fields, it was necessary to develop an alternative method to deflect the antennae without the use of electric fields that prevent electrophysiological analysis due to electrical 'noise'. We, therefore, developed a method combining magnetic field stimulation with the application of fine iron powder to the antennae to mimic the movements of the antennae caused by electric fields. Without iron powder, magnetic fields of varying strength did not have an effect on antennal movement ($F_{1,15}$=2.29, P>0.05), demonstrating that magnetic fields *per se* did not influence the movement of antennae without iron powder (Fig. 3A). Following coating of the antennae with iron powder, magnetic fields deflected the antennae toward the coil tip (Fig. 3B).

Similar antennal deflections were generated for both field types (electric or magnetic) at four potential pairings. For a given pairing, antennal deflection did not differ between field types (Fig. 3B) (N=5, P>0.05 in all cases), demonstrating that the electrical and magnetic forces acting on the antennae at each pairing had similar effects on the antennae. Antennal deflection caused by a 20 V magnetic coil potential was therefore analogous to a deflection elicited by a 3 kV electric potential; deflection due to a 25 V magnetic coil potential was the same as a 4 kV electric potential; deflection by a 30 V magnetic coil potentials similar to a 5 kV electric potential; and 35 V was the same as 6 kV.

Increasing the magnetic or electric field strength by increasing the potential had a proportional effect on antennal deflection. Regression analysis showed that as the magnetic potential was increased the antennal deflection became significantly greater (b=0.84, t=2.55, P<0.05) (Fig. 3D). There was no significant difference between the regression slopes of antennal deflection caused by magnetic and electric fields as the voltage potential was altered (t=0.35, d.f.=1, P>0.05).

Antennal displacement evokes interneurone activity in VNC

Extracellular recordings of neural activity were made from the VNC to investigate whether deflection of the antennae led to elevated levels of activity in intersegmental interneurones in the VNC. Control experiments using antennae not coated with iron particles showed that exposure to magnetic fields was not associated with changes in antennal deflection and VNC activity when magnetic potentials were applied (N=5, t=0.18, P<0.05), indicating that magnetic fields *per se* did not influence neural activity (Fig. 4A,Ai). Deflecting a coated antenna with a magnetic field resulted in a significant increase in VNC activity (N=5, t=3.4, P<0.05) and a significant deflection of the antennae (Fig. 4B,Bi).

VNC activity was also recorded after restricting antennal movement at the scape, therefore, preventing the mechanosensory

