The effect of electric stimuli on German cockroach behaviour

by

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Abstract

Some insects reportedly associate with electrical circuits while others avoid electric fields. This thesis presents evidence that electrical circuits modify the behaviour of several insects, attracting or arresting *Blattella germanica*, *Supella longipalpa*, *Lepisma saccharina*, *Thermobia domestica* and *Forficula auricularia,* and repelling *Periplaneta americana*. Based on extensive experimentation, it appears that primarily the electric component of electromagnetic fields contributes to the attraction and/or arrestment response of *B. germanica.* Furthermore, I present evidence that *B. germanica* may utilise electro-communication. The evidence includes (1) the attraction of virgin males, but not mated males, virgin females or nymphs, to specific electromagnetic fields; (2) recordings of electrical pulses associated with insect presence; (3) greater incidence of electrical pulses in groups of females and males than in unisexual groups of males or females; and (4) exhibition of pre-copulatory wing raising behaviour by males exposed to electrical pulses as recorded from females and reproduced.

Keywords: German cockroach, *Blattella germanica*, electric fields, electro-communication, attraction/arrestment

Dedication

For my Dad.

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The text of this dissertation includes manuscripts formatted for future submission. The co-author Dr. Gerhard Gries listed in these publications directed and supervised the research which forms the basis for the dissertation.

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1. Is there an electrosensory modality in the German cockroach, *Blattella germanica*?

1.1. Sensory modalities utilised as communication signals and foraging cues in arthropods

Insects and other arthropods interpret their environment by means of various sensory modalities, including vision, audition, olfaction and touch (Bradbury and Vehrencamp 1998). With these senses, insects gather information about their surroundings, reducing uncertainty and responding to environmental and social parameters in a manner that will maximize their chances for survival and reproduction (Greenfield 2002). Animals gather information as signals which are shaped by natural selection to convey specific information, or as cues which provide information through their chance association with environmental parameters or other organisms' behaviour or metabolism (Otte 1974, Krebs and Dawkins 1984, Danchin *et al.* 2004).

A semiochemical is a message bearing chemical emitted by plants or animals that induces a behavioral or physiological response in another organism (Wyatt 2003). Insects detect volatile semiochemicals by olfaction and surface-bound semiochemicals by gustation (Gerber 2009, Sato and Touhara 2009). Semiochemicals are referred to as pheromones if the target organism is a conspecific (Wyatt 2003). They are communication signals that help coordinate behavior such as courtship, mating, aggregation, dispersal and oviposition (Birch 1988).

Insects also utilise vibratosensory modalities, in the form of audition of airborne vibrations and tactile sensation of substrate-borne vibration (Claridge 2006, Virant-Doberlet and Zorovic 2006). Substrate-borne vibrations act as communication signals in insects and spiders (Klamring 1985, Cokl and Virant-Doberlet 2003, Hill 2008) or as cues for the detection of interspecific competitors or potential predators (Castellanos and Barbosa 2006, Evans *et al.* 2009). Insects of many taxa, including but not limited to,

Coleoptera, Lepidoptera, Dictyoptera and Orthoptera, produce sound for communication through a variety of mechanisms such as stridulation, percussion, vibration, clicks, and air expulsion (Nelson and Fraser 1980, Ewing 1989, Jang and Greenfield 1996, Boulard 2006, Wessel 2006).

Insects utilise vision to interpret absolute, directional and motion-associated attributes of visible (colour), ultraviolet or polarised light (Osorio and Vorobyev 2008). The Sulfur butterflies *Colias eurytheme* and *C. philodice* flash ultraviolet-reflective wings during courtship displays (Silberglied and Taylor 1978), whereas fireflies use bioluminescent signals for communication (Lall *et al.* 1980). As foraging cues, colour and pattern are particularly important for many species of herbivorous insects (Briscoe and Chittka 2001). Polarised light and sunlight are used as navigational cues by bees and desert ants (Wehner and Muller 2007, Kraft *et al.* 2011).

The magnetic sense is an unusual sensory modality which allows honey bees, *Apis mellifera*, and termites to utilise the earth's magnetic field as an orientation cue (Walker 1997). Resource-derived infrared radiation is yet another rare foraging cue exploited by the Western conifer seed bug, *Leptoglossus occidentalis*, and the kissing bug *Rhodnius prolixus* to locate conifer cones and vertebrate hosts, respectively (Schmitz and Bleckmann 2000, Takács *et al.* 2009).

1.2. Is there potential for electroreception and electro-communication in insects?

Electroreception is a rare sensory modality in the animal kingdom and it is yet to be demonstrated in any arthropoda. Passive electroreception is found in platypus, some amphibians and cartilaginous fishes. It involves specialized receptors that detect electric field cues in the environment, usually for the purpose of navigation or prey location (Himstedt and Schmidt 1982, Scheich *et al.* 1986, Zupanc and Bullock 2006). Active electroreception, wherein the animal generates electrical pulses and uses deviations in the resultant fields to interpret the environment, is found in African mormyriforms, South American gymnotiforms, and several groups of catfish (Zupanc and Bullock 2006). Some species have developed electro-communication, wherein the animal-generated electrical

pulses and the resultant electric fields are utilized as signals, mediating social interactions such as courtship and dominance (Hopkins 1974, Kramer 1990, 1997).

Electroreception is thought to occur only in aquatic vertebrates, due to the high conductivity of electrical information in water and the assumed imperviousness of invertebrate exoskeletons to electrical sensation (Bullock 1999). However, American cockroaches, crayfish and other invertebrates assumed to lack true electroreceptive capabilities nonetheless exhibit electrosensitivity, in that they behaviourally respond to the presence of electric fields (Patullo and MacMillan 2010, Jackson *et al.* 2011). American cockroaches, cabbage loopers, cigarette beetles and vinegar flies avoid, or are repelled from, areas associated with electric fields (Perumpral *et al.* 1978, Hunt *et al.* 2005, Newland *et al.* 2008, Matsuda 2011). In addition, anecdotal information suggests that German cockroaches aggregate in response to the presence of electric fields (Gries, personal communication).

With electroreceptors not yet identified in invertebrates, behavioural responses of invertebrates to electric fields are often considered artifacts. However, if invertebrates respond to electrical stimuli in biologically relevant ways, they must be able to receive and interpret electrical information, even though pertinent electroreceptors are not yet known.

1.3. Communication signals in the German cockroach, *Blattella germanica*

German cockroaches are hemi-metabolous insects that colonize human dwellings and form mixed aggregations of males, females and juveniles with overlapping generations (Cornwell 1968, Rivault 1989, 1990). They are generally nocturnal, seeking food and water at night, and retreating to harbourages during the day (Ross and Mullins 1995).

German cockroaches aggregate in response to suitable microhabitats and microclimates, and to the presence of conspecifics and conspecific-associated cues (Ogata 1976, Cornwell 1968, Jeanson and Fournier 2005). While they tend to settle in dark, enclosed areas associated with warmth and moisture, the current or past presence

of conspecifics makes it more likely that individuals will settle at a given location (Berthold and Wilson 1967, Cornwell 1968, Ogata 1976, Jeanson and Fournier 2005). Cuticular extracts induce both aggregation and arrestment behaviour, and frass contains attractive pheromone (Sakuma and Fukami 1990, 1993, Rivault *et al.* 1998). In addition, females and nymphs produce sounds that mediate attraction or arrestment of conspecifics (Mistal *et al.* 2000, Wijenberg *et al.* 2008).

Courtship and mate-finding in German cockroaches is mediated by pheromone and tactile signals which induce sexual behaviours (Roth and Barth 1967, Nishida *et al.* 1979, Schal *et al.* 1999, Nojima *et al.* 2005). Sensing the female's long-range sex pheromone, the male engages in searching behaviour (Liang and Schal 1993, Nojima *et al.* 2005). When a male finds a female, he antennates with her. This results in tactile stimulation and facilitates the exchange of contact pheromone from her antennae to his, releasing his full courtship display (Roth and Willis 1952, Schal *et al.* 1997). The male then spins 180^0 and raises his wings 90^0, presenting his tergal glands to the female and secreting a phago-stimulatory nuptial secretion for the female to feed upon, thus positioning her for copulation and allowing him to attempt copulation (Roth and Willis 1952, Nojima *et al.* 1999, Kugimiya *et al.* 2003).

Depending on how long information persists in the environment, how far it can travel, and how resistant it is to environmental noise, different modalities have varying degrees of efficacy in differing environments (Bradbury and Vehrencamp 1998, Goodenough *et al.* 2010). In some cases, redundancy of information in the form of multimodal signals and cues may ensure that important tasks such as mate location or courtship are completed (Johnstone 1996, Hauser 1997, Ay *et al.* 2007, Wilgers *et al.* 2011). For example, electrical fish use electric fields to locate potential mates in murky water where vision is compromised (Hagedorn and Heiligenberg 1985). Similarly, pheromonal courtship signals of German cockroaches may be ineffective in pheromone-saturated and crowded microhabitats where electrosensory signals may constitute alternate means of communication.

1.4. Thesis organisation and research objectives

My thesis is organized into four chapters. Following the introductory chapter, there are two research chapters and a final concluding chapter summarizing the major findings. The research chapters are prepared as manuscripts which - after some revisions - will be submitted for publication. Accordingly, each chapter is presented in the style and format prescribed by the target journal and comprises several sections which may include abstract, introduction, materials and methods, results, discussion and a reference list.

In Chapter 2, I report the response of several insects to electrified coils. Anecdotal reports of urban insects found near electrical circuits, and published evidence of insects responding to electric fields, suggested a potential behaviour-modifying effect associated with electrical circuits. Thus, I conducted bioassays to determine whether insects are attracted to, or repelled by, electrified coils. I found that German cockroaches, Brown-banded cockroaches (*Supella longipalpa*), Common silverfish (*Lepisma saccharina*), firebrats (*Thermobia domestica*) and European earwigs (*Forficula auricularia*) are attracted to, or arrested by, electrified coils, whereas American cockroaches (*Periplaneta americana*) are repelled. I also found that electromagnetic fields with the magnetic component of the field nulled, still attracted German cockroaches, suggesting that the electric component of the field may contribute to the attraction and/or arrestment response of German cockroaches.

In Chapter 3, I explore the potential for electrocommunication in German cockroach. I present data suggesting that German cockroaches utilize electric pulses as part of their decision-making process during mate-finding and courtship. I show that sexually receptive, virgin males intensify courtship behaviour in the presence of electric fields and prefer to shelter in harborages associated with electromagnetic fields. Furthermore, I show that German cockroaches are associated with electric pulses and that there is a greater incidence of these pulses in mixed groups of females and males than in unisexual groups of males or females. When male German cockroaches were exposed to pulses, as recorded from females and artificially reproduced, they responded with increased courtship behaviour. I conclude that German cockroaches may use electrical discharges as communication signals and that these signals may serve as fail

safe means in microhabitats where the effect of olfactory and auditory signal are compromised.

In Chapter 4, I highlight the main results and conclusions of my thesis.

