

RESEARCH ARTICLE

Static electric fields modify the locomotory behaviour of cockroaches

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Accepted 1 March 2011

SUMMARY

Static electric fields are found throughout the environment and there is growing interest in how electric fields influence insect behaviour. Here we have analysed the locomotory behaviour of cockroaches (*Periplaneta americana*) in response to static electric fields at levels equal to and above those found in the natural environment. Walking behaviour (including velocity, distance moved, turn angle and time spent walking) were analysed as cockroaches approached an electric field boundary in an open arena, and also when continuously exposed to an electric field. On approaching an electric field boundary, the greater the electric field strength the more likely a cockroach would be to turn away from, or be repulsed by, the electric field. Cockroaches completely exposed to electric fields showed significant changes in locomotion by covering less distance, walking slowly and turning more often. This study highlights the importance of electric fields on the normal locomotory behaviour of insects.

Key words: static electric field, high voltage, walking, locomotion, insect.

INTRODUCTION

Natural electric fields exist between the Earth's surface and the outer atmosphere and are generated by a variety of sources including a global electric circuit that is produced and maintained predominantly by thunderstorms (Adlerman and Williams, 1996; Bering et al., 1998; Williams, 1994), which can generate a difference in electrical potential between the Earth's surface and outer atmosphere of approximately 250 kV. This potential difference results in naturally occurring electric fields at ground level of 100–300 V m⁻¹ (Adlerman and Williams, 1996; Bering et al., 1998; Israel, 1971; Reiter, 1993; Rycroft et al., 2000; Williams, 1994). High voltage power lines and electrical equipment contribute to man-made electric fields in the environment by generating electromagnetic and electrostatic fields many orders of magnitude greater than those that occur naturally. For example, quasi-static electric fields beneath power lines vary according to operating voltage, yet can reach up to 11 kV m⁻¹ at ground level (Bracken et al., 2005) and are far higher at closer proximity to the power line (Fews et al., 1999a; Fews et al., 1999b), whereas electric fields surrounding electrical equipment reach over 20 kV m⁻¹ (Repacholi and Greenebaum, 1999). Interactions between materials also generate electric fields, such as those generated when we walk across a carpet, that may reach up to 30 kV m⁻¹ (Chubb and Malinverni, 1993) in a process termed triboelectrification. Insects may accumulate a net electric charge produced when walking on specific surfaces (Colin et al., 1991; Edwards, 1962; Jackson and McGonigle, 2005; Yes'Kov and Sapozhnikov, 1976), and during flight by the wings rubbing against the body or within the air (Gan-Mor et al., 1995; Yes'Kov and Sapozhnikov, 1976).

Relatively few studies have focused on the responses of animals, and insects in particular, to static electric fields. Those studies have shown that static electric fields can cause involuntary movements of appendages, such as the antennae (Maw, 1961; Yes'Kov and Sapozhnikov, 1976) and the wings (Bindokas et al., 1989; Watson et al., 1997). Deflection of hairs on the legs of spiders has also been

reported when individuals are exposed to electric fields similar to those beneath power lines (Orlov and Romanenko, 1989). It has recently been shown that cockroaches are able to detect electric fields by means of their antennae (Hunt et al., 2005; Newland et al., 2008) and these movements underpin avoidance behaviour. The antennae are highly active and flexible appendages that are present on all insects (Okada and Toh, 2001; Schneider, 1964) and in cockroaches they contribute to escape responses via the activation of mechanoreceptors at the base of the antennae during movement (Comer et al., 1994; Stierle et al., 1994). Thus deflection leads to the activation of descending interneurons that, in turn, mediate avoidance movements (Newland et al., 2008).

Even fewer studies have attempted to quantify the effects of static electric fields on the locomotory movements of insects and these have shown that changes in movement are correlated with electric field strength (Edwards, 1960; Maw, 1961; Maw, 1962; Watson et al., 1997). Flying insects presented with a choice of a static electric field or no field exhibit a preference for no field (Perumpral et al., 1978), yet it is not known whether such preferences are exhibited by terrestrial walking insects confronted with static electric fields and how such environments may alter normal locomotory behaviour. Given that static electric fields from power lines can have deleterious effects on some insect populations (e.g. bees) (Bindokas et al., 1988) under certain environmental conditions, it is pertinent to determine how static electric fields affect insect locomotion, and also to consider the possibility of using electric fields as barriers to insect movement. In this study we therefore quantify how the locomotory behaviour of cockroaches is modified by exposure to electric fields of varying strengths.