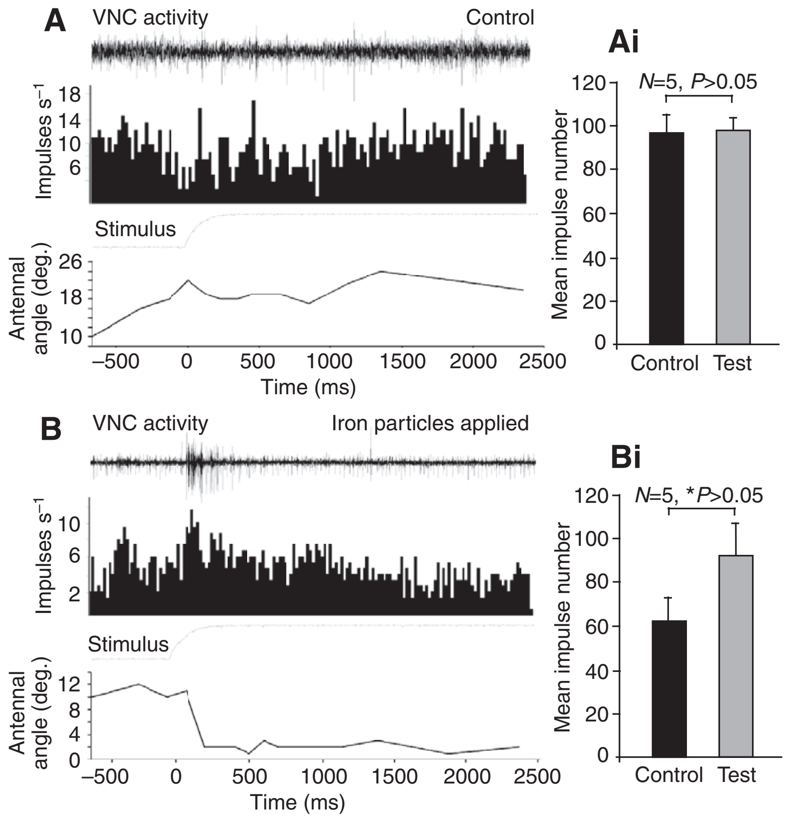

Fig. 4. Antennal movement and associated ventral nerve cord (VNC) activity before and after stimulus onset in individuals with (A) uncoated and (B) coated antennae. (A) A representative recording showing that the application of a magnetic field (25 V) to an uncoated antenna caused no change in antennal deflection in control individuals and no change in VNC activity after stimulus onset. (Ai) Graph showing mean impulse number (± s.e.m.) recorded from the VNC 320 ms before (control) and 320 ms after stimulation (test) of the antennae during magnetic field stimulation from five individuals. Magnetic field stimulation alone caused no change in impulse number. (B) Representative recording from an individual with a coated antenna, showing antennal deflection and increased VNC activity after stimulus onset (25 V). (Bi) Stimulating coated antennae caused a significant increase in impulse number after stimulus onset (test) compared with before (control) (N=5, t=3.4, P<0.05).

input that caused avoidance behaviour (see Fig. 2E). Fixing the scape reduced antennal deflection (Fig. 5A,B) (N=5, t=0.25, P>0.05) and reduced VNC activity (Fig. 5A,C) (N=5, t=0.5, P>0.05).

Behavioural responses to magnetic fields

To confirm that antennal deflection caused by magnetic fields in fixed animals could affect the ability of cockroaches to avoid magnetic fields during free movement, we placed individuals with antennae coated with iron particles in a Y-tube apparatus combined with electromagnets (Fig. 6A). Control trials with no magnetic fields showed that cockroaches with coated antennae exhibited no side preference (N=32, P>0.05). However, cockroaches did not appear to significantly avoid magnetic fields (N=27, P>0.05). This was most likely due to the antennae on insects with iron particles sticking to the magnets and thereby completely abolishing normal avoidance patterns. However, as with electric field avoidance (Fig. 1C), individuals took significantly longer to make a decision when approaching the magnetic field than when no magnetic fields were present (Fig. 6B) (N=44, P<0.01). Moreover, control studies showed that magnetic fields alone did not have an effect on behaviour as there was no significant difference in the decision time taken by cockroaches in the Y-tube (Fig. 6B) (N=40, P>0.05).

DISCUSSION

We have demonstrated clearly that cockroaches avoid static electric fields, just as they do friction charged surfaces (Hunt et al., 2005). Cockroaches actively avoided the charged arm of a choice chamber indicating that electric fields can be detected and the information used to generate avoidance responses. These findings support previous observations, for example Watson (Watson, 1984), who showed that *Drosophila* movement is also correlated with field strength. Our results suggest that cockroaches exhibited a ‘threshold’ of avoidance at static electric field strengths of 8–10 kV m^{-1}. Atmospheric electric fields have been reported to cause behavioural changes in insects (Edwards, 1960a; Maw, 1962) and static electric fields up to 20 kV m^{-1} can be generated by equipment such as televisions. Underneath high voltage power lines, static electric fields can reach 11 kV m^{-1} at ground level and far higher at closer proximity to the power line (Fews et al., 1999a; Fews et al., 1999b). The results of the present study showed that avoidance and behavioural changes occurred in free-moving cockroaches confronted with static electric fields of 8 kV m^{-1} and above. Therefore, this finding implies that static electric fields from household and office equipment could cause changes in insect behaviour. In addition, our results may explain previous observations that suggest that the flying activity of insects is altered near high voltage power lines (Orlov, 1990; Orlov and Babenko, 1987).