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2. Response of diverse insects to electrified coils*

2.1. Abstract

Anecdotal evidence suggests that cockroaches respond to electrical appliances or outlets. Our objectives were to determine the effect of field-inducing sources and field attributes on attraction of German cockroaches, *Blattella germanica* (Blattodea: Blattellidae), and to test those parameters found effective for attraction of *B. germanica* for attraction of other urban insects. In two-choice large-arena experiments, significantly more female, but not nymph, *B. germanica* settled in or near electrified coils with static or fluctuating electromagnetic fields produced by low-level AC or DC than in control coils without current. Electromagnetic fields with the magnetic, but not the electric, component of the field nulled still attracted *B. germanica,* suggesting that the electric component of the field may contribute to the attraction and/or arrestment response of *B. germanica.* DC-powered coils with static electromagnetic fields also attracted/arrested Brown-banded cockroaches, *Supella longipalpa* (Blattodea: Blattellidae), Common silverfish, *Lepisma saccharina,* firebrats, *Thermobia domestica* (both Thysanura: Lepismatidae), and European earwigs, *Forficula auricularia* (Dermaptera: Forficulidae), but they repelled American cockroaches, *Periplaneta americana* (Blattaria: Blattidae). If proven attractive, rather than arrestant, electrified coils may offer non-toxic alternatives to pesticides for selective insect control in urban environments.

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2.2. Introduction

Insects of diverse taxa inhabit human dwellings. They include, but are not limited to, German cockroaches, *Blattella germanica* (Blattodea: Blattellidae), American cockroaches, *Periplaneta americana* (L.) (Blattaria: Blattidae), Brown-banded cockroaches (Dictyoptera: Blattidae), *Supella longipalpa* (Fabricius) (Blattodea: Blattellidae), Common silverfish, *Lepisma saccharina* (L.) (Thysanura: Lepismatidae), firebrats, *Thermobia domestica* (Packard) (Thysanura: Lepismatidae), and European earwigs, *Forficula auricularia* (L.) (Dermaptera: Forficulidae).

Cockroaches have adverse effects on human or pet health in that they may serve as reservoirs and mechanical transmission agents of human pathogens (Fotedar and Verma 1991; Gliniewicz and Grzegorzak 2003) and allergens associated with asthma (Rosenstreich and Slavin 1997). Silverfish and firebrats are generally considered aesthetically displeasing. In addition, they eat a wide variety of materials including glue, wallpaper paste, book bindings, paper, photographs, starch in clothing, cotton, linen, fabrics as well as stored dry food products and leather, which can result in significant damage to human possessions (Capinera 2001). The presence of silverfish may also trigger sensitisation in children with respiratory allergy (Boquete et al. 2008). Earwigs too are aesthetically displeasing, and large numbers may become a nuisance (Hedges 2004). They seek refuge indoors when outside conditions become harsh (Hedges 2004) but pose no health hazards and generally starve to death indoors.

Most attempts to control urban insect infestations include sanitation procedures which entail the removal of potential insect harbourages and food sources (Rust et al. 1995). This approach, however, may not be entirely effective because even completely sanitized apartments can become re-infested with insects from surrounding areas (Shahraki and Ibrahim 2010). Insecticide-based insect control tactics remain the prevailing pest management practice in urban areas of North America (Davis et al. 1992; Horton and Fincher 2011). While insecticides often eradicate insect infestations, they have undesired side effects on humans and pets, enter bodily fluids, and act as neurotoxins (Whitemore et al. 1994; Eskenazi et al. 1999; Landrigan 2001; Jamal et al. 2002). For these reasons, insecticides applied in urban environments are typically formulated such that the risk of chance contact by non-target organisms is minimal and

toxins are effective only when directly contacted by target insects. Manipulation of insect behaviour can supplement or replace insecticide applications for insect control. This can be achieved with stimuli including communication signals or foraging cues that induce or inhibit insect responses (Bell and Cardé 1984; Cardé and Bell 1995; Foster and Harris 1997).

The most widely used tactic in pest control programs for modifying the behaviour of insects is the deployment of long-range attractants *sensu* Kennedy[1] (1974) that lure insects to a trap or killing station (Ebeling and Reierson 1974; Lanier 1990; Schal and Hamilton 1990). These attractants can be synthetic replicas of long-range pheromonal, auditory, or visual insect communication signals or cues (Gillespie and Quiring 1987; Walker 1988; Lanier 1990; Howse 1998; Witzgall et al. 2010).

Options for modifying the behaviour of urban insect pests are limited in number and scope. There are no long-range attractants for specific management of silverfish, firebrats or earwigs. Long-range attractants for cockroaches include aggregation and sex pheromones (Sakuma and Fukami 1990; Liang and Schal 1993; Liang et al. 1998; Nojima 2005), auditory cues (Mistal et al. 2000; Wijenberg et al. 2008) and food-based attractants (Karimifar et al. 2011), but only food attractants have been implemented operationally (Schal and Hamilton 1990).

Anecdotal evidence suggests that certain urban insects tend to be found in areas associated with electric circuits. Stimuli associated with such circuits include heat, vibration, and electromagnetic fields. Insects have been shown previously to behaviourally respond to electric fields with aversive reactions. A proprioreceptor at the antennal base of American cockroaches detects electric fields, resulting in an avoidance response (Hunt et al. 2005; Newland et al. 2008; Jackson et al. 2011). The Cabbage looper, *Trichoplusia ni,* avoids static electric fields (Perumpral et al. 1978). Cigarette beetles (Anobiidae) and vinegar flies (Drosophilidae) are repelled from screens associated with electric fields (Matsuda 2011). Other organisms modify their behaviour in the presence of high electric fields, responding to their presence with involuntary movements of antennae and wings, aversion and avoidance behaviour, and with altered

[1] An organism is attracted over long-range if the distance to the stimulus exceeds a few body lengths of the organism.

patterns of oviposition (Edwards 1960, 1961; Maw 1961; Watson et al. 1997).

If electric fields can alter an insect's behaviour, they may prove useful when associated with insect trapping and control devices. If attractive properties associated with electrical circuits were to be shown to lure urban insects to traps or killing stations, these properties could be exploited and developed as novel, insecticide-free and earth-friendly tools in urban pest control.

My objectives were (1) to determine the effect of field-inducing sources and field attributes on attraction of German cockroaches, and (2) to test those parameters found effective for attraction of German cockroaches for attraction of American cockroaches, brown-banded cockroaches, common firebrats, common silverfish, and European earwigs.

2.3. Methods

2.3.1. Experimental insects

Start-up colonies of German and Brown-banded cockroaches were obtained from the insectary of SC Johnson and Son (Racine, WI, USA). Prior to onset of experiments, the German cockroach colony was supplemented with specimens captured in apartment buildings in Vancouver (BC, Canada). American cockroaches were obtained from SFU's insectary (Burnaby, BC, Canada). Cockroaches were reared in Plexiglas™ cages (30 × 60 × 45 cm) fitted with two mesh-covered openings for ventilation. The cages were maintained at 25 ± 1 °C and 40–70% r.h., with a photoperiod of L14:D10. Shelter was provided by crumpled paper towels and panels of narrowly spaced particle board. The diet consisted of ground Purina dog chow (Ralston Purina, St. Louis, MO, USA), apple slices, and water. Eclosed adults were collected every 2nd day, and males and females were placed in separate cages. Males, females, or late-instar nymphs were isolated two days prior to experiments.

Common silverfish, firebrats and European earwigs were obtained from colonies at SFU's insectary (Woodbury and Gries 2007, 2008; Hehar and Gries 2008).

2.3.2. General methods

Two-choice experiments were conducted to determine whether German cockroaches prefer to settle in shelters associated with specific test stimuli. All experiments were deployed in a Plexiglas™ arena (Figure 2.1) containing two shelters at opposite positions equidistant from the centre and edges. Positions of treatment and control shelters were alternated between replicates, and rotated 90° after two replicates. Unless otherwise stated, glass tubes (Length (L) = 11 cm, Diameter (D) = 4.7 cm) wrapped in copper wire (enamel-coated, 28 gauge; Resistance (Ω) = 21 ohms, 319 turns, 1 layer, Inductance = 2.6 mH, Coil constant = 34 Gauss/ampere) served as shelters, hereafter referred to as coils. Infrared (IR) radiation from coils was recorded with a mid-range IR (3-5 µm) AGEMA Thermovision 550 camera (FLIR Systems Ltd., Burlington, ON, Canada). All thermographic images were analyzed post hoc, using ThermaCam Reporter 2000 Pro (FLIR Systems Ltd., Burlington, ON, Canada) software to calculate the mean temperature of coils. Between replicates, bioassay arenas and shelters were cleaned with non-polar detergent and hexane.

For each replicate, a Petri dish containing groups of insects was placed at the centre of the arena. One hour later, at the beginning of the scotophase during which insects forage, they were released and their position was recorded 19 h later. For each experiment, the proportion of responding insects settling in or near treatment or control shelters was analyzed by a two-sided t-test, using JMP™ 8 software (SAS®, Cary, NC, USA).

2.3.3. Specific experiments

2.3.3.1. Exps. 1, 2: Effect of white noise (and the electromagnetic field associated therewith)

Experiments 1 and 2 (Table 1) were designed to determine whether German cockroaches prefer shelters associated with white noise and the electromagnetic field associated therewith. Shelters consisted of an inverted plastic cup (15 × 12 cm) housing a HD 202 II Sennheiser speaker (Sennheiser Electronic, Wedemark, Germany, Nominal impedance = 32 ohms) (Figure 1). The voltage source for each speaker was a line out connector on an Intel Pentium 2.54 GHz computer equipped with a white noise generator developed using National Instrument's LabVIEW 7 (National Instruments,

Austin, TX, USA). A white noise signal (f = 20-20000 Hz) was directed through a relay box to the treatment speaker. The control speaker was powered but kept silent. As a result, one speaker emitted a Gaussian white noise auditory stimulus (σ = 0.5 volts, 55 dB) and the associated electromagnetic field; the other speaker generated neither auditory nor electromagnetic stimuli. The software continued to replay the white noise stimulus until stopped manually. In each replicate of experiment 1, 40 virgin, 1- to 3-wk-old females were released. In each replicate of experiment 2, 30 late-instar male and female nymphs were released. Responders were defined as insects inside or within 2.5 cm of a shelter.

2.3.3.2. Exps. 3, 4: Effect of a fluctuating electromagnetic field

In experiments 3 and 4 (Table 1), we tested whether German cockroaches prefer shelters associated with fluctuating electromagnetic fields without an audible component. The treatment coil received a Gaussian white noise voltage signal via the line out connector on a computer equipped with a white noise generator (see above), resulting in current producing an electromagnetic field with fluctuations spanning the range 20-20000 Hz with white noise characteristics up to 1 kHz and pink noise characteristics, where the intensity of the noise is inversely proportional to the frequency, at frequencies > 1 kHz. The auditory component of the noise signal was not emitted. In experiments 3 and 4, the electromagnetic field within the coil was measured as < 0.05 mT and 0.05-1.00 mT, respectively, using a F.W. Bell Model 6010 Gauss/ Teslameter (Bell Technologies, Sypris, Ontario, Canada), a unit capable of reporting the true RMS value of the time-varying component of the field. Measurements were taken using an axial probe (F.W. Bell, Model HAD61-2508-15) placed centrally in the coil. In both experiments the control coil received no white noise signal or electromagnetic field.