MATERIALS AND METHODS

Cockroaches (*Periplaneta americana* Linnaeus 1758) were maintained at the School of Biological Sciences, University of Southampton, Southampton, UK, and raised at 28±1°C (mean ±

s.e.m.) with $30\pm4\%$ relative humidity under a 12h:12h light:dark regime. Egg cases and young nymphs were regularly isolated for instar determination. All experiments were carried out on third and fourth instar cockroaches of both sexes for two reasons. First, using small cockroaches allowed us to minimise the size of the experimental arena to fit within the field of view of the video system used for analyses (see below); second, small body size allowed us to reduce the magnitude of the applied voltages used to evoke behavioural responses (from the equation $V=Ed$, where V is voltage, E is electric field and d is distance).

Experimental arena

Cockroaches were exposed to static electric fields produced by an aluminium wire mesh semi-circle (130 mm radius, mesh size 2.8 mm, Locker Wire Weavers Ltd, Cheshire, UK) positioned above and to one side of a glass arena (190×30 mm, diameter×height; Fig. 1A). The mesh was connected to a high voltage power supply (Brandenburg Alpha III, Dudley, West Midlands, UK). An identical earthed wire mesh semi-circle was placed on the opposite side, with a gap (30 mm) between the meshes to localise the electric field to the side of the arena on which the field was applied. The arena was placed on white paper (210 mm diameter), beneath which an earthed wire mesh semi-circle (130 mm radius) was positioned, acting as a parallel earth plate. The arena was covered by a glass sheet (205×205×3 mm) to hold the mesh

sections in place and prevent air movement within the arena and positioned on a black medium-density fibreboard (298×298×15 mm) on which reference points were marked to ensure a consistent arena position for video analysis. This glass, and the glass arena itself, has a negligible effect on the electric field inside the arena. The setup was contained within an earthed enclosure to reduce visual input, air movement and external electric fields. Cockroach behaviour within the arena was filmed for 10 min using a digital camera (Sanyo VCB-3372P, 1/3" CCD, 560 lines; Japan) with lens (Computar® 03A; Japan) and recorded onto DVD (Panasonic DMR-E55EB; Osaka, Japan) at 25 frames s⁻¹.

Experimental procedure

The experimental protocol followed a randomised complete block design (RCBD) using six voltage levels of 0, 1, 2, 3, 4 and 5 kV applied to the mesh. These voltages were chosen to determine the range of electric fields that cockroaches would respond to. Twenty-one repeats were carried out for each voltage, and three blocks of treatments were performed each day to control for any time or day effects (Wyatt, 1997). Control tests using an arena with no electric field were also included in the RCBD.

At the beginning of each day, third and fourth instar cockroaches (mean \pm s.e.m. body length = 8.13 ± 0.7 mm, $N=126$) were selected randomly from culture and isolated in preparation for analysis. Before each trial began, the arena was set up as in