The detection of static electric fields

Some animals have evolved specialised means of detecting forces such as the Earth’s magnetic and electric fields. For example, magnetite (Fe_3O_4) is deposited in specific regions of certain insects and birds, allowing them to detect magnetic fields (Maher, 1998; Wiltschko and Wiltschko, 2006). Likewise, some aquatic animals can perceive the Earth’s magnetic field using specific structures, such as the ampullary organs (Kalmijn, 1971; Kalmijn, 1982). The ampullary organs are also used to generate and detect weak electric fields within sea- and freshwater; an ability that is utilised during prey localization, communication and navigation (Heiligenberg and Bastian, 1984; Hopkins, 1988; Kalmijn, 1988).

Given the evolution of specific structures to detect the many external cues in the environment, a key focus of the present study was to determine whether insects have also evolved specific sensory structures to detect electric fields. We found through ablation studies that the antennae were crucial for the detection of electric fields and without them a cockroach is not able to avoid a static electric field.

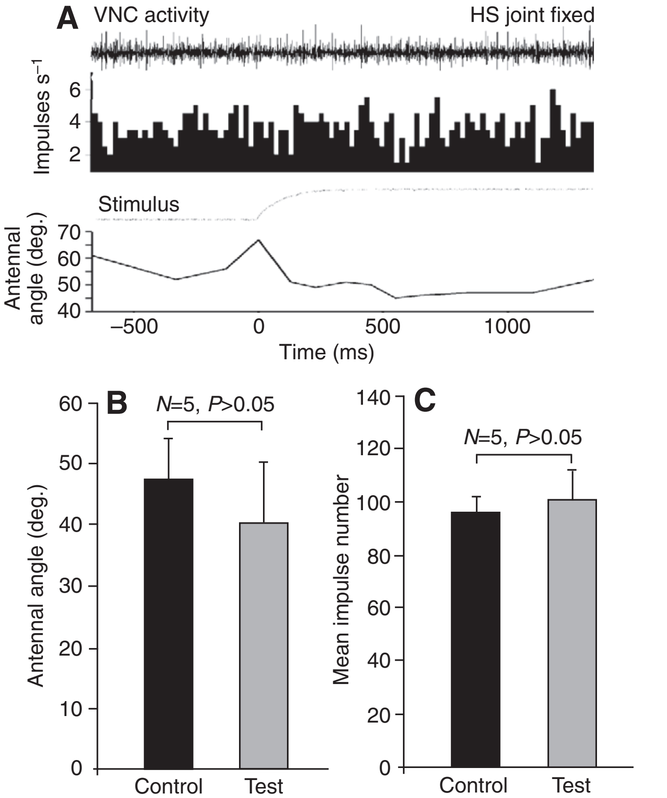

Fig. 5. The role of antennal hair plates during antennal deflection. (A) An example showing that with the head–scape joint fixed there was little antennal movement and no evoked activity in the ventral nerve cord (VNC). (B) Magnetic field stimulation (25 V) did not produce a significant deflection of the antennae with the head–scape joint fixed (test N=4, t=–1.9, P>0.05). (C) VNC activity did not significantly change when antennae were deflected using magnetic fields with the head–scape joint fixed (test N=5, t=0.5, P>0.05).

Further fixation studies revealed that hair plates at the base of the scape (S-HPs) were crucially required for an animal to avoid an electric field. The influences of electric fields on other slender, elongated structures, such as human hairs have previously been reported (Chapman et al., 2005; Shimizu and Shimizu, 2003; Shimizu and Shimizu, 2004). Our results show that the detection of static electric fields by cockroaches can be attributed to the activation of an established sensory system and not one that has evolved specifically for the purpose.