For each replicate of each of experiments 3 and 4, 30 1- to 3-wk-old virgin females were released. In Experiment 3, responding insects were defined as those found inside the coil. When we increased the strength of the field in experiment 4 (see above), insects sheltered under the coil rather than inside, which prompted us to include them as responders.

2.3.3.3. Exp. 5: Effect of a fluctuating electromagnetic field produced by direct current (DC)

In experiment 5 (Table 1), we tested whether German cockroaches prefer coils associated with a fluctuating electromagnetic field generated by a battery-powered device. An electromagnetic field (< 0.02 mT), with fluctuations spanning the range of 20-20000 Hz within the coil, was produced by playing back recorded white noise on a continuous loop through the line out connector on a rechargeable, battery-powered, portable CD player and by running the signal to a coil. The auditory component of the white-noise stimulus was not generated. At the beginning of each replicate, 30 1- to 3-wk-old virgin females were released and those found inside the coil at the conclusion of the experiment were considered responders.

2.3.3.4. Exp. 6: Effect of a static electromagnetic field produced by DC

In experiment 6 (Table 1), we tested whether German cockroaches prefer coils associated with DC-driven, static electromagnetic fields. Current was driven through a coil using a 13-V motorcycle battery. A rheostat (Science Technical Centre, Simon Fraser University) in series with the coil was used to limit the current and maintain the voltage across the coil at 200-500 mV (< 0.11 mT within the coil). For each replicate, 30 1- to 3-wk-old virgin females were released and those found inside and beneath the coil at the conclusion of the experiment were considered responders.

2.3.3.5. Exps. 7, 8: Effect of the magnetic or electric component of the electromagnetic field

In experiments 7 and 8 (Table 1), we tested whether the magnetic or electric component of an electromagnetic field mediates the response of German cockroaches. Double-wound rather than single-wound coils (L = 11 cm, D = 4.7 cm, enamel-coated, 28 gauge, R ≈ 21 ohms, 330 turns, 1 layer, Inductance $= 1.7 \times 10^3$ mH) were deployed. Current [Current (I) = 21.7] was run through the coils using a regulated current source (Appendix 1) at a steady 20 V. Current was run through the coils in either an antiparallel sense, thus cancelling the magnetic field produced by each winding and generating a null-magnetic field, or in a parallel sense, thus summing the magnetic field produced by each winding and generating a field with both an electric and magnetic component. Coils were run in-series so that the current was identical and could be switched between the

antiparallel and parallel sense between treatments. Due to the winding, the electric field, although present in each coil, was not consistent across coils. In experiment 7, antiparallel-wound treatment coils had a nulled-magnetic field and parallel-wound control coils had an 'active'-magnetic field. In experiment 8, the antiparallel double-wound treatment coil had no magnetic field, whereas the unplugged antiparallel-wound control coil had neither an electric nor a magnetic component. In each replicate of experiments 7 and 8, 10 (Exp. 7) and 15 (Exp. 8) 1- to 3-wk-old virgin females were released and those found inside the coils were considered responders.

2.3.3.6. Exps 9-13: Effect of static, DC-driven electromagnetic fields on various insect species

In experiments 9-13 (Table 2), we tested the effect of DC-driven, static electromagnetic fields on behavioral responses of mixed groups of firebrats (Exp 9), European earwigs (Exp. 10), common silverfish (Exp. 11), Brown-banded cockroaches (Exp. 12), and American cockroaches (Exp. 13). The experimental design was identical to that described for experiment 6. Responders were defined as insects found in or under the coil at the conclusion of the experiment.

2.4. Results

2.4.1. Exps. 1, 2: Effect of white noise (and the electromagnetic field associated therewith)

In experiment 1 (Table 1), significantly more female German cockroaches were found in treatment shelters with the white noise stimulus than in silent control shelters ($t = 8.16$, $P \leq 0.0001$; Fig. 2.2). In experiment 2 (Table 1), there was no significant difference in the proportion of German cockroach nymphs in treatment and control shelters ($t = -0.61$, $P > 0.05$; Fig. 2.2).

2.4.2. Exps. 3, 4: Effect of fluctuating electromagnetic fields

In experiments 3 (field strength of test stimulus: < 0.05 mT) and 4 (field strength of test stimulus: 0.05-1 mT) (Table 1), significantly more female German cockroaches

were found in coils associated with fluctuating electromagnetic fields than in control coils (Exp. 3: t = 4.57, $P \leq 0.001$; Exp. 4: t = 4.54, $P \leq 0.0011$; Fig. 2.3).

2.4.3. Exp. 5: Effect of fluctuating electromagnetic fields generated by DC

Significantly more female German cockroaches were found in treatment coils associated with a fluctuating electromagnetic field generated by a DC-powered sourcethan in control coils (t = 20.77, $P \leq 0.0001$; Fig. 2.4).

2.4.4. Exp. 6: Effect of static electromagnetic fields driven by DC

Significantly more female German cockroaches were found in and around coils associated with static electromagnetic fields driven by a DC source than in control coils (t = 17.14, $P \leq 0.007$; Fig. 2.4).

2.4.5. Exps. 7, 8: Effect of the magnetic or electric component of the electromagnetic field

In experiment 7, there was no significant difference in the number of female German cockroaches found in coils associated either with a nulled magnetic or an 'active' magnetic field (t = -0.26, $P \leq 0.79$; Fig. 2.5). In experiment 8, significantly more female German cockroaches were found in electrified coils with a nulled magnetic but an effective electric field component (t = 18.64 value, $P \leq 0.0001$; Fig. 2.5) than in non-electrified coils. Combined these results seem to suggest that female German cockroaches respond to the electric rather than the magnetic component of electromagnetic fields associated with electrified coils.

2.4.6. Exps. 9-13: Effect of static, DC-driven electromagnetic fields on various apterous insects

In experiments 9-12, significantly more insects were found in and around electrified treatment coils than in control coils, indicating a widespread preference by apterous insects for the electromagnetic field associated with electrified coils [Exp. 9 (firebrats): t = -9.8, $P \leq 0.0001$; Exp. 10 (European earwigs): t = -4.93, $P \leq 0.0003$; Exp. 11 (common silverfish): t = -2.25, $P \leq 0.041$; Exp. 12 (Brown-banded cockroaches): t = -

4.54, $P \leq 0.0005$; Fig. 2.6). In experiment 13, American cockroaches were found significantly more often in control coils than in treatment coils (t = -5.87, $P \leq 0.0002$; Fig. 2.6), indicating the possibility of a repellent effect associated with electrified coils.

2.5. Discussion

Our data support the conclusion that German cockroaches, Brown-banded cockroaches, common silverfish, firebrats and European earwigs, but not American cockroaches, are attracted to, or arrested by, electrified coils.

Attributes associated with electrified coils that may have induced attraction or arrestment of bioassay insects include electromagnetic fields with both electric and magnetic components, vibration and heat. In a series of experiments, we have attempted to determine the attributes that mediate the insects' response. Vibration, and any sound associated with such vibration, was absent from coils associated with steady fields. Yet, these coils still elicited responses from German cockroaches, eliminating vibration as a potential behaviour-modifying stimulus.

Thermographic images of electrified and non-electrified coils revealed temperature differences of < 0.1 ºC, but German cockroaches may not be able to discern between such subtle temperature changes. Such small temperature differences are not likely to affect life history traits, foraging decisions or any elements of reproductive or courtship behaviour. This is different, however, in snakes. IR receptors of crotaline snakes (Moiseenkóvà et al. 2003) and Python snakes (Grace et al. 1999) aid in locating warm-bodied prey or hosts, and temperature differentials as little as 0.003 °C elicit neurological and behavioral responses, respectively (Noble and Schmidt 1937; Bullock and Diecke 1956).

German cockroaches continued to respond to coils in which the magnetic component of the electromagnetic field was nullified, indicating that the magnetic component may not mediate attraction. The electric component of the electromagnetic field may have a behaviour-modifying effect either by itself, or possibly in combination with heat. It would have been associated with both fluctuating and steady fields, and in both expressions of the double-wound coils.

The active space or attractive range of electrified coils is yet to be determined. They may have attracted bioassay insects or merely arrested them when they approached. If the coils' attributes were to serve as long-range attractants, coils would be useful as baits to bring insects into traps or to killing stations containing a toxin, such as abamectin, boric acid, fipronil, hydramethylnon, indoxacarb or midacloprid (Horton and Fincher 2011).

A wide variety of conventional devices for trapping urban insects could be fitted with an electrified coil, offering an alternative to semiochemical baits. Alternatively, these devices may be supplemented with additional attractants including, but not limited to, pheromones (Mayer 1991), food semiochemicals (Karimifar et al. 2011) and/or acoustic attractants (Mistal et al. 2000; Wijenberg et al. 2008).

Both the frequency and intensity of electromagnetic fields associated with electrified coils for optimal attraction or arrestment of insects are yet to be determined. Moreover, they may vary and may need to be optimized for each target species. The intensity of fields to be perceived by insects will need to exceed the background level but must not be too high to possibly become repulsive.

If proven attractive, rather than merely arrestant, electrified coils may offer viable, earth-friendly, less hazardous and non-toxic alternatives to pesticides for insect control in urban environments.

2.6. References

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2.7. Tables

Table 2.1 Overview of stimuli and bioassay insects (nymph or adult German cockroaches) tested in experiments 1-8.

Exp.	N[1]	Insects[1]	Delivery apparatus	Stimuli tested		Location of responding insects
				Treament	Control	
1	6	30 females	Loud speaker	White noise	Silence	Inside or within 2.5 cm of shelter
2	6	30 late-instar nymphs	Loud speaker	White noise	No white noise	Inside or within 2.5 cm of shelter
3	6	30 females	Single-wound coil	White noise-driven AC[2], fluctuating electromagnetic field < 0.05 mT, no sound	No current	Inside coil
4	6	30 females	Single-wound coil	White noise-driven AC, fluctuating electromagnetic field 0.05-1.00 mT, no sound	No current	Inside or under coil
5	6	30 females	Single-wound coil	AC, fluctuating electromagnetic field, vibration	No current	Inside coil
6	6	30 females	Single-wound coil	DC[3], static electromagnetic field, no vibration	No current	Inside or under coil
7	10	10 females	Double-wound coil (treatment: antiparallel; control: parallel)	DC, static electromagnetic field with nulled magnetic field component, no vibration	DC current, static electromagnetic field, no vibration	Inside coil
8	10	15 females	Double-wound, anti-parallel coil	DC, static electromagnetic field, nulled magnetic field component, no vibration	No current	Inside coil

[1]*All females were* 1- to 3-wk-old virgins
[2]*AC = alternating current*
[3]*DC = direct current*

Table 2.2 Overview of stimuli and insects tested in experiments 9-13.

Exp.	N[1]	Insects	Delivery apparatus	Stimuli tested[6]	
				Treatment	Control
9	7	Firebrats[1]	Single-wound coil	DC current, static electromagnetic field	No current
10	7	Earwigs[2]	Single-wound coil	DC current, static electromagnetic field	No current
11	8	Common silverfish[3]	Single-wound coil	DC current, static electromagnetic field	No current
12	8	Brown-banded cockroaches[4]	Single-wound coil	DC current, static electromagnetic field	No current
13	6	American cockroaches[5]	Single-wound coil	DC current, static electromagnetic field	No current

[1]Mixed group of 20 insects including males, females and nymphs;
[2]Mixed group of 10 insects including males and females;
[3]Mixed group of 10 insects including males, females and nymphs;
[4]Mixed group of 5 insects including males, females and nymphs;
[5]Mixed group of 5 insects including males and females);
[6]Responding insects were inside or under treatment or control coils.