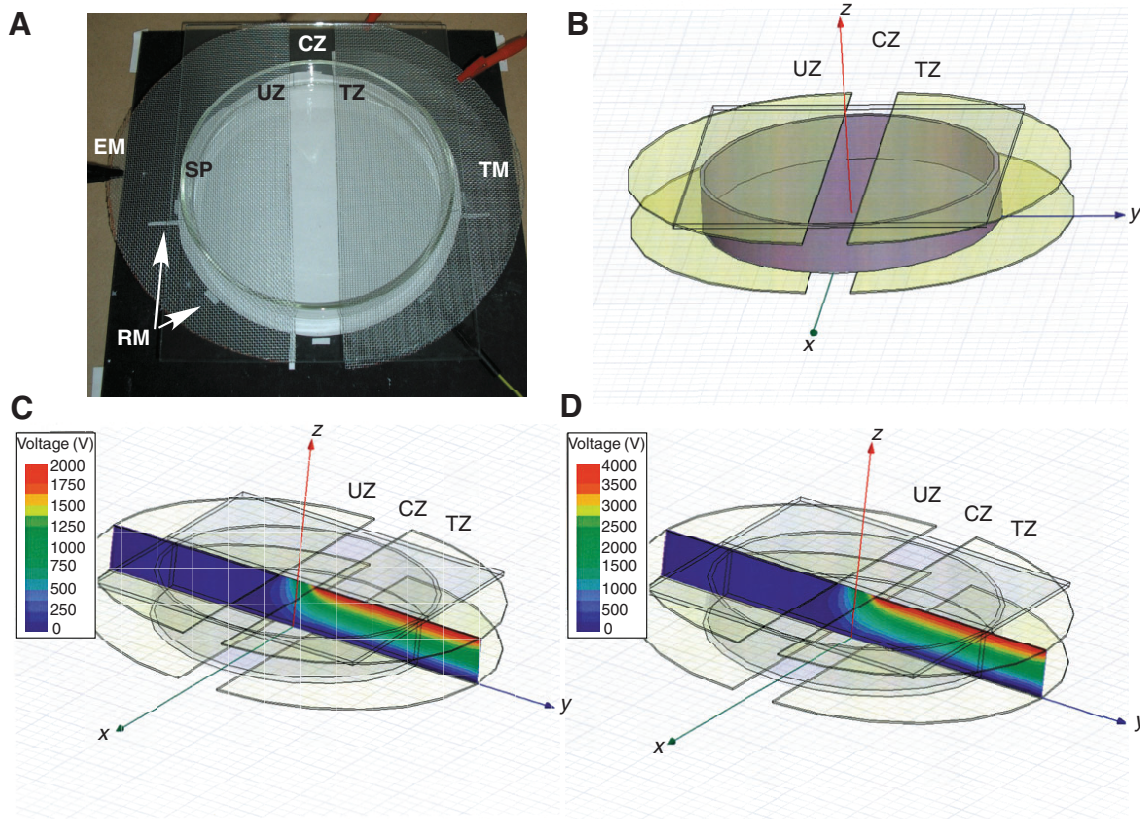


Fig. 1. The circular arena and electric field models. (A) In the arena, the earth mesh (EM) ensured that the electric field emitted from the treated mesh (TM) was localised to the treated zone (TZ). The electric field was localised vertically using a mesh semi-circle positioned below the treated mesh and connected to earth via an earth wire. The arena was positioned using the reference marks (RM). Each trial began when the cockroach passed a start point (SP) after a 2 min rest period. CZ, central zone; UZ, untreated zone. (B) Maxwell® model of the arena based on the materials and dimensions of the arena in A. (C) Section through a Maxwell® three-dimensional electric field visualisation with an applied voltage of 2 kV shows that there were no electric fields within the UZ in which the mesh above the arena was grounded. Electric fields were mainly restricted to the TZ with some spread into the CZ. (D) With an applied voltage of 4 kV, the extent of spread within the CZ did not differ substantially from that at 2 kV.

Fig. 1A and aligned with the reference marks. The glass sheet was temporarily removed and a cockroach was carefully placed into the central zone of the arena using storkbill forceps. The glass sheet was replaced, mesh sections were repositioned and the cockroach was allowed to rest for 2 min. After the rest period, video recording was started and the high voltage power supply was turned on at the appropriate voltage when the cockroach was positioned at the start point (Fig. 1A).

After 10 min, the power supply was turned off and the cockroach was removed. All mesh sections were rotated 90 deg clockwise to control for any room effects and two further trials were carried out with different cockroaches before washing the arena. The washing procedure involved soaking the arena in hot 5% Decon90[®] solution (55°C; Fisher Scientific, Loughborough, UK) for 15 min and then rinsing it in distilled water. Any potential remaining pheromone traces were removed by liberally washing the arena with 100% acetone. The arena was then placed in a drying chamber at 110°C for a minimum of 10 min to remove the acetone. The arena was cooled to room temperature before being used for experimental tests. All experiments were carried out under red light at $22.9 \pm 1.8^\circ\text{C}$ and $38.6 \pm 6\%$ relative humidity.

Behavioural analysis

The effects of varying field strength on cockroach locomotor activity and the distribution of cockroaches within the arena were analysed using video analysis software (EthoVision[®] 3.1, Noldus Information Technology, Wageningen, The Netherlands). Comparisons of cockroach behaviour between each zone (untreated, central and treated) were made using five behavioural parameters measured in each zone: time spent walking (s), distance moved (cm), velocity (cm s^{-1}), absolute unsigned meander (deg cm^{-1}) and absolute unsigned angular velocity (deg s^{-1}). Meander was calculated from the equation: $\text{meander} = \text{relative turn angle} / \text{distance moved}$. EthoVision[®] automatically assigned and logged the *x*- and *y*-coordinates of the centre of each individual at 12 samples s^{-1} for the 10 min trial duration.

The effect of field strength on each behavioural parameter in each zone was tested using one-way ANOVA with *post hoc t*-tests after the assumptions of normal distribution and homogeneity of variance of the data had been met (Kolmogorov–Smirnov and Levene's test, respectively). Data that did not meet the assumptions were log

transformed and re-tested (Sokal and Rohlf, 1995). Differences between the zones for each behaviour, at each voltage potential, were investigated using independent *t*-tests. All tests were carried out using SPSS (version 12, IBM, Somers, NY, USA) and significance was determined at the $P < 0.05$ level.

