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The ecology of electricity and electroreception

Sam J. England* [ID] and Daniel Robert [ID]

School of Biological Sciences, Life Sciences Building, University of Bristol, 24 Tyndall Avenue, Bristol, BS8 1TQ, U.K.

ABSTRACT

Electricity, the interaction between electrically charged objects, is widely known to be fundamental to the functioning of living systems. However, this appreciation has largely been restricted to the scale of atoms, molecules, and cells. By contrast, the role of electricity at the ecological scale has historically been largely neglected, characterised by punctuated islands of research infrequently connected to one another. Recently, however, an understanding of the ubiquity of electrical forces within the natural environment has begun to grow, along with a realisation of the multitude of ecological interactions that these forces may influence. Herein, we provide the first comprehensive collation and synthesis of research in this emerging field of electric ecology. This includes assessments of the role electricity plays in the natural ecology of predator–prey interactions, pollination, and animal dispersal, among many others, as well as the impact of anthropogenic activity on these systems. A detailed introduction to the ecology and physiology of electroreception – the biological detection of ecologically relevant electric fields – is also provided. Further to this, we suggest avenues for future research that show particular promise, most notably those investigating the recently discovered sense of aerial electroreception.

Key words: sensory biology, animal behaviour, electrostatics, electric fields, static charge, atmospheric electricity, neuroethology, physiology, aerial electroreception, anthropogenic noise.

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* Address for correspondence (Tel: +447947472915; E-mail: sam.england@bristol.ac.uk)

I. INTRODUCTION

Electromagnetism is one of the four fundamental forces of the universe. Therefore, electromagnetic interactions inevitably influence the biotic world in a multitude of ways. There are two primary manifestations of electromagnetism: the magnetic field (magnetism), and the electric field (electricity); which when oscillating in synchronicity produce electromagnetic waves, i.e. light (Maxwell, 1865). For a summary and

definition of the key electric and magnetic terminology used within this review, see Table 1. Whilst electromagnetic waves, and to some extent magnetic fields, have in many ways driven the rise and evolution of life on Earth, the influence of electric fields alone should not be understated.

An electric field exists around any electrically charged object, exerting a repulsive force on like charges, and an attractive force on opposite charges (Coulomb, 1785). The electrodynamic interactions of electrons and protons largely

Table 1. A list of electromagnetic terminology with associated definitions and SI units where applicable

Term	Definition	Units (if applicable)
Charge	A property possessed by some objects that allows them to create and interact with electric and magnetic fields. Opposite charges attract each other, whilst like charges repel each other.	Coulombs (C)
Electricity	The phenomena resulting from the interactions between charged objects.	—
Electric field (electric field strength)	The field around a charged object that will exert a force on other charged objects. The force exerted on a charge is proportional to the electric field strength.	Volts per metre (V/m)
Magnetism	The phenomena resulting from the movement of electrical charges.	—
Magnetic field	The field around a moving electrical charge (/magnetic material) that will exert a force on other moving electrical charges (/magnetic materials).	Tesla (T)
Electromagnetism	The combined physical phenomena associated with electricity and magnetism.	—
Electromagnetic wave	A propagating wave consisting of synchronised oscillations of electric and magnetic fields. Also known as 'light'.	—
Current	The net flow of electrical charge through an object/space.	Amperes (A)
Conductor/conduction	A material that allows current to flow through it.	—
Conductance	A measure of how well a particular object allows current to flow through it.	Siemens (S)
Conductivity	A material property that indicates how well a substance conducts electricity, independent of the dimensions of that substance.	Siemens per metre (S/m)
Resistance	Inverse of conductance. How much a particular object resists current flowing through it.	Ohms (Ω)
Resistivity	Inverse of conductivity. A material property indicating how well a substance resists the flow of current through it, independent of the dimensions of that substance.	Ohm metres (Ωm)
Insulator/insulation	A material that does not allow current to flow freely through it (possesses high resistivity/low conductivity).	—
Polarisation	The net movement of charge within an object such that the distribution of charge is no longer symmetrical, resulting in an apparent electric field emanating from the object. Will sometimes be referred to as 'charge separation' if occuring within a conductor.	—
Dielectric	An insulating material that can be polarised when placed within an electric field.	—
Potential	The amount of energy theoretically required to move a unit of charge from a reference point (usually the electrical ground or a point infinitely far away) to the point in question.	Volts (V)
Voltage	The difference in potential between two points.	Volts (V)
Ground/earth	A point or object defined as being at zero potential. This will often be a conductor directly connected into the actual physical ground/earth. The ground can effectively be seen as an infinite source of charge carriers and therefore can act efficiently as a current sink.	—
Capacitance	The amount of charge an object can hold at a particular voltage.	Farads (F)
Electrostatic induction	The induction of current or polarisation within a material due to an applied electric field.	—
Electromagnetic induction	The induction of current or polarisation within a material due to a varying magnetic field.	—
Permittivity	A measure of the polarisability of a material, which has consequences for how much electric fields are attenuated within that material.	Farads per metre (F/m)
Relative permittivity	The ratio of the permittivity of a material to the permittivity of a vacuum, i.e. how much weaker an electric field between two charges would be in this material compared to in a vacuum. Also known as the 'Dielectric constant'.	Dimensionless