2.8. Figure captions

Fig. 2.1 Arena olfactometer to test the preference of bioassay insects for one of two test stimuli. 1. Plexiglas^{TM} arena (h = 0.40 m, diam = 1.25 m); 2. Petri dish from which bioassay insects are released; 3. shelter (15 × 12 cm); 4. speaker housing; 5. Sennheisser speaker; 6. glass tubing (11.5 × 4.7 cm); 7. copper electrical coil (enamel-coated, 28 gauge; resistance ~ 21 ohms); 8. current generator; 9. coaxial cable (L = 4 m).

Fig. 2.2 Mean (+ SE) number of female or nymph *Blattella germanica* in experiments 1 and 2 (Table 1) settling in or near shelters associated with speakers which emitted white noise or were kept silent. In experiment 1, the asterisk (*) above a bar indicates a significant preference for the test stimulus; two-sided t-test, $P \leq 0.05$.

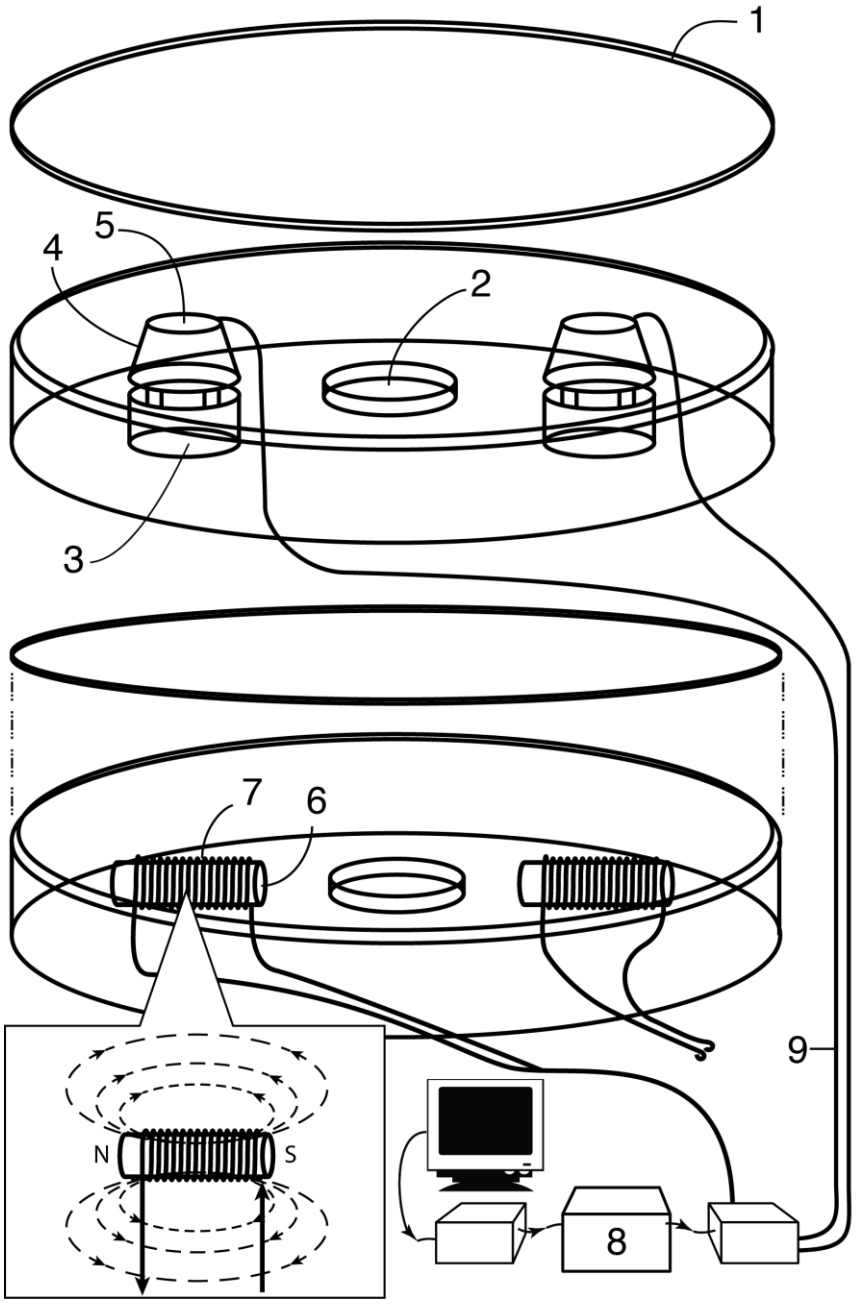
Fig. 2.3 Mean (+ SE) number of female *Blattella germanica* in experiments 3 and 4 (Table 1) settling inside or under coils associated with or without fluctuating electromagnetic fields (EF). In each experiment, an asterisk (*) above a bar indicates a significant preference for the test stimulus; two-sided t-test, $P \leq 0.05$.

Fig. 2.4 Mean (+ SE) number of female *Blattella germanica* in experiments 5 and 6 (Table 1) settling inside or under coils associated with or without fluctuating electromagnetic fields (EF) (Exp. 5), or associated with or without static electromagnetic fields (EF) produced by direct current (DC) (Exp.6). In each experiment, an asterisk (*) above a bar indicates a significant preference for the test stimulus; two-sided t-test, $P \leq 0.05$.

Fig. 2.5 Mean (+ SE) number of female *Blattella germanic*a in experiment 7 (Table 1) settling in coils associated with a static electromagnetic field (EF) produced by direct current (DC) with the magnetic (but not the electric) field component nulled (S1) or not (S2), or in experiment 8 (Table 1) settling in a coil associated with S1 or without any electromagnetic field. In each experiment, an asterisk (*) above a bar indicates a significant preference for the test stimulus; two-sided t-test, $P \leq 0.05$.

Fig. 2.6 Mean (+ SE) numbers of firebrats (Exp. 9), European earwigs (exp. 10), common silverfish (Exp. 11), Brown-banded cockroaches (Exp. 12), and American cockroaches (Exp. 13) (Table 2) settling inside or under coils associated with or without static electromagnetic fields (EF) produced by direct current (DC). In each experiment, an asterisk (*) above a bar indicates a significant preference for the respective stimulus; two-sided t-test, $P \leq 0.05$.

2.9. Figures



Gries _RW_fig 1

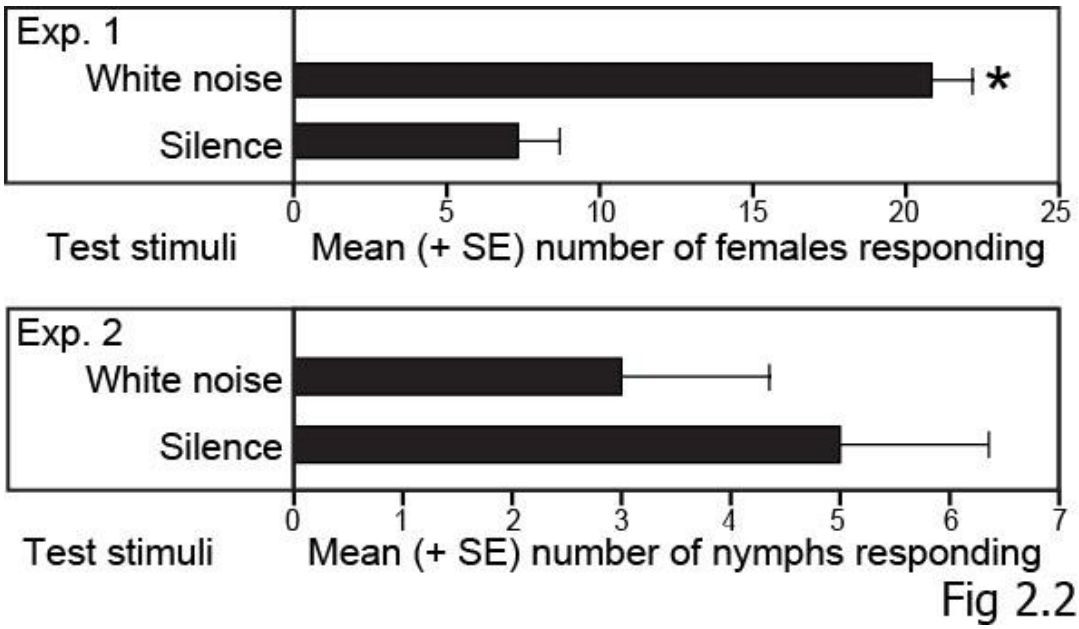

Exp. 1
White noise
Silence
*
0
5
10
15
20
25
Test stimuli
Mean (+ SE) number of females responding
Exp. 2
White noise
Silence
0
1
2
3
4
5
6
7
Test stimuli
Mean (+ SE) number of nymphs responding

Fig 2.2

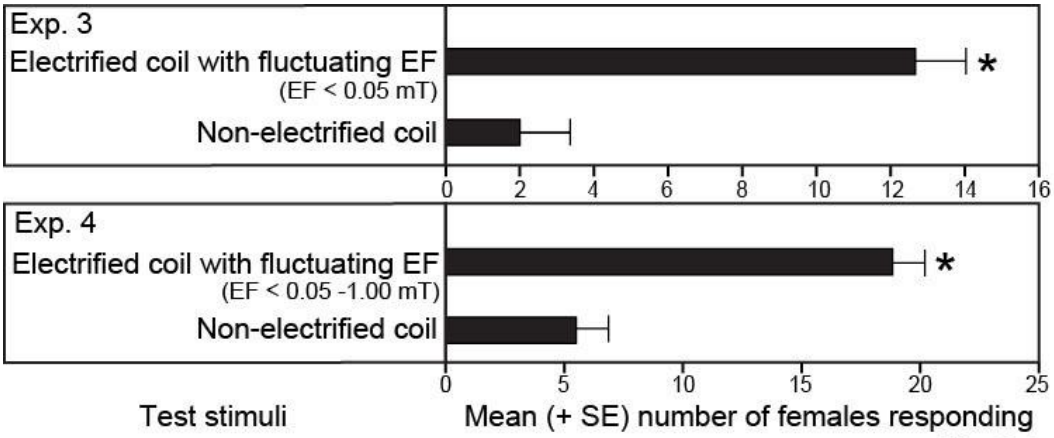

Exp. 3
Electrified coil with fluctuating EF
(EF < 0.05 mT)
Non-electrified coil
*
0
2
4
6
8
10
12
14
16
Exp. 4
Electrified coil with fluctuating EF
(EF < 0.05 -1.00 mT)
Non-electrified coil
*
0
5
10
15
20
25
Test stimuli
Mean (+ SE) number of females responding