Cockroaches approaching a static electric field are subject to considerable electrical forces, clearly illustrated by the antennal deflection observed through high-speed video caused by attraction forces pulling the antennae to the electrode. Before encountering an electric field, the charges on a cockroach are randomly distributed (Fig. 7A). When approaching a positively charged electrode, as used in our experiments, this induces an uneven charge distribution on the cockroach with negative charges attracted towards the electrode and, hence, leading to a passive bending of the antennae towards the electrode by the attraction of opposite charges (Fig. 7B). The imposed deflection of the antennae is detected by sensory receptors leading to a marked bending of the antennae as they are actively withdrawn from the forces attracting them to the electrode. Thus, the cockroaches use their antennae as multi-modal sensors to detect many external cues (Bell and Adiyodi, 1981). Electric fields cause displacement of the antennae about the head–scape joint, deflecting S-HP sensilla. There are three S-HPs on adult cockroach antennae located on the dorsal, medial and lateral surfaces (Staudacher et al., 2005) that detect antennal position in all planes (Okada and Toh, 2001). We have clearly established that it is the displacement of the antennae by electrical forces that are detected by the S-HP mechanoreceptors, enabling an animal to perceive static electric fields. The antennae are known to play a crucial role in insect behaviour and their deflection evokes avoidance or escape movements (Camhi and Johnson, 1999; Comer et al., 2003; Cowan et al., 2006; Okada and Toh, 2006). Information on antennal position is not only provided by the hair plates on the scape but also from pedicel hair plates, from the flagella and from internal movement detectors (Comer et al., 2003; Okada and Toh, 2000; Okada and Toh, 2006; Staudacher et al., 2005). Together, they provide information about deflection of the antennae in all planes of movement (Okada and Toh, 2001; Staudacher et al., 2005).

A number of studies have shown that the activation of proprio- and exteroceptors on the antennae mediate escape, and other locomotor activities, in response to antennal stimulation (Camhi and Johnson, 1999; Comer et al., 2003; Cowan et al., 2006; Okada and Toh, 2006). Hence, displacement of the antennae by electric fields activates sensory receptors involved in generating avoidance responses. The scape hair plates mediate a variety of behaviours, not only in cockroaches but also in a number of insects including locusts (Gewecke, 1974), stick insects (Durr et al., 2001), bees (Kloppenburg, 1995) and crickets (Staudacher et al., 2005). Such behaviours include locomotion and flight, antennal avoidance reflexes and object orientation (Gewecke, 1974; Okada and Toh, 2000; Sherman and Dickinson, 2004; Staudacher et al., 2005).

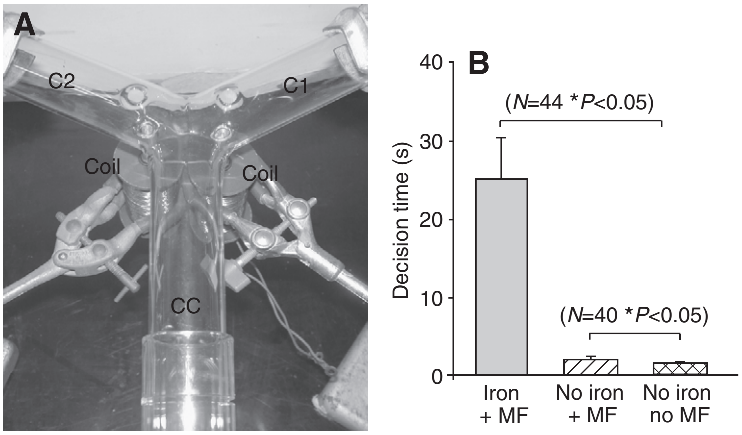

Fig. 6. Avoidance of magnetic fields (MF) by animals with iron-particle-coated antennae. (A) Photograph of the electromagnet Y-tube apparatus. The distal end of an electromagnet (Coil) was positioned at the entrance to both the anterior pathways. C1 and C2, chambers; CC, central chamber. (B) The time taken by cockroaches confronted by MF to make a decision within the Y-tube apparatus. The time in the decision zone was greater when cockroaches were exposed to MF (N=40, P<0.05). The decision time did not differ between individuals exposed and not exposed to MF without iron powder (N=40, P>0.05). MF did, however, have an effect on cockroach decision time when antennae were coated with iron particles (N=44, P<0.05).