Visualising static electric fields

Due to the small size of the arena, in which it was impossible to measure directly the level of electric fields, we used Maxwell[®] (ANSYS, Canonsburg, PA, USA) three-dimensional analytical and visualization software for electromagnetic field simulation to calculate the extent of electric fields within the experimental arena. Maxwell[®] uses finite element methods to solve Laplace partial differential equation of the electric potential for given materials and boundary conditions. Using Maxwell[®], we generated a theoretical model of electric fields based on the real dimensions and properties of materials of the test arena (Fig. 1A,B) to visualise the electric fields (Fig. 1C,D). The wire mesh electrodes were modelled as solid conducting plates as the size of the mesh was small, which is a reasonable approximation for a static electric field. The accuracy of the Maxwell[®] solution was improved by refining the mesh so that the modelling errors were less than 1%.

RESULTS

The static electric fields within the test arena were calculated using Maxwell[®] software based on the properties, both materials and geometry, of the model (Fig. 1B) that were based on the real test arena (Fig. 1A). From the visualisations shown in Fig. 1C,D, it is clear that electric fields were mainly restricted to the treated zone with some spread to the central zone but none in the untreated zone, in which the mesh above the arena was grounded. The field strengths within the central zone did not differ substantially between 2 and 4 kV (Fig. 1C,D).

To analyse the effects of static electric fields on cockroach behaviour, individual cockroaches were placed into the test arena and different electric fields were applied. Under control conditions with no electric field, the walking tracks generated using EthoVision[®] analysis showed that individual cockroaches walked in all areas of the arena but commonly at the outer perimeter (Fig. 2). This type of walking behaviour is typical of cockroaches, which

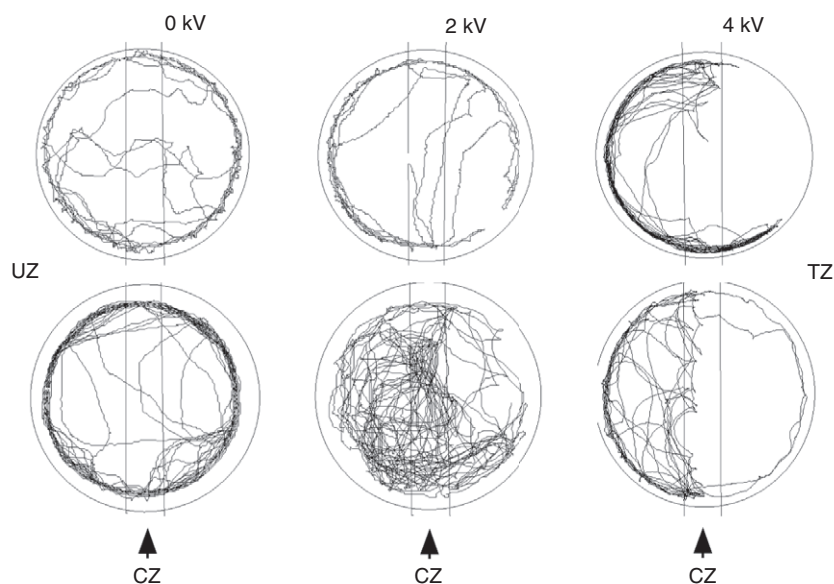


Fig. 2. Walking tracks of cockroaches under electric fields. Two representative examples of the walking tracks of cockroaches generated using EthoVision[®] at each of three test voltages, 0, 2 and 4 kV, are shown. For each example, the UZ is shown on the left of each diagram and the TZ on the right.