Fig 2.3

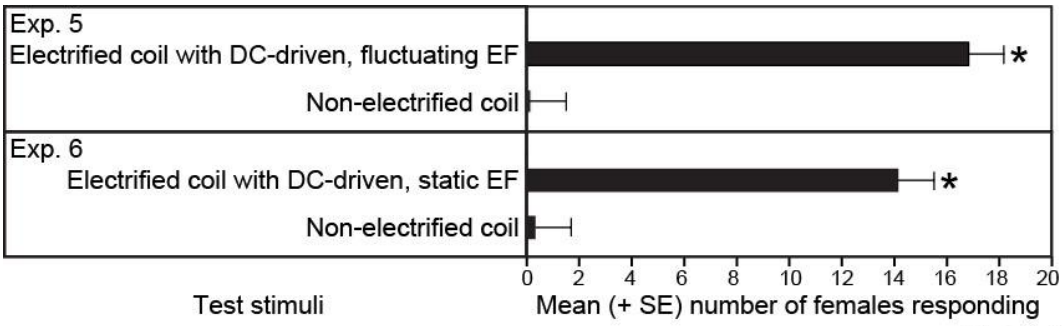

Exp. 5
Electrified coil with DC-driven, fluctuating EF
Non-electrified coil
Exp. 6
Electrified coil with DC-driven, static EF
Non-electrified coil
*
*
0 2 4 6 8 10 12 14 16 18 20
Test stimuli
Mean (+ SE) number of females responding

Fig. 2.4

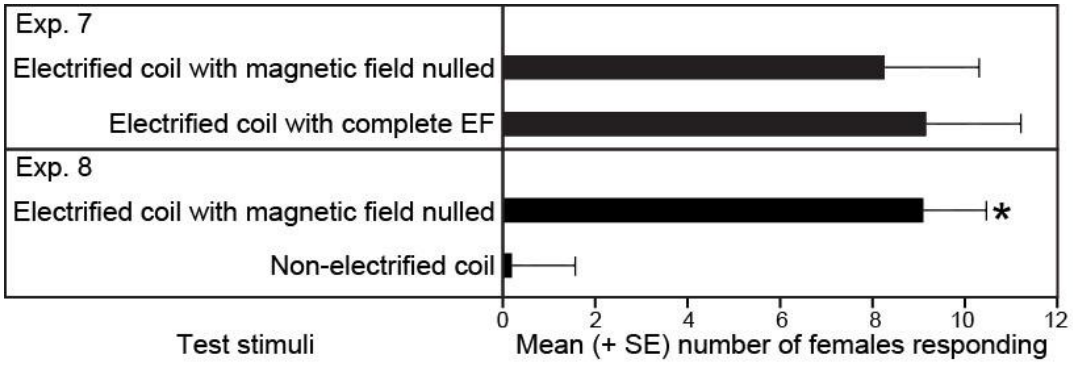

Exp. 7
Electrified coil with magnetic field nulled
Electrified coil with complete EF
Exp. 8
Electrified coil with magnetic field nulled
*
Non-electrified coil
0
2
4
6
8
10
12
Test stimuli
Mean (+ SE) number of females responding

Fig 2.5

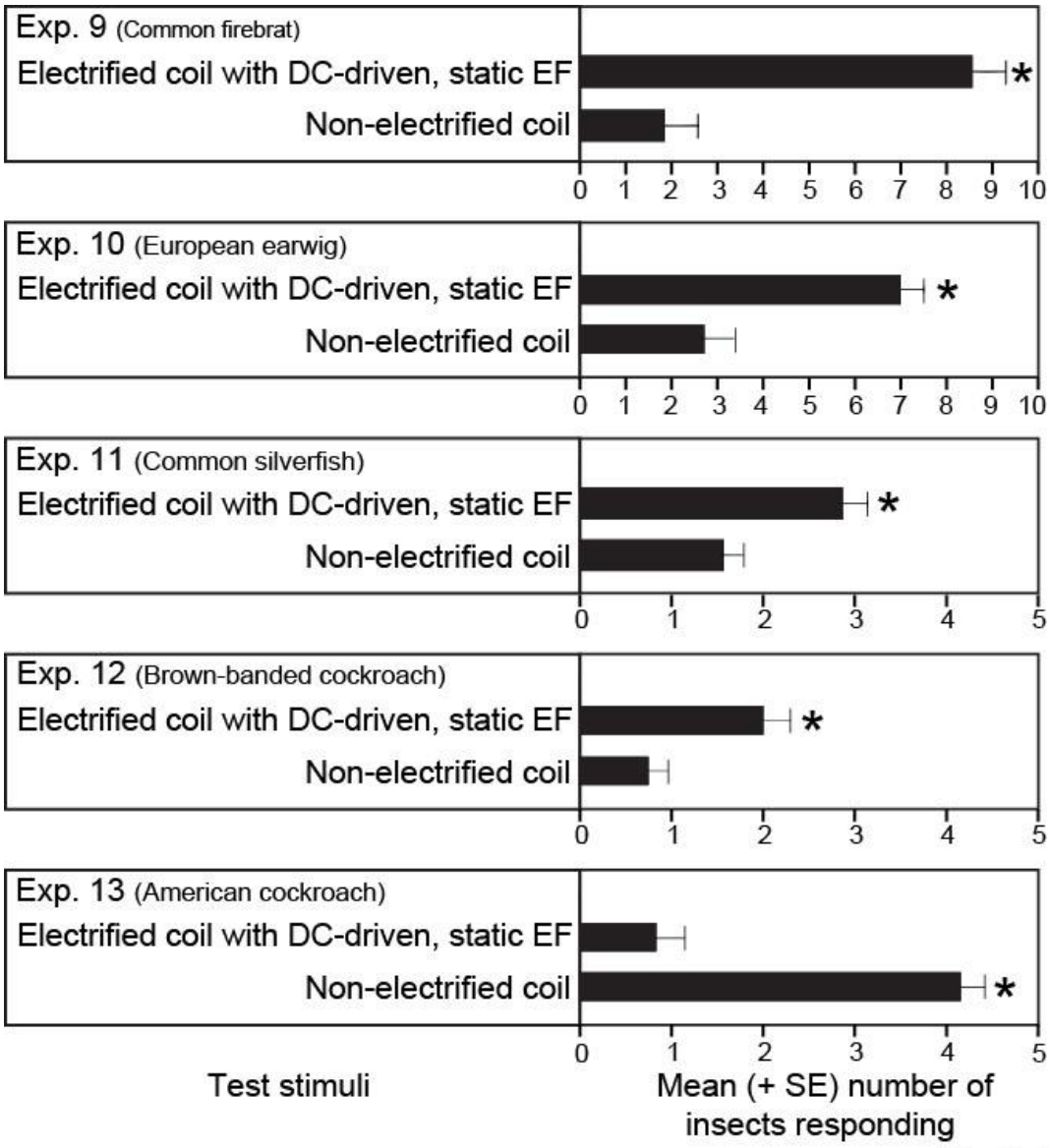
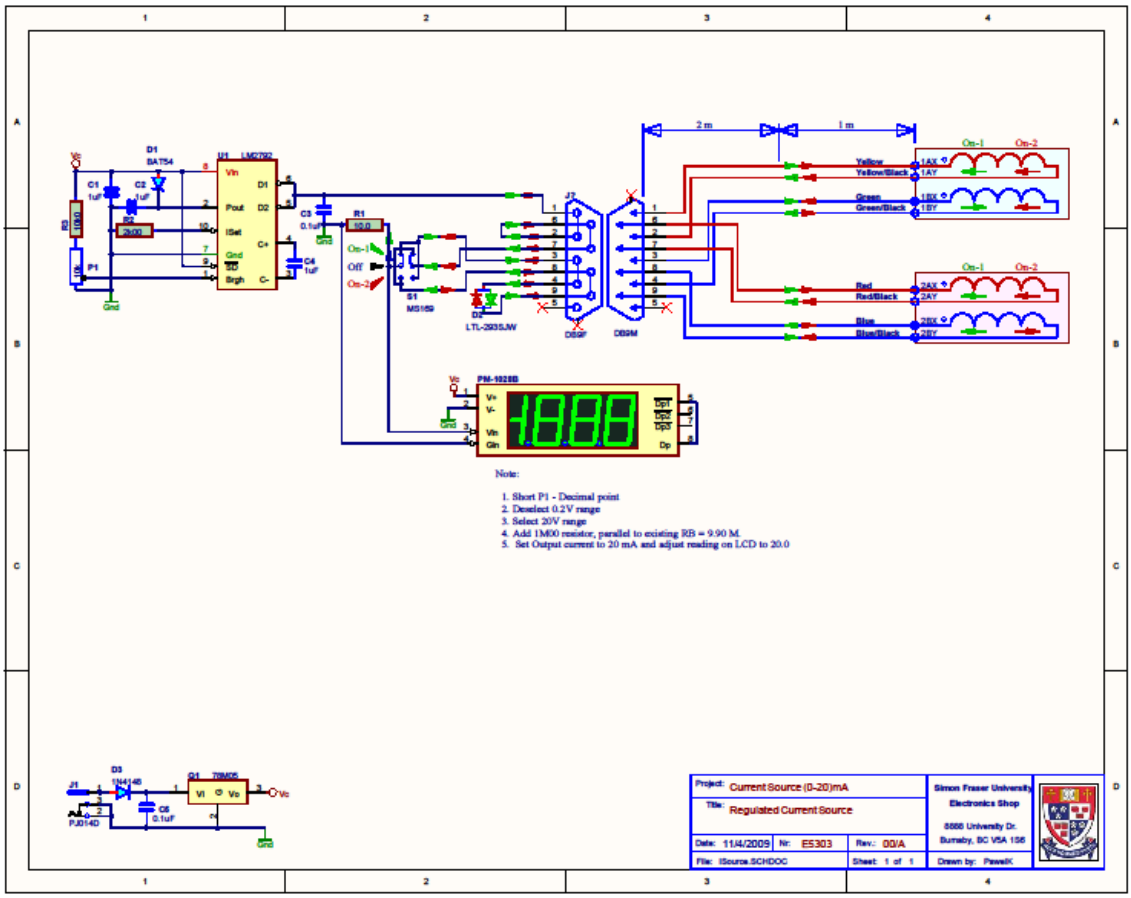

Exp. 9 (Common firebrat)
Electrified coil with DC-driven, static EF
Non-electrified coil
0 1 2 3 4 5 6 7 8 9 10
Exp. 10 (European earwig)
Electrified coil with DC-driven, static EF
Non-electrified coil
0 1 2 3 4 5 6 7 8 9 10
Exp. 11 (Common silverfish)
Electrified coil with DC-driven, static EF
Non-electrified coil
0 1 2 3 4 5
Exp. 12 (Brown-banded cockroach)
Electrified coil with DC-driven, static EF
Non-electrified coil
0 1 2 3 4 5
Exp. 13 (American cockroach)
Electrified coil with DC-driven, static EF
Non-electrified coil
0 1 2 3 4 5
Test stimuli
Mean (+ SE) number of insects responding

Fig 2.6

2.10 Appendix 1: Regulated current source with double wound coils



3. Sparks are flying during sexual communication in German cockroaches*

3.1. Abstract

Common communication signals used by animals have visual, auditory, vibratory or olfactory characteristics[1]. Electrocommunication is rare but does occur in some species of fish that generate electric signals for information conveyance[2]. Electrocommunication is thought to be restricted to aquatic organisms due to superb conductivity of electrical information in water[3]. Here we present evidence for electro-communication in the German cockroach, *Blattella germanica*, in terrestrial environments. The evidence includes (*i*) attraction of virgin males, but not mated males, and virgin females or nymphs, to specific electromagnetic fields, (*ii*) recordings of electrical pulses from German cockroaches that resemble electric pulse characteristics reported in fish[4]; (*iii*) greater incidence of electrical pulses in solitary females than in solitary males, and in mixed groups of females and males than in unisexual groups of males or females; and (*iv*) exhibition of pre-copulatory wing-raising behaviour by males exposed to electrical pulses as recorded from females and reproduced by a waveform generator. Electrical discharges as communication signals in German cockroaches may serve as a back-up system in those microhabitats where olfactory and auditory noise habituate the insects' sensory system and preclude effective communication.