dictate the chemistry of both the abiotic and biotic world, and thus the structure of life. However, the bulk distribution and mobility of these charged particles within a material also result in electric fields manifesting their influence on biology at scales much larger than atoms and small molecules. For example, the folding of proteins, which predominantly determines their function, is governed significantly by electrostatic interactions (Zhou & Pang, 2018). It is also well appreciated that electrical interactions are responsible for a great number of cellular functions, in particular cell signalling (Lipscombe & Toro, 2014). Even at the scale of organs and organisms, the functioning of the nervous system in animals and plants relies upon electricity to generate and transmit information, in the form of propagating action potentials (Nicholls *et al.*, 2001). However, one facet of the role of electric fields in biology has remained notably underappreciated: the ecology of electric fields. Recent work has highlighted that indeed a plethora of electrical interactions take place at the ecological scale, in terms of an organism's interactions with the physical abiotic environment, as well as conspecifics and other organisms. This article intends to review our current knowledge on the influence of electric fields at the ecological scale, including the sensory ecology of the biological detection of these fields: electroreception. Particular emphasis and detail will be given to the recently discovered field of aerial electroreception, as this provides some of the most exciting and potentially fruitful opportunities for further research. This review also aims to integrate aerial electroreception into the wider context of electroreception research by comparing and contrasting between aerial

and aquatic examples, identifying common trends whilst appreciating their distinctiveness.

II. SOURCES OF ECOLOGICALLY RELEVANT ELECTRIC FIELDS

(1) Abiotic electric field sources

It is first important to consider the presence of electric fields of abiotic origin. Arguably, the primary abiotic electric field source experienced by terrestrial organisms on Earth is the atmospheric potential gradient (APG) (Hunting *et al.*, 2021c). The APG is an electric field oriented vertically in the Earth's atmosphere, such that, within the vast majority of biologically inhabited altitudes (Imshenetsky, Lysenko & Kazakov, 1978; Womack, Bohannan & Green, 2010), the electric potential increases with altitude (Wilson, 1903). Near to the Earth's surface, in fair-weather conditions, the strength of the APG is on the order of 100 V m^{-1}, but can increase by an order of magnitude, or even invert, during certain meteorological conditions, most notably thunderstorms (Wilson, 1903; Bennett & Harrison, 2007). The APG is largely created by a potential difference between the ionosphere and the Earth's surface and is constantly maintained by the global atmospheric electric circuit, wherein thunderstorms generate electric current upwards in the atmosphere, towards the ionosphere; this current is simultaneously counteracted elsewhere on the planet in fair-weather regions by gradual currents flowing back down to the ground (Rycroft, Israelsson & Price, 2000; Rycroft *et al.*, 2012).