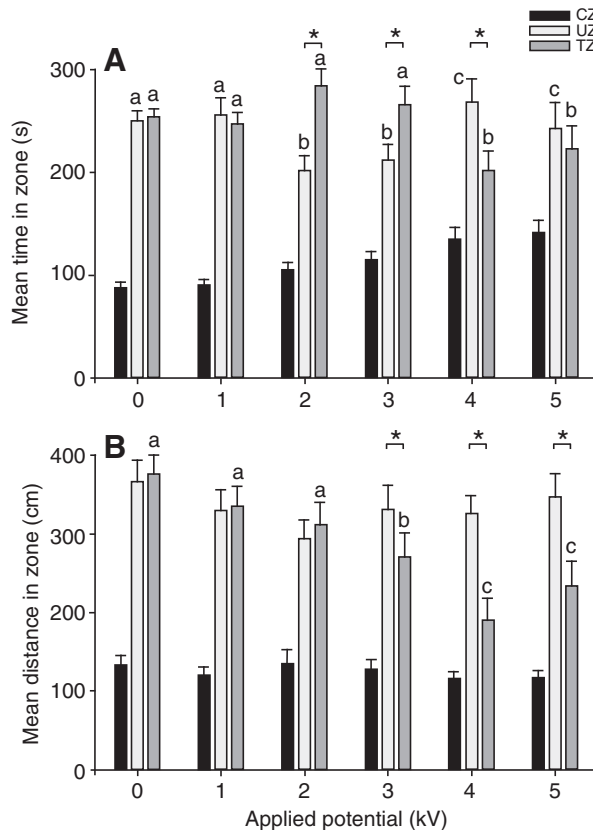


Fig. 3. Effects of electric fields on walking behaviour. (A) The effect of applied voltage on the mean (\pm s.e.m.) time cockroaches spent in each zone of the arena. The electric fields caused by the applied voltages significantly affected the time spent in the CZ, TZ and UZ ($P<0.05$). (B) The effect of applied voltage on the mean (\pm s.e.m.) distance cockroaches moved in each zone. Distance moved in the TZ significantly decreased as the applied voltage potential increased (3 kV and above; $d.f.=118$, $P<0.05$ in both cases). Different letters indicate significant differences within a zone between voltage potentials. Asterisks indicate significant differences between zones.

tend to follow edges during walking (Camhi and Johnson, 1999). With 0 V (control) applied to the treated zone, cockroaches spent a similar amount of time within the treated and untreated zones (Student's t -test, $t=0.173$, $d.f.=40$, $P>0.05$). Similarly, the distance moved within the treated and untreated zones was not significantly different ($t=0.166$, $d.f.=40$, $P>0.05$), indicating that cockroaches show no side-specific preferences within the arena.

In addition, many other temporal parameters of movement were similar on both sides of the arena under control conditions (0 kV). Analysis of mean velocity ($t=-0.125$, $d.f.=40$, $P>0.05$), meander ($t=-0.267$, $d.f.=40$, $P>0.05$) and angular velocity ($t=-0.176$, $d.f.=40$, $P>0.05$) showed that they were similar on both sides of the arena. Together, these results indicate that cockroaches were not susceptible to external stimuli causing side bias and that the resulting changes in behaviour described below are the result of the applied electric fields.

Time spent within zones

The region of the arena favoured by cockroaches differed as the applied electrode voltage increased (Figs 2, 3). For example, the greater the applied voltage the greater the mean time spent in the untreated zone ($F_{5,118}=3.37$, $P<0.05$; $F_{5,120}=2.66$, $P<0.05$) (Fig. 3A).

At intermediate applied voltages (2 and 3 kV), cockroaches spent more time in the treated than the untreated zone ($t=4.188$, $d.f.=40$, $P<0.05$; $t=1.88$, $d.f.=40$, $P<0.05$, respectively). This behaviour was reversed at 4 kV, when cockroaches avoided the electric field generated within the treated zone and spent significantly less time in the treated zone in comparison to 1–3 kV ($d.f.=118$, $P<0.05$ for all cases). In addition, cockroaches spent more time in the untreated zone at 4 kV ($t=2.746$, $d.f.=40$, $P<0.05$).

Cockroaches also spent significantly more time in the central zone as the applied voltage potential was increased from 0 to 5 kV ($F_{5,120}=7.05$, $P<0.05$). This could be attributed to decreased locomotion and/or higher turning rates in that zone (parameters that are described below). The shorter overall time spent in the central zone compared with adjacent zones ($N=40$, $P<0.05$ in all cases) simply reflects the smaller area of the central zone compared with the treated and untreated zones.

In addition, the wall-following behaviour typically shown under control conditions would break down at voltages of 2 kV and above, with animals crossing and re-crossing the arena or following the edge of the electric field (Fig. 2).

Distance moved in zones

The distances moved by cockroaches in the untreated zone did not differ significantly as the applied voltages were increased from 1 to 5 kV ($F_{5,120}=0.996$, $P>0.05$; Fig. 3B). Cockroaches in the treated zone, however, covered significantly less distance at the same applied voltages ($F_{5,118}=5.841$, $P<0.05$). *Post hoc* analysis revealed that this effect was most apparent at applied voltages of 3 kV and above ($d.f.=118$, $P>0.05$ in all cases). The distance that cockroaches moved was only affected when a cockroach was under an electric field. This was clearly demonstrated by the results showing that the distance travelled by individuals subjected to an electric field in the central zone did not differ as the applied voltage was increased ($F_{5,120}=0.77$, $P>0.05$). Together, these results demonstrate that the distance travelled by cockroaches was reduced only for cockroaches continuously exposed to a static electric field.

Velocity of walking movements

There was a significant inverse relationship between the velocity of walking of cockroaches within the treated zone and the applied voltage ($F_{5,118}=6.38$, $P<0.05$; Fig. 4A). This further supports the notion that locomotion was attenuated when cockroaches were subjected to increasing field strengths. The decrease in velocity was only evident in response to electric fields caused by applied voltages of 2 kV and higher ($d.f.=118$, $P<0.05$ in all cases), which were adequate to cause slower movement in the treated zone compared with the untreated zone ($d.f.=40$, $P<0.05$ in all cases).