*This chapter is presented in manuscript form. A modified version will submitted for publication with the following authors: Rosanna Wijenberg, Michael Hayden, Onour Moeri, Gerhard Gries

3.2. Main body

Many fish, several amphibians and monotreme mammals have independently evolved the ability to perceive weak electric fields with specialized receptors (electroreception)[5-9]. This passive electric sense is useful to avoid obstacles or detect prey[10]. Some weakly electric fish, such as mormyriforms and gymnotiforms, not only receive electrical cues, they possess electric organs which generate electric signals in the form of pulsed charges, resulting in electric fields that generate a pattern of current flow in the water[11]. They “electrocommunicate” during territorial disputes, mate attraction, and courtship[12,13]. Their electric organs are located on their tail, along the side of their body or on their head, and produce electric discharges ranging between millivolts to a few volts with pulse- or wave-type pattern[14]. Pulse-type electrical discharges are brief, often multi-phasic and intermittent. Wave-type electrical discharges have a sine wave-like pattern, and are often sustained monophasic pulses. All types of electroreceptors thus far described in fish comprise a sensory epithelium composed of a transducer that converts external electrical stimuli into internal neural responses[15].

There is no evidence for electro-communication in terrestrial vertebrates or invertebrates. Air as a conductive medium for electrical information is inferior to water, and the exoskeleton of invertebrates has been assumed impervious to electrical sensation[3]. Yet, American cockroaches, *Periplanata americana,* some freshwater crustaceans, and other invertebrates exhibit electrosensitivity and behaviorally respond to electric fields[16,17]. Here we provide evidence that German cockroaches electrocommunicate, in that they discharge, and behaviourally respond to electrical information during sexual communication.

We had observed that male German cockroaches exhibit pre-copulatory behaviour in the presence of electromagnetic fields (Wijenberg & Gries, unpublished observations). We surmised that German cockroaches may be deploying electrical signals in the context of sexual communication, and that only individuals sexually mature and receptive respond. To test this, we offered uniform groups of virgin males, mated males, virgin females, or last-instar nymphs (the state preceding adults), and mixed groups of such insects, a choice of two shelters (Fig. 1a). Both were fitted with a copper disc but just one generated an electromagnetic field (Fig. 1b). Only older virgin males were attracted to, and settled in, the shelter associated with the field (Fig. 1c), suggesting that the insects' response to electrical information is contingent upon their sexual maturity, gender and mating status.

If an electric field was capable of inducing pre-copulatory wing-raising in males, it would further indicate a role in the context of sexual communication and reproduction. Wing-raising is a courtship behaviour during which the male raises his wings 90º (see supplemental video) and presents his tergal gland to the female who then mounts the male, feeds on the gland's nuptial secretion, and thus assumes a position suitable for copulation with the male[18]. To test whether an electric field elicits wing-raising behaviour, and to determine the field's characteristics inducing it, we placed males into glass jars and exposed them to oscillating fields of different frequency or intensity or with or without electric component, and with gradient or uniform characteristics (Fig. 2a). We found that the electric component of electromagnetic fields induced wing-raising in males. At a fixed field intensity (1300 – 1400 V/m at exposure surface) but varying frequency, most males wing-raised at 10 KHz (Fig. 2b); at a fixed frequency (10 kHz), progressively more males wing raised with increasing input voltage (Fig. 2b). Males did not respond to fields

without an electrical component, or without a gradient (as tested by exposing insects to a field generated between two plates of opposing potential (Fig. 2c). These data revealed that the electric rather than the magnetic component of the field appears to trigger the wing-raising response, and that males respond to the field gradient rather than to a uniform field. However, we cannot entirely rule out the magnetic component may just have been attenuated in the shielded treatment. That virgin males responded, but mated males, sexually immature males and virgin females did not (Fig. 1c), further supports a function of the field as a courtship signal, apparently destined for virgin males, and produced by, or associated with, females. If so, one would predict more electrical activity associated with solitary females, and groups of females and males, than with solitary males and unisexual groups of females or males. Indeed, we found more electrical pulses in recordings of solitary females than in recordings of solitary males. Mixed groups of females and males had more pulses than unisexual groups, but only during the first 5 seconds of 20-second recordings (Fig. 3d). That there were electrical pulses in recordings of solitary males (data not shown) and in unisexual groups of males (Fig. 3d), suggests that the pulses may also play roles outside the context of courtship and reproduction.

To record and characterize the electrical pulses associated with German cockroaches, insects were placed in a Petri dish positioned between copper mesh capacitor plates (Fig. 3a). Concurrent video recordings of the insects allowed observations of their behaviour during recorded potential differences between plates. These recordings revealed electrical pulses of solitary, bi-phasic waveforms, a frequency ranging between 300-700 kHz, and an intensity (referred to the amplifier input) of order

100 µV (Fig. 3b). These electric pulse characteristics resemble those reported in weakly electric fish.

Wing-raising of males in response to such electrical pulses recorded from females (Fig. 3b), or reproduced at the same intensity and frequency (Fig. 4a), would be strong evidence that female-associated pulses serve as sexual communication signals. When we exposed groups of males to such pulses (Fig. 4b), many males indeed exhibited pre-copulatory wing-raising behaviour (Fig. 4c).

We are currently unaware of the mechanisms of pulse production and reception. Females may produce charge or they may pick up charge through friction with substrate, and then transfer it to a prospective mate. Frictional charge, however, may not account for the rather stereotypical waveform we recorded. Males may sense charge through structures associated with their antennae as has been demonstrated in American cockroaches[19]. However, as the hair receptors evolved to sense surfaces in front of cockroaches, and to then trigger an avoidance response, the authors[19] conclude that the reception of electric stimuli by American cockroaches does not serve as true electroreception, let alone communication.

With the mechanisms of electrical pulse production and reception not yet fully understood, and a history of scepticism in the scientific community towards invertebrates and non-aquatic animals being electroreceptive, or even electrocommunicative, it is noteworthy that the original and now fully accepted concept of electrocommunication in weakly electric fish was initially rejected. The effect of electric fields on the animals' behaviour was deemed due to noxious stimulation of sense organs and nerves[15]. Our findings that groups of German cockroach males, but not single males, exhibited pre-

copulatory wing-raising when exposed to electric fields (Fig. 2d) suggest that this behaviour is not a reflex response to noxious neural stimulation, but that it does occur in response to a courtship signal that typically is coupled to the presence of another German cockroach. Moreover, even though the exoskeleton of invertebrates might reduce their sensitivity to electrical stimuli, an electrical sense could function in aquatic invertebrates, as shown for crayfish[17]. With our study, evidence is emerging that it does function even in terrestrial invertebrates.

To claim electrocommunication in German cockroaches, and to term insect-associated electrical pulses as communication signals, we need to demonstrate intent on part of the sender, a behavioral response from the receiver, and adaptive benefit to one or both participant(s)[1]. We have shown attraction and wing-raising responses of virgin males to female-associated pulses, and the ensuing mating would benefit both partners. Intent is more difficult to prove as we don't know yet the mode of signal production. However, increased pulse incidence in solitary female insects and in female-male pairings (Fig. 3d), and the behavioral response of virgin males to female-associated pulses (Fig. 4c), may indicate evolutionary intent on the part of the female sender[21].

The communication system of German cockroaches is already complex and includes pheromonal[22,23] and auditory[24] signals and cues. Electrical discharges, as yet another type of communication signal, may serve as a back-up or fail-safe system in those microhabitats where olfactory or auditory noise precludes effective communication. Electrocommunication with localized, low-amplitude and intermittent signals may not habituate the insects' sensory system and remain discernible against a noisy background.

3.3. Methods summary

3.3.1. Experimental insects.

German cockroaches were reared as previously described[24].

3.3.2. Attraction of German cockroaches to electromagnetic fields.

Paired shelters in an arena inside a grounded aluminum box were fitted with a copper disc, of which one generated an electromagnetic field (Fig. 1b). For each replicate, the presence of 30 insects in or near a shelter was recorded.

3.3.3. Wing-raising behaviour of male German cockroaches in response to electromagnetic or electric fields.

Paired glass jars on a grounded base were fitted above the lid with a copper disc (Fig. 2a) generated a sine-wave electromagnetic field or no field. The effect of field intensity or frequency on the insects' response was tested by keeping one parameter constant while varying the other. To test the effect of the field's electric component, a grounded aluminum foil was placed between the disc and the jar (Fig. 2a). To compare the effect of a uniform or gradient field, two copper plates were placed equidistant alongside or above the jar (Fig. 2a). To test the effect of group size on the insects' wing-raising response, they were tested singly or in groups of 3.

3.3.4. Electric pulses produced by German cockroaches.

Insects were placed in a Petri dish positioned between copper mesh capacitor plates within a Plexiglas box (Fig. 3a). Concurrent video recordings of the insects allowed observation of their behaviour during recorded potential differences between plates. Numbers of electric pulses produced by males, females, or males and females

were analyzed by ANOVA. Pulse characteristics associated with solitary males or females were analyzed with t-test ($\alpha = 0.05$).

3.3.5. Wing-raising of German cockroach males in response to electrical pulses from a waveform generator.

Virgin males were placed in a glass container with a copper wire inserted through a small hole (Fig. 4b). The wire was charged to emit pulses (treatment) or it was grounded to emit no pulses (control).

3.4. Methods

3.4.1. Experimental insects.

German cockroaches were obtained and reared as previously described[24].

3.4.2. Attraction of German cockroaches to electromagnetic fields.

A Plexiglas™ arena (Diameter (D) = 1.2 m, Height (h) = 0.4 m) was housed in a grounded, shielding aluminum box (h = 0.60, length × width = 1.53 × 1.22 m; wall thickness: 0.25 cm) which was fitted with four electrically-shielded, warm-white, 3-V LEDs producing a 10-h dark: 14-h light photoperiod (Fig. 1a). Two black plastic shelters (h = 10, length × width = 8 × 8 cm) were placed at opposite positions in the arena and fitted with a copper disc (D = 4.0 cm, Thickness = 0.01 cm) 10 cm above the grounded floor. Unlike the control disc, the treatment disc generated an electromagnetic field (Fig. 1b) generated by a Fluke 5200 AC voltage source (Fluke Corporation, Everett, WA, USA). We measured the electrical potential in the vicinity of the copper disc, with a 1 Volt charge on it, using a wire probe and oscilloscope (Techtronics TDS 2). The measurements were taken in one plain from the center of the copper disc in a 1 cm grid

extending 3 cm above, 9 cm below and 6 cm to either side of the center of the disc. We then used these measurements to calculate and map the electric field intensity in volts/ meter. For each replicate, treatment and control discs were randomly assigned to each shelter, and 30 insects randomly selected from the laboratory colony were released in the center of the arena 2 h prior to the dark phase. Eighteen hours later, insects in or near (1.5 cm) a shelter were recorded as responders. Between replicates, shelters were replaced and the arena was cleaned with 95% ethanol and Fischerbrand Sparkleen (Fisher Scientific Company, Ottawa, Ontario, Canada). Proportions of responding insects were analyzed with a χ^2 test ($\alpha = 0.05$).