It is also worth mentioning the electrical charges of atmospheric precipitation. Individual raindrops generally carry non-negligible electrostatic charges (Wilson, 1903). These charges vary in polarity, even within the same rainfall, but negative charges appear to be marginally more common (Wilson, 1903; Chalmers & Pasquill, 1938; Chauzy & Despiau, 1980; Bennett & Harrison, 2007). The magnitude of charge carried is also highly variable but is typically in the region of 0.1–1000 pC, depending on meteorological conditions and the size of the raindrop (Banerji & Lele, 1932; Chalmers & Pasquill, 1938; Smith, 1955; Chauzy & Despiau, 1980). Snowflakes and hailstones have also been shown to carry electrostatic charges (Chalmers & Pasquill, 1938; Latham, Mason & Blackett, 1961).

In the aquatic environment, a major abiotic source of electric fields is the Earth's geomagnetic field. Whilst the geomagnetic field itself is not an electric field, any time-varying magnetic field will induce an electric field (Faraday, 1832; Maxwell, 1865). Therefore, because the geomagnetic field varies spatially, when water or animals move through the geomagnetic field, this can be viewed as a temporal variation in magnetic field from the reference point of the moving object, and therefore electric currents are electromagnetically induced in the water or animal (Kalmijn, 1974). The magnitudes of these motion-induced electric fields are not negligible, with a fish moving at 1 m s^{-1} likely to induce electric fields as strong as 0.4 μV cm^{-1}, and electric fields induced by water motion typically measuring around 0.05–0.25 μV cm^{-1} (Barber & Longuet-Higgins, 1948; Kalmijn, 1974). By the same electromagnetic principles, temporal variations in the ambient magnetic field, for example those caused by magnetic storms, will similarly induce electric fields in the Earth's crust and mantle, including the oceans (Kalmijn, 1974). These are generally referred to as telluric, or Earth currents, and in coastal or continental shelf waters (where oceanic telluric currents are at their highest), they are typically on the order of 0.01 μV cm^{-1} in magnitude (Kalmijn, 1974).

(2) Electric fields around plants

Plants are known to be electrically conductive (Corbet, Beament & Eisikowitch, 1982; Gora & Yanoviak, 2015). Therefore, because they are connected into the ground, but protrude above it, the vertical electric field of the APG will cause accumulation of negative charges within the plant *via* electrostatic induction. This results in most plants usually exhibiting a negative surface potential relative to the surrounding air, and thus electric fields will be present around most plants exposed to the APG in typical conditions; a prediction backed up by measurements (Maw, 1962). The strength and shape of these electric fields is dependent largely on the morphology, height, and conductance of the plant, as well as the local atmospheric conditions and the structure of the nearby abiotic and biotic landscape. Typically, however, electric field magnitudes on the order of 1–100 kV m^{-1} within centimetres of the plant surface are likely (Bowker & Crenshaw, 2007b). Notably, plant parts with a high geometrical aspect ratio, such as reproductive floral structures, will exhibit the greatest local electric field strengths (Dai & Law, 1995; Vaknin *et al.*, 2001), potentially reaching 1 MV m^{-1} or more within a few millimetres of the plant surface (Bowker & Crenshaw, 2007b). Furthermore, because of their electrical conductivity, plants, especially tall trees and vegetation, will shield large portions of their surroundings from the vertical APG, effectively nullifying, greatly reducing, or even inverting the electric field strength underneath their canopy (Arnold, Pierce & Whitson, 1965; Williams, Markson & Heckman, 2005; Clarke, Morley & Robert, 2017; Hunting, England & Robert, 2021b).

Individual pollen grains also carry electric charge (Vercoulen *et al.*, 1992; Bowker & Crenshaw, 2007a). Available measurements suggest a typical magnitude of roughly 1 fC, with some pollen grains reaching charges as high as 40 fC (Bowker & Crenshaw, 2007a). Both positive and negative polarities of charge are reportedly common on pollen grains (Bowker & Crenshaw, 2007a), however, other studies have found negative pollen charges to be far more prevalent (Vercoulen *et al.*, 1992).