Walking velocity was also attenuated within the central zone as the applied voltage was increased ($F_{5,120}=5.82$, $P<0.05$), and was most apparent for applied voltages of 3 kV and above ($d.f.=120$, $P>0.05$ for both cases). Control tests (0 V) showed that there were no significant differences between the central, treated or untreated zones ($N=40$, $P>0.05$ in all cases).

Absolute meander

Cockroaches exhibited greater turning, or sinuosity, when subject to electric fields within the treated zone as the applied voltage was increased ($F_{5,120}=11.8$, $P<0.05$; Fig. 4B). Increasing the field strength also caused an increase in turning behaviour, or meander, within the central zone ($F_{5,118}=8.873$, $P<0.05$). Hence, cockroach sinuosity increased when individuals were both positioned within and confronted by static electric fields.

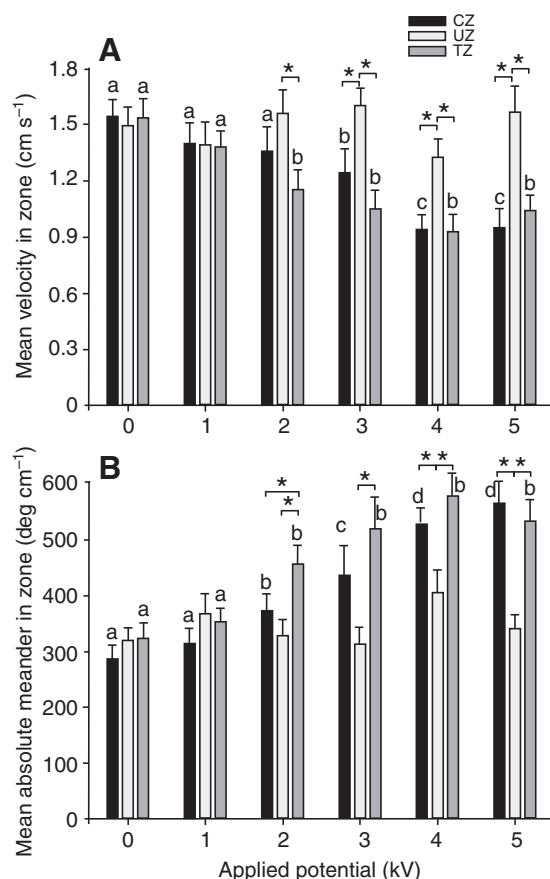


Fig. 4. Electric fields influence walking speed and turning behaviour. (A) The effect of applied voltage on the mean (\pm s.e.m.) velocity of cockroaches in each zone of the arena. A significant effect of voltage potential on velocity occurred in the CZ and TZ. Cockroach velocity in the UZ was not affected by field strength. Different letters indicate significant decreases in the velocity within zones as the applied voltage was changed. Asterisks indicate significant differences between zones. (B) The effect of applied voltage on the mean (\pm s.e.m.) absolute meander of cockroaches in each zone of the arena. Raising the voltage significantly increased meander in both the CZ and the TZ (2 kV and above; d.f.=120, $P<0.05$; d.f.=118, $P<0.05$, respectively), yet meander in the UZ was not affected. Differences between the zones indicate increased sinuosity in the TZ compared with the CZ or UZ when a 2 kV potential was applied ($t=2.39$, d.f.=42, $P<0.05$; $t=3.17$, d.f.=42, $P<0.05$). Meander was greater in the CZ than the UZ at 4 kV potentials and above ($t=1.99$, d.f.=42, $P<0.05$; $t=4.04$, d.f.=42, $P<0.05$). Different letters indicate significant differences within a zone between voltage potentials. Asterisks indicate significant differences between zones.

Increased turning was apparent within both the treated and central zones when cockroaches were exposed to applied potentials of 2 kV (d.f.=118, $P<0.05$ in all cases). Meander was significantly more frequent in the treated zone compared with the central and the untreated zones ($t=1.98$, d.f.=42, $P<0.05$; $t=4.04$, d.f.=42, $P<0.05$, respectively) at applied voltages of 2 kV and above.