3.4.3. Pre-mating wing-raising behavior of male German cockroaches in response to electromagnetic or electric fields.

Paired glass jars (D = 4 cm, h = 5 cm) were placed on a grounded base, and a copper disc was positioned 1 cm above each lid (Fig. 2a). The disc was charged via a Fluke 5200 AC generator to generate a sin-wave electromagnetic field or it was grounded and generated no field. The relative importance of the field's voltage (V) or frequency (kHz) on the insects' wing-raising response was tested by keeping one field parameter (Input Voltage (rms) = 120 V or Frequency = 10 kHz) constant while varying the other (Input Voltage (rms) = 0, 15, 30, 60, 90, 120 V or Frequency = 0, 0.1, 1, 10, 100 kHz). To test the effect of the electric component of the field on the insects' wing-raising response, a grounded aluminum foil was placed between the disc and the jar (Fig. 2a). To compare the effect of a uniform or gradient field, the disc was replaced with two copper plates (7 × 4 × 0.02 cm each) placed equidistant (d = 10 cm) alongside or above the jar placed above a rubber base (Fig. 2a). The jar was placed above a rubber base. In all experiments described above, virgin 10-d-old male cockroaches were

collected from the laboratory colony, randomly assigned to groups of 5, and placed in test jars. To test the effect of group size on the wing-raising response of cockroaches, they were tested singly or in groups of 3. A response was recorded when a male raised his wings > 45^0 to its body axis. Experiments with two test stimuli were analyzed with two-sided t-test, and those with 4-6 test stimuli were analyzed with ANOVA. In all experiments $\alpha = 0.05$.

3.4.4. Electric pulses produced by German cockroaches.

In each of 10 replicates, a single 10-d-old virgin male or female, pairs of a virgin male and a female, or unisex pairings of two males or two females were randomly selected from the laboratory colony and placed in a Petri dish (D = 1.25, h = 3.5 cm). The Petri dish was positioned between two capacitor plates (distance between capacitor plates = 1.5 cm, D = 6 cm) made from copper mesh (1 mm grid, Wire diameter = 0.2 mm) and mounted within a Plexiglas^{TM} box (5 × 5 × 5 cm). Each plate was connected to a wire in a shielded twisted-pair cable. Via its shielding, the cable was connected to the grounded BNC feedthrough of a shielding aluminum box (see above) and to a Stanford Research Systems preamplifier with AC coupling, 1×10^4 gain, a high-pass filter (300 Hz), and a low-pass filter (30000 Hz) so any data below 300 Hz or above 30000 Hz associated with the insects was not collected. The roll-off for both filters was 6 dB/octave. Any potential difference between the plates was relayed to a computer fitted with the data acquisition software Labview 7 (National Instruments, Austin, TX, USA). Concurrent video recordings of the insects (Labview Joint-time Frequency Analyzer with AVI Video Playback) allowed observations of their behaviour during recorded potential differences. Numbers of electric pulses produced by single insects, paired males, paired females, or one male and one female (see above), during each of four consecutive 5-sec intervals

were analyzed by ANOVA. Pulse characteristics [intensity (V); frequency (Hz)] associated with solitary males or females (N = 10 each) were analyzed with t-test (α = 0.05).

3.4.5. Wing-raising of German cockroach males in response to electrical pulses produced by a waveform generator.

A model pulse (Fig. 4a) with 100 25-µs points, an intensity of 100 mV and a frequency of 400 Hz was generated using an Agilent 33120A Function/Arbitrary Waveform Generator. The pulse was programmed according to parameters recorded from virgin, 10-d-old females (see Fig. 3b). It is important to note that any low (under 300 Hz) or high frequency (above 30000 Hz) components of this pulse were filtered out upon acquisition and were thus absent from our model pulse. To bioassay the response of insects to model pulses generated 10 times per second, groups (N = 16) of five 10-d-old virgin males were placed in a glass container (2.5 × 2.5 × 5 cm), with a copper wire (L = 2 cm, gauge = 28), inserted through a small hole (Fig. 4b). The wire was charged to emit model pulses (treatment) or it was grounded to emit no pulses (control). The order of testing treatment or control stimuli for 10 min each was randomly assigned. Numbers of wing raises in response to stimuli were analyzed by two-sided t-test (α = 0.05). Data were also analyzed by ANOVA to determine whether the wing-raising responses varied over time.

3.4.6. References

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3.4.7. Figure captions

Figure 3.1 – **Attraction of German cockroaches to electromagnetic fields. a,** Design of behavioural experiments**. b,** Map of the electrical field strength in the vicinity of the copper disc (120 V rms, 10 kHz). **c,** Response of 30 10-d-old virgin or mated males, 30 virgin females, 30 late-instar nymphs, and a group of seven males, seven females and 16 nymphs in two-choice experiments (10 replicates each) to electromagnetic fields (EF). Only virgin males were significantly attracted to, or arrested by, the electromagnetic field (χ^2 test, $P \leq 0.001$).

Figure 3.2 – **Pre-mating, wing raising behavior of male cockroaches in response to electromagnetic or electric fields. a,** Experimental designs for testing wing raising response. **b,** Effect of the fields' input voltage (V) or frequency (kHz) on the insects' wing raising response. **c**, Effect of field-generating copper discs or plates being charged or grounded, shielded or non-shielded, and emitting gradient or uniform fields on the insects' wing raising response. **d**, Effect of group size (single males versus 3-male groups) on the insects' wing raising response.

Figure 3.3 – **Electric pulses produced by German cockroaches**. **a**, Experimental design to record electric pulses from test insects. **b**, Analysis of waveform (1), frequency (2) and time-frequency pulse intensity (3); brighter colors in (3) indicate more intense frequency components. **c**, Comparison of pulse intensity (V), frequency

(Hz), and number of pulses produced by solitary males or females (N = 10 each); there was a statistically significant difference in the number of pulses, but not in pulse intensity or frequency, between males and females (t-test, $P \leq 0.05$). **d**, Number of electric pulses produced by males, females, or males and females (see above), during each of four consecutive 5-min intervals. Within groups, bars with different lower-case letters indicate significant differences in the number of pulses between test intervals; same-color bars with different upper-case letters indicate significant differences in the number of pulses between groups for the same test interval.

Figure 3.4 – **Wing raising of male German cockroaches in response to electrical pulses produced by a waveform generator**. **a**, Model pulse resembling insect-produced pulse. **b**, Experimental design to test wing-raising of males in response to model pulses. **c**, Number of wing-raises in 10 minutes in response to test stimuli.