Plants, especially those found in the aquatic environment, will additionally be electric field sources due to transmembrane potentials resulting from differences in electrochemical

concentrations between the inside of the plant and its external surroundings. This is discussed in detail in Section II.4.

(3) Electrostatic charges of animals

Any electrically insulated object, including an animal, is likely to accumulate charge as it moves through its environment, *via* a mechanism known as triboelectrification, or the triboelectric effect. The triboelectric effect describes the phenomenon wherein the separation of two materials formerly in contact with each other results in an anti-symmetrical deposition of charge on their surfaces. Whilst this effect is usually small, with repetition such as when rubbing two materials against each other, significant differences in charge can be created. The same principle applies to animals walking across and brushing past objects in their environment, including friction with the air when in flight. As such, one would expect many, if not the majority of, animals in the terrestrial environment to carry non-negligible electric charges. This has long been noted in many taxa, but most comprehensively in insects, which tend to accumulate charges whilst in flight (Edwards, 1960a, 1962b; Erickson, 1975; Gan-Mor et al., 1995; Clarke et al., 2013), walking (McGonigle & Jackson, 2002; McGonigle, Jackson & Davidson, 2002; Jackson & McGonigle, 2005), or otherwise in contact with a surface (Edwards, 1962a; Colin, Richard & Chauzy, 1991). These charges are generally, but not exclusively, positive, which places insects near to the top of the triboelectric series (Edwards, 1962a; Clarke et al., 2017), meaning that they will almost always be electron donors in triboelectric interactions. Measures of the electric charge carried by an object or animal are given either as total charge, measured in Coulombs (C), or as surface potentials, measured in Volts (V). Comparison or conversion between the two quantities requires knowledge of the capacitance of the object or animal, measured in Farads (F). The typical electrostatic charges of insects range between 1 and 1000 pC (Fig. 1). Of note is the observation that the amount of charge carried by insects is generally higher in field measurements as compared to laboratory measurements (Montgomery, Koh & Robert, 2019).

Outside of insects, charges have been measured on hummingbirds as high as +800 pC (Badger et al., 2015). Furthermore, reptiles also build up significant positive charges (Vonstille & Stille III, 1994; Izadi, Stewart & Penlidis, 2014), with surface potentials purportedly on the order of 100–1000 V (Vonstille & Stille III, 1994). Electrostatic charges of mammals or amphibians have not been well characterised; however, it is known that the fur of cats and rabbits lies very near to the top of the triboelectric series (Clarke et al., 2017), meaning it readily accumulates positive charge. This likely applies to most mammalian taxa with keratinous fur. Amphibians are unlikely to accumulate significant electrostatic charge due to the presumably high conductivity of their moist skin, and the generally wet or very humid environments that they inhabit. Similarly, for fully aquatic fauna, accumulating electrostatic charge is challenging due to the higher electrical conductivity of the surrounding water, which allows for much faster dissipation of charge than in air.