Absolute angular velocity

Increasing the applied voltage also had a significant effect on the rate of turning, or angular velocity, in cockroaches confronted with, and subjected to, electric fields ($F_{5,120}=9.19$, $P<0.05$; $F_{5,118}=8.33$, $P<0.05$, respectively; Fig. 5). Applied voltages of 4 kV and above evoked an increased angular velocity in the central zone (d.f.=120, $P<0.05$ in both cases), whereas 2 kV potentials were adequate to

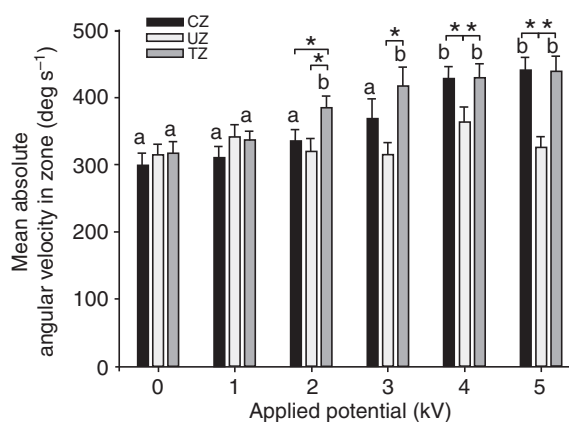


Fig. 5. The effect of applied voltage on the mean (\pm s.e.m.) angular velocity of cockroaches in each zone of the arena. Increasing the applied voltage led to a significantly increased angular velocity in the CZ and the TZ ($P<0.05$ in both cases) whereas it was unaffected in the UZ. Significant increases in angular velocity occurred in the CZ at 4 kV and above (d.f.=120, $P<0.05$). Angular velocity significantly increased within the TZ when a 2 kV potential was applied (d.f.=118, $P<0.05$) and was greater than in the CZ and the UZ at 2 kV ($t=2.58$, d.f.=40, $P<0.05$; $t=-2.88$, d.f.=40, $P<0.05$, respectively). Potentials of 4 kV were required to elicit greater angular velocity within the CZ compared with the UZ ($t=2.43$, d.f.=40, $P<0.05$; $t=4.42$, d.f.=40, $P<0.05$, respectively). Different letters indicate significant differences within a zone between voltage potentials. Asterisks indicate significant differences between zones.

elicit a greater angular velocity within the treated zone (d.f.=118, $P<0.05$).

DISCUSSION

Fabre first suggested that invertebrates respond to atmospheric electric fields following observations of heightened activity of dung beetles before a thunderstorm (Fabre, 1918). Subsequent laboratory studies that exposed insects to electric fields of magnitudes similar to those within the atmosphere have also provided evidence that insects could respond to naturally occurring electric fields. For example, Maw (Maw, 1961) found that mosquitoes would aggregate in regions of high atmospheric field strength, and the fruit fly, *Drosophila melanogaster*, and the blow fly, *Calliphora vicina*, show decreased locomotion when exposed to fields of $\sim 0.5 \text{ kV m}^{-1}$ and above (Edwards, 1960). More recent field studies have also shown decreased flying activity and decreased foraging of insects in the vicinity of power lines, in addition to lowered populations (Bindokas et al., 1988; Orlov, 1990; Orlov and Babenko, 1987).

Our results reveal distinct changes in the locomotory behaviour of free-moving cockroaches when encountering or walking within electrostatic fields likely to be generated in the environment. For example, electrostatic fields were found to act as aversive stimuli with cockroaches being less likely to walk under them the greater the field strength and, when within an electric field, their locomotory performance was significantly altered.

Modification of locomotory behaviour under electric fields

Watson et al. showed that exposure of *Drosophila* to a static electric field resulted in the flies attempting to move out of the field (Watson et al., 1997). Similarly, we found that at applied potentials of 2 and 3 kV (equivalent to electric field strengths of $66\text{--}100 \text{ kV m}^{-1}$, from the equation $V=Ed$) cockroaches walked less in terms of distance in electric fields compared with at lower applied voltages; however,

this was associated with more time spent in the field. This apparent dichotomy can be explained by the changes observed in walking behaviour of animals in electric fields where they frequently paused, covered less distance, walked more slowly and turned more often. The walking velocity of cockroaches subjected to 66–100 kV m⁻¹ static electric fields within the treated zone decreased compared with controls, supporting the notion that insects often paused, resulting in intermittent movement. These changes in behaviour would result in more time spent in the field, as was found in the present study, even though it may evoke avoidance at high field strengths (as has been shown previously) (Newland et al., 2008). At greater field strengths of 133 kV m⁻¹ and above, velocity continued to decrease, causing cockroaches to slow down rather than elicit more pausing. Such a response is termed inverse orthokinesis, and commonly occurs in insects in response to odours and mechanical stimuli (Kennedy, 1977; Kennedy, 1978). Earwigs, *Forficula* spp., slow down in response to tactile stimulation and have a tendency to remain in crevices, and do so by thigmotaxis – turning towards and slowing down in response to mechanical contact (Fraenkel and Gunn, 1961; Jeanson et al., 2003). Our studies show that when there was no electric field present, cockroaches would often walk around the perimeter of the arena. When electric fields were applied, this type of behaviour often broke down, with cockroaches crossing and re-crossing the arena. Cockroaches are normally highly thigmotactic and their antennae play an important role in detecting mechanical stimuli and mediating responses to walls (Camhi and Johnson, 1999; Cowan et al., 2006). Given the influences of electrical fields on the antennae of cockroaches (Hunt et al., 2005; Newland et al., 2008), any disruption to their normal movement by static electric fields (Newland et al., 2008) is likely to lead to a substantial changes in walking behaviour and be responsible for the arrestment of free-moving cockroaches exposed to electric fields, as we have shown here. In addition, obstacle negotiation in cockroaches also requires sensory input from the antennae (Harley et al., 2009), and any disruption in the normal movements of the antennae is likely to impair the negotiation around objects.