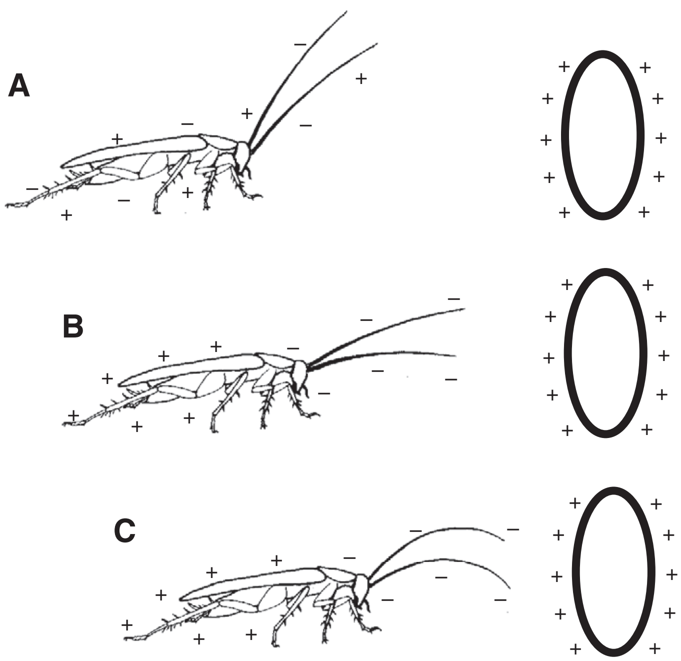

Fig. 7. Summary of effects of electric fields on the cockroach. (A) Before encountering a positively charged electrode the electrical charges on a cockroach are randomly distributed (+ and –, positive and negative charges, respectively). (B) As a cockroach approaches a positively charged electrode the electric field induces an uneven charge distribution on the cockroach with negative charges being attracted to the antennae, which, in turn, causes passive deflection of the antennae towards the electrode as opposite charges are attracted. (C) The passive deflection of the antennae is detected by sensory receptors at their base (the head–scape hair plate) that generates a withdrawal of the antennae away from the electrode leading to a pronounced bending of the antennae.

Notably, the basal joints play an important role in triggering cockroach escape away from the direction of an antennal stimulus (Comer et al., 1994; Ye et al., 2003). Together, the influences of electric fields on antennae and the behaviour mediated by scape hair plates may therefore underpin the avoidance evoked by cockroaches confronted with static electric fields.

Descending interneurones and the avoidance of static electric fields

To demonstrate that antennal deflection caused by electrical forces could lead to changes in the activity of interneurones involved in avoidance responses, we developed a method of deflecting the antennae using magnetic fields to mimic the deflections caused by electric fields. These experiments showed that the magnetic fields themselves did not cause a change in behaviour of the insects but that when combined with deflection of the antennae covered in iron powder they did.

Stimulation of the antennae has a substantial effect on thoracic motor output, believed to be controlled by connections between descending mechanosensory interneurones (DMIs) and thoracic interneurones (TIs) (Ritzmann and Pollack, 1994; Ritzmann and Pollack, 1998). We showed that the activity of the VNCs, which is likely to result from DMIs activation (Burdohan and Comer, 1996; Ye and Comer, 1996), increased when the antennae were deflected using magnetic stimulation, suggesting that the DMIs responded to antennal deflection. Previous studies have shown that the DMIs converge onto TIs and cause TI excitation and, subsequently, movement (Ritzmann et al., 1991). Given the similarities in the influences of magnetic and electric fields on cockroach antennae, our results suggest that the DMIs are, at the very least, partly involved in mediating the avoidance of static electric fields.

Mechanosensory afferents from both the head–scape and scape–pedicel joints project primarily to the deutocerebrum *via* the antennal lobe (Okada and Toh, 2000; Staudacher et al., 2005). Mechanosensory neurones do not connect directly with DMIs in the antennal lobe (Burdohan and Comer, 1996) but branch within the deutocerebrum (Staudacher et al., 2005), with the DMIs passing down the VNC, ultimately activating leg motor neurones *via* the TIs. Stimulation of exteroceptors at the head–scape joint can, therefore, elicit motor output (Burdohan and Comer, 1996; Ritzmann and Pollack, 1994) but preventing activation will prevent motor output.

We show that cockroaches are able to detect static electrical fields and avoid them. They do this not with a specialised detection system but by virtue of having long antennae that are easily charged and displaced by electric fields. This raises the possibility that other insects may also respond to electric fields in the same way and potentially may lead to the development of alternative measures of pest control.

This work was made possible by an award from the NERC to C.W.J. and P.L.N., a travel award to E.P.H. from the Company of Biologists and an award from the Ministry of Science, Sport, Culture and Technology to M.T.

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