(4) Transmembrane potentials, myogenic potentials, and electrogenesis

As a result of the biophysics and chemistry of the eukaryotic body, almost all animals and plants will be sources of electric fields irrespective of the triboelectric charging of their surfaces. These electric fields have two primary sources; transmembrane potentials, and myogenic potentials. Transmembrane potentials, defined here as the potential difference between the interior and exterior of an organism, exist around almost all living organisms, due to differences in electrochemical concentrations between the inside of the organism and its environment (Kalmijn, 1974). These electrochemical potentials largely arise from the active transport of ions through the outer wall of the organism, in the pursuit of maintaining internal homeostasis. Ultimately, these transmembrane potentials result in DC electric fields being emitted from most animals and plants. Generally, the magnitude of transmembrane potentials is low enough such that, due to the high resistivity of air, the resultant electric currents in the terrestrial environment are too weak to propagate over distances that would be considered ecologically relevant in most conceivable circumstances. However, the conductivity of water is sufficiently high to allow even very small potentials to generate notable electric currents within the surrounding water, and thus these electrical cues can propagate at higher magnitudes for greater distances in the aquatic environment. Transmembrane potentials, measured within 1 mm of the skin of a variety of vertebrate and invertebrate taxa, are typically on the order of 100 µV (Kalmijn, 1974; Wilkens & Hofmann, 2005), resulting in electric field strengths of around 100 µV cm^{-1} within 1 cm of the animal, decreasing to around 0.1 µV cm^{-1} at about 10 cm away (Kalmijn, 1974). The magnitude of transmembrane potentials is greatly increased around openings of the body cavity, such as the mouth, gills, and anus, as well as open wounds (Kalmijn, 1974). Of particular note is the order of magnitude increase in transmembrane potential observed in wounded crustaceans *versus* unwounded counterparts, rising to as high as 1250 µV, measured at 1 mm (Kalmijn, 1974). The electric field resulting from the transmembrane potential of animals will exhibit very low frequency modulations (typically less than 5 Hz), caused by body movement of the animal, as well as opening and closing of body cavity entrances, such as the gills (Kalmijn, 1974; Wilkens & Hofmann, 2005).

The second primary intrinsic source of electric fields around most eumetazoans is myogenic nervous activity. Specifically, the firing of action potentials within the muscles of animals produces electric fields that leak out into the surrounding environment. These external myogenic potentials are usually of slightly lower magnitude, but higher frequency, than transmembrane potentials; typically on the order of 10–100 µV with frequencies generally greater than 10 Hz
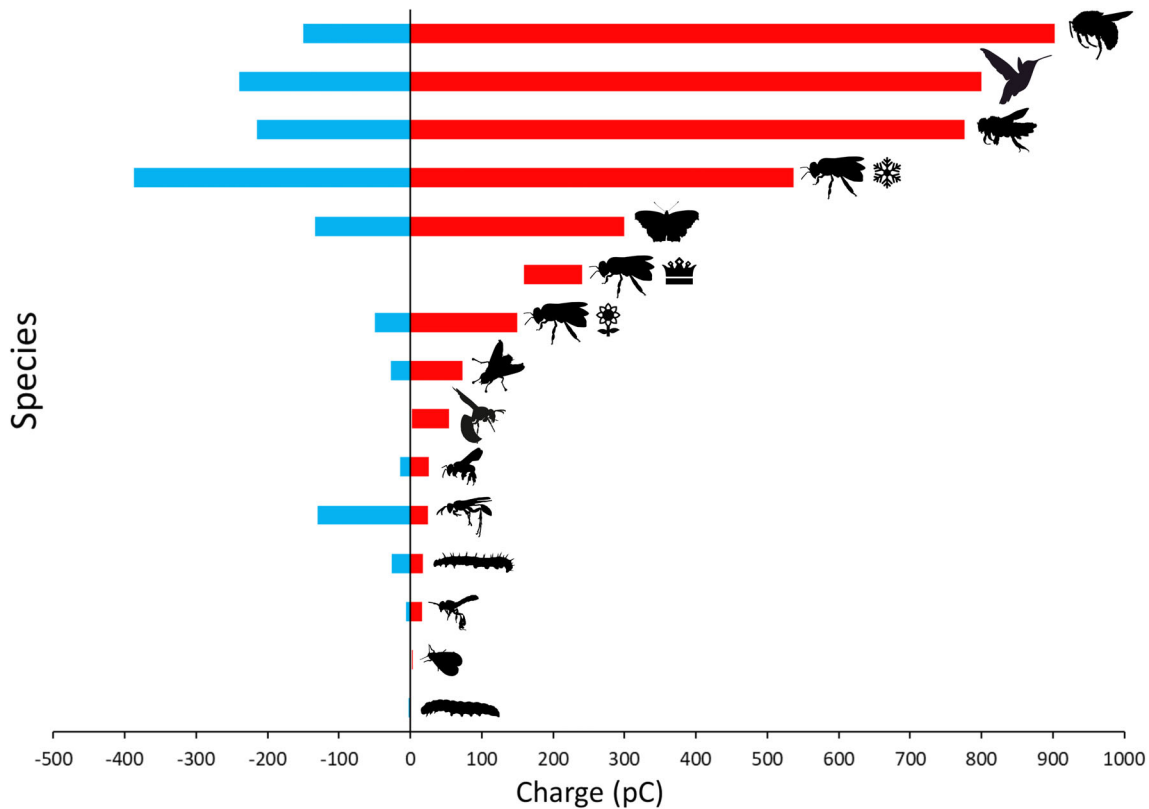
Fig. 1. Ranges of net electrostatic charge measured on animals, taken from existing literature. From top to bottom: bumblebees, *Bombus terrestris*, $N = 798$ (Clarke *et al.*, 2013; Montgomery, 2020); Anna's hummingbird, *Calypte anna*, $N = 194$ (Badger *et al.*, 2015); red mason bee, *Osmia bicornis*, $N = 85$ (Montgomery, 2020); wintering honeybees, *Apis mellifera*, $N = 352$ (Colin *et al.*, 1992); European peacock butterfly, *Aglais io*, $N = 72$ (S.J. England & D. Robert, in preparation); queen honeybee, $N = 1$, two replicates (Colin *et al.*, 1992); foraging honeybees, $N = 339$ (Colin *et al.*, 1992); housefly, *Musca domestica*, $N = 10$ (McGonigle & Jackson, 2002); common wasp, *Vespula vulgaris*, $N = 18$ (Montgomery, 2020); stingless bee, *Scaptotrigona subobscuripennis*, $N = 144$ (S.J. England & D. Robert, in preparation); paper wasp, *Mischocyttarus* spp., $N = 22$ (S.J England, X. Miranda & D. Robert, in preparation); European peacock caterpillar, $N = 44$ (S.J. England & D. Robert, in preparation); stingless bee, *Tetragonisca angustula*, $N = 157$ (S.J. England & D. Robert, in preparation); silverleaf whitefly, *Bemisia tabaci*, $N = 40$ (Lapidot *et al.*, 2020); cinnabar caterpillar, *Tyria jacobaeae*, $N = 5$ (S.J. England & D. Robert, in preparation). Where exact minimum and maximum values were not provided in the source text, estimates of these values were extracted from figures.