In cockroaches, the antennae are involved in the detection of electric fields (Newland et al., 2008) whereas *Drosophila* may utilise sensory systems at the bases of the wings, as the wings appear to be ‘pulled open’ in the direction of the electrostatic field. Given the lack of effect of other sensory structures (Hunt et al., 2005), the changes in walking behavior shown by the animals analysed in this study are therefore likely to be mediated by antennal deflection and activation of interneurons encoding directional information from the antennae (Newland et al., 2008; Ritzmann and Pollack, 1994; Ritzmann and Pollack, 1998).

Avoidance of electric fields

It has been shown that flying insects, such as cabbage loopers, presented with a choice of a static electric field or no field exhibit a preference away from the field (Perumpral et al., 1978); more recently, Hunt et al. (Hunt et al., 2005) and Newland et al. (Newland et al., 2008) showed similar preferences in cockroaches. The present study goes further and demonstrates that at applied voltages in the range of 2–5 kV, equivalent to substantial field strengths of 66–166 kV m⁻¹, cockroaches spent less time in the field and were less likely to enter a field at greater field strengths. Cockroaches have been shown to avoid an electrostatic field in one arm of a Y-choice chamber (Newland et al., 2008) in which a circular ‘barrier’ type electric field was generated, and to friction-charged dielectric surfaces (Hunt et al., 2005). Vertebrates such as mice and pigs exposed to 60 Hz electric fields (similar orders of magnitude to those

found in the environment), when given a choice, spend more time out of the field rather than under it (Hjerresen et al., 1982). It is not yet known how and why animals avoid fields, although studies in invertebrates and vertebrates have provided some clues as the forces elicited by electric fields deflect sensory appendages (Newland et al., 2008) and bend hairs of humans (Shimizu and Shimizu, 2003; Shimizu and Shimizu, 2004). Extreme static electric fields can also have harmful effects on organisms. For example, chromosomal aberrations have been shown to occur in plants and invertebrates (McCann et al., 1998; McCann et al., 1993), and adverse effects on cell membrane transport (Funk and Monsees, 2006) have been reported in organisms exposed to extremely low frequency electric fields for more than 24 h. In *Drosophila*, chromosome mutation has been revealed at field strengths of 330 kV m⁻¹ (Portnov et al., 1975) and Edwards (Edwards, 1961) has shown a slowed development and reduced fecundity in phantom hemlock loopers. These high electric levels are extremely rare and transient in the natural environment (such as those caused by lightning), so that although animals undoubtedly respond to electric fields, their avoidance responses to them are unlikely to have evolved as specific defence mechanisms. Because more common man-made electric fields of these magnitudes, which *Drosophila* have also been shown to respond to (Edwards, 1960), have only been present in the environment following the wide-scale use of electricity for industrial and residential use since the 19th century, it is again unlikely that specific receptors have evolved over this short time scale.

The results of this study demonstrate that the behaviour of free-moving cockroaches is significantly influenced by static electric fields and that the responses are related to field strength. Given the avoidance of electric fields previously reported in other insects (Maw 1964; Perumpral et al., 1978) and also exhibited by cockroaches (Newland et al., 2008), it is clear that many free-moving animals show a number of altered behaviours when exposed to static electric fields. In cockroaches, this was most apparent at high field strengths, which could be considered to be acting at repellent levels. Understanding the normal behavioural responses of cockroaches to static electric fields not only advances current knowledge of the influences of electric fields on insects, but also is important in developing pest control methods based on insect avoidance of electric fields (Foster and Harris, 1997).

ACKNOWLEDGEMENTS

We are grateful to our Southampton colleagues for their helpful comments on early versions of the manuscript. This work was made possible by an award from the Natural Environment Research Council to C.W.J. and P.L.N.

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