3.4.8. Figures

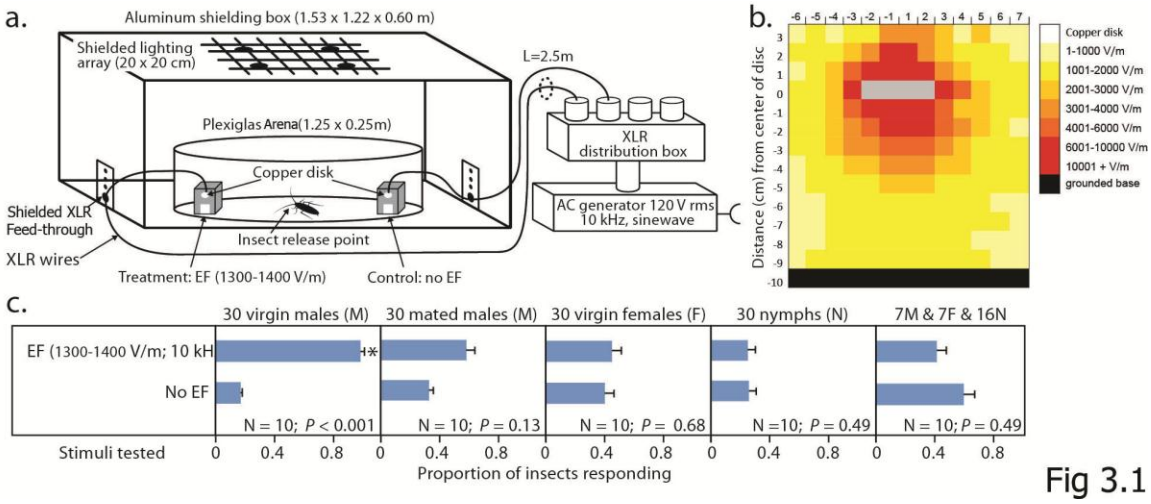

Fig 3.1

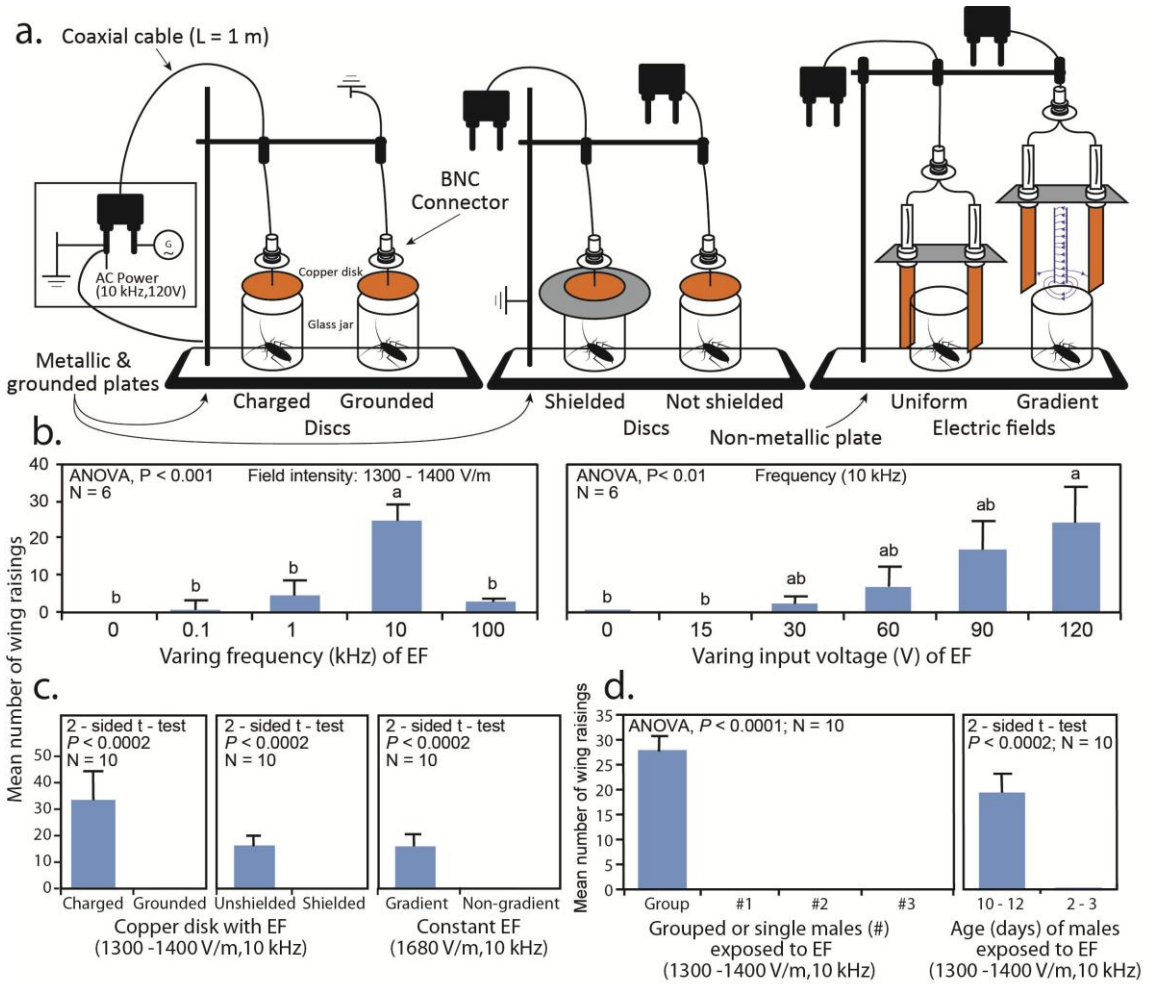
a.
Coaxial cable (L = 1 m)
BNC Connector
AC Power (10 kHz,120V)
Copper disk
Glass jar
Metallic & grounded plates
Charged
Grounded
Discs
Shielded
Not shielded
Discs
Non-metallic plate
Uniform
Gradient
Electric fields
b.
ANOVA, P < 0.001
N = 6
Field intensity: 1300 - 1400 V/m
Mean number of wing raisings
Varing frequency (kHz) of EF
ANOVA, P< 0.01
N = 6
Frequency (10 kHz)
Varing input voltage (V) of EF
c.
2 - sided t - test
P < 0.0002
N = 10
Charged Grounded
Copper disk with EF
(1300 -1400 V/m,10 kHz)
Unshielded Shielded
Gradient Non-gradient
Constant EF
(1680 V/m,10 kHz)
d.
ANOVA, P < 0.0001; N = 10
Group
#1
#2
#3
Grouped or single males (#)
exposed to EF
(1300 -1400 V/m,10 kHz)
2 - sided t - test
P < 0.0002; N = 10
10 - 12
2 - 3
Age (days) of males
exposed to EF
(1300 -1400 V/m,10 kHz)

Fig 3.2

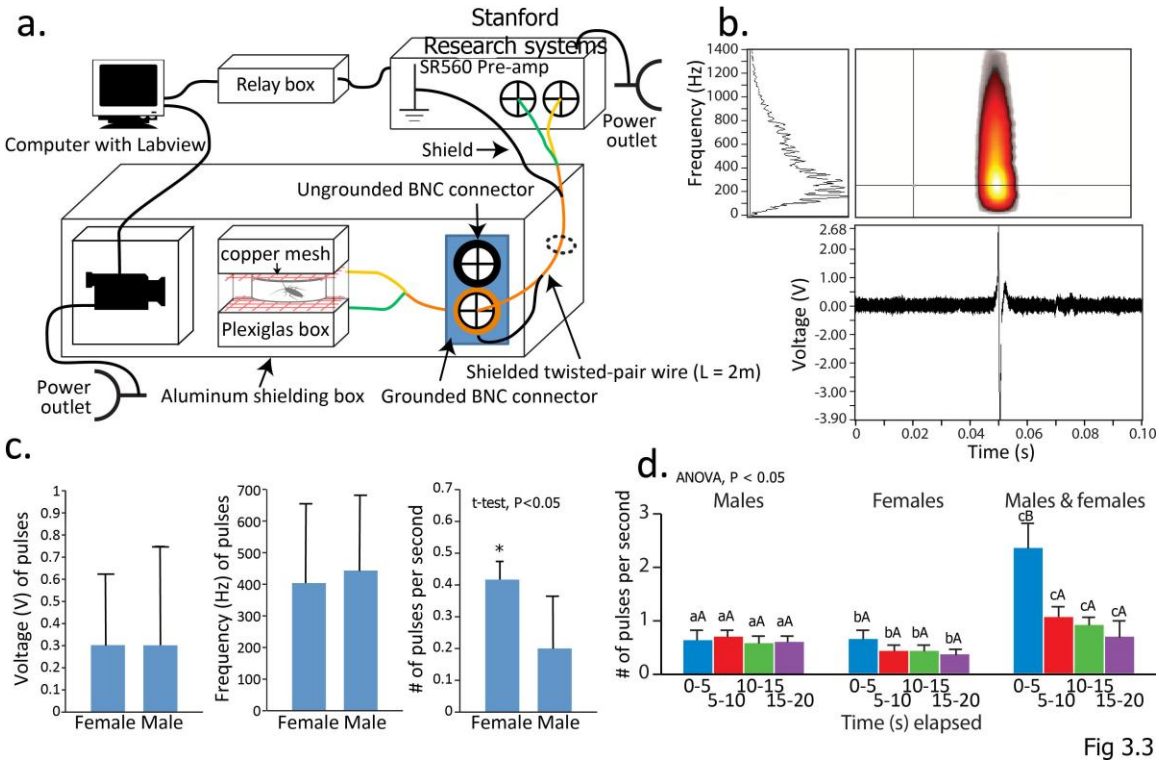
a.
Stanford
Research systems
SR560 Pre-amp
Relay box
Computer with Labview
Power outlet
Shield
Ungrounded BNC connector
copper mesh
Plexiglas box
Power outlet
Aluminum shielding box
Grounded BNC connector
Shielded twisted-pair wire (L = 2m)
b.
Frequency (Hz)
Voltage (V)
Time (s)
c.
Voltage (V) of pulses
Female Male
Frequency (Hz) of pulses
Female Male
t-test, P<0.05
# of pulses per second
Female Male
d.
ANOVA, P < 0.05
Males
Females
Males & females
# of pulses per second
0-5
5-10
10-15
15-20
Time (s) elapsed

Fig 3.3

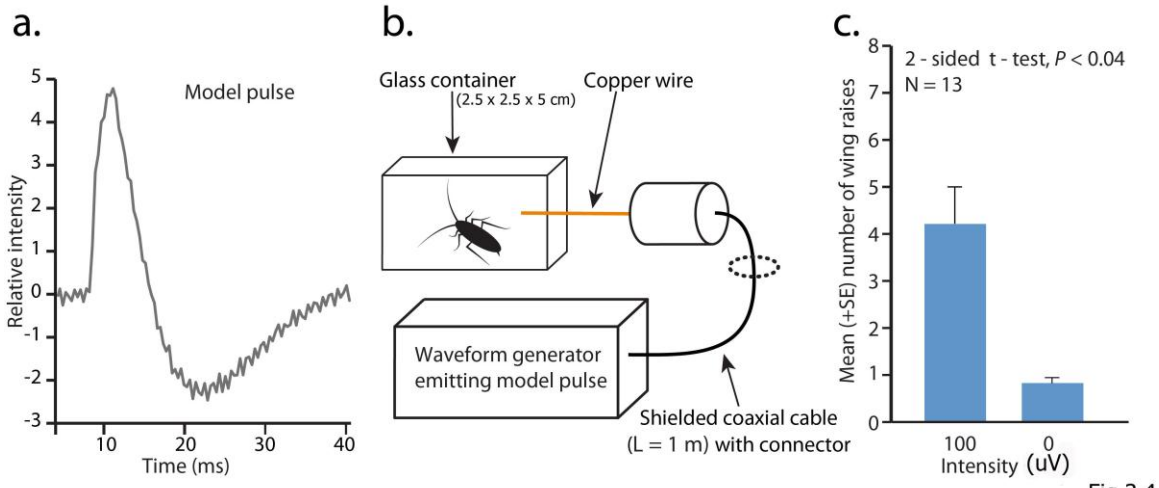
a.
Model pulse
Relative intensity
5
4
3
2
1
0
-1
-2
-3
10
20
30
40
Time (ms)
b.
Glass container
(2.5 x 2.5 x 5 cm)
Copper wire
Waveform generator
emitting model pulse
Shielded coaxial cable
(L = 1 m) with connector
c.
2 - sided t - test, P < 0.04
N = 13
Mean (+SE) number of wing raises
8
7
6
5
4
3
2
1
0
100
0
Intensity (uV)

Fig 3.4

4. Concluding summary

I have investigated the response of various insects to electric stimuli and explored the potential for electrocommunication in the German cockroach.

My main results and conclusions are as follows:

1. In binary-choice arena assays with treatment and control coils, female German cockroaches (a) preferred to shelter in coils associated with fluctuating electromagnetic fields (≤ 0.05 mT and 0.05 -1 mT) generated by AC and DC; (b) preferred to shelter in coils associated with static electromagnetic fields (< 0.11 mT) produced by DC; (c) failed to distinguish between electrified coils associated with a nulled magnetic or an 'active' magnetic field; and (d) preferred electrified coils associated with a nulled magnetic field over non-electrified coils.

2. In binary-choice arena assays with treatment and control coils, Brown-banded cockroaches, common silverfish, firebrats and European earwigs preferred to shelter in coils associated with static electromagnetic fields (< 0.11 mT) generated by DC, whereas American cockroaches were repelled by them.

3. In wing-raising bioassays, virgin male German cockroaches exhibited increased pre-copulatory wing-raising behaviour when exposed to electromagnetic fields, but ceased to do so when exposed to electromagnetic fields with the electric component shielded or without a gradient.

4. Sexually immature males, mated males and virgin females of German cockroaches did not exhibit increased pre-copulatory behaviour in the presence of an electric field.

5. Virgin males, but not mated males, virgin females or nymphs, of the German cockroach, are attracted to specific electromagnetic fields.

6. German cockroaches were associated with pulses of shifting electrical potential. More of these electrical pulses were present in recordings of solitary females than in

recordings of solitary males, and more pulses were present in recordings of mixed groups of females and males than in unisexual groups of males or females.

7. Virgin male German cockroaches exhibit increased pre-copulatory wing-raising behaviour when exposed to electric pulses as recorded from females and reproduced at biologically relevant levels by a waveform generator.

8. To summarize, studying communication in the German cochroach, I have demonstrated a behavioural response (wing raising) by a 'receiver' to a biologically relevant stimulus (an electric pulse) associated with a potential 'sender', thus providing evidence that electric pulses may serve as electrocommunication signals in German cockroaches. The nature of the behavioural response suggests a courtship purpose.

I have demonstrated courtship response by males to a model pulse and surmise that the pulse incidence may provide information during courtship that helps coordinate mating. If detection of pulses were to increase mating success, this would benefit both the 'sender' and the 'receiver'. Such benefits could select for the evolution of electroreception or electrocommunication. The mechanisms of electric pulse production and reception are not yet understood and would be a intriguing to unravel.