(Kalmijn, 1974; Wilkens & Hofmann, 2005). Therefore, like transmembrane potentials, myogenic potentials do not produce significant currents in air, due to its low conductivity, but are able to propagate well in the aquatic environment.

In addition to these incidental electric fields produced by animals and plants, some fish actively generate electric fields with specialised organs. This is known as electrogenesis. There are two main types of electrogenic fish, the strongly electric fish, and the weakly electric fish. Strongly electric fish produce electric potentials from around 10 V up to 860 V (Bennett, 1971*a*; Zupanc & Bullock, 2005; de Santana *et al.*, 2019), whereas the weakly electric fish generally produce potentials on the order of 100–1000 mV (Bennett, 1971*a*; Zupanc & Bullock, 2005). Electrogenesis in both strongly and weakly electric fish is performed by modified muscle and nerve tissues, known as the electric organ (Bennett, 1971*a*). The potentials produced by the electric organ are referred to as electric organ discharges (EODs)

and originate from the cumulative contribution of many electrocytes; specialised cells that produce electric potentials by actively transporting large quantities of ions across their membranes (Bennett, 1971*a*; Crampton, 2019). Whilst the transmembrane potentials produced by electrocytes are not markedly different from other cells, it is their structural arrangement and synchronicity in firing that is largely responsible for the remarkable external potentials produced by the electric organ in its entirety. The EODs of strongly electric fish are of high enough magnitude such that they can constitute a stunning or startling function (discussed in Section III.2), whereas in the weakly electric fish, they facilitate active electroreception and communication (discussed in detail in Section IV.2). The category of weakly electric fish can be further divided into pulse-type and wave-type varieties. Pulse-type animals produce EODs in pulses, which are relatively brief in comparison to the length of electrical silence between them. On the other hand, wave-type fish

generate EODs in a quasi-sinusoidal pattern, in which pulses and silences are of comparable length to each other (Zupanc & Bullock, 2005). A small number of fish species are capable of producing both strongly and weakly electric EODs, with separate electric organs (Bennett, 1970, 1971*a*).

(5) Anthropogenic electric field sources

As with almost all aspects of ecology in the modern day, it is also important to discuss the presence and impact of anthropogenic factors, and therefore anthropogenic electric field sources warrant discussion. Electric fields of human origin have increased exponentially since the industrial revolution, with almost every electrical appliance, device, or infrastructure component emitting electric fields into the environment to some degree. The most significant anthropogenic electric field source is high-voltage power cables and transmission lines, both above ground and submarine. In the terrestrial environment, overhead transmission lines are typically held at voltages on the order of 100 kV, higher than 750 kV in some cases, and as such can produce electric fields in excess of 30 kV m^{-1} at ground level (Repacholi & Greenebaum, 1999; Gonen, 2011). Some household appliances are also capable of producing electric field strengths of this magnitude at very short distances, but more typically these fields are on the order of 100 V m^{-1} (Repacholi & Greenebaum, 1999). In the aquatic environment, subsea cables are emerging as an increasingly prevalent anthropogenic electric field source due to the acceleration in development of offshore energy production. Whilst the cables are usually insulated and shielded to prevent current and electric field leakage, magnetic fields produced by the current in the cable are still emitted into the surrounding water, which subsequently can create electric fields in the water *via* electromagnetic induction. These induced electric fields are thought to have magnitudes between 0.5 and 100 μV m^{-1} (Gill, Bartlett & Thomsen, 2012), which although seemingly small compared to values in the terrestrial environment, are well within the detection ranges of most aquatic electroreceptive organisms (Peters, Eeuwes & Bretschneider, 2007).

In the context of anthropogenic electric field sources, it is also worth mentioning the triboelectric properties of synthetic materials. Generally speaking, synthetic materials and fibres sit at very extreme ends of the triboelectric series, meaning that they often build up negative or positive charges at much greater magnitudes than naturally occurring materials (Henniker, 1962; Zou *et al.*, 2019). The consequence of this is that the electric fields around clothed humans, as well as many anthropogenic structures, are likely to be much higher in magnitude than those around similarly sized animals or natural structures.

III. THE PHYSICAL ECOLOGY OF ELECTRIC FIELDS

The presence of electric fields around organisms and in the environment has many potential ecological consequences. Whilst electroreception provides some of the more complex and well-studied examples of the influence of electric fields at the ecological scale, there are many more underappreciated facets of electric ecology that do not involve the biological detection of electric fields. Instead, these functional aspects relate to physical electrical interactions between organism(s) and their environment; termed here the 'physical ecology' of electric fields. An overview of our current knowledge of this physical, non-sensory, ecology is provided herein.

(1) Electrostatics in pollination and seed dispersal

One ecological function well known to be facilitated in part by electrostatic forces is plant pollination. For example, the electric fields surrounding plants and their charged pollinators are sufficient for contactless pollen transfer, wherein pollen is electrostatically attracted onto the surface of nearby insects (Corbet *et al.*, 1982; Vaknin *et al.*, 2000; Clarke *et al.*, 2017) and hummingbirds (Badger *et al.*, 2015), and *vice versa*. It has even been suggested that buzz pollination, wherein sudden expulsion of pollen is triggered by the vibration of a visiting pollinator, may be facilitated by triboelectric charging of pollen grains vibrating against the walls of the anther (Corbet & Huang, 2014). The electric field around flowers, which is particularly strong around morphological features of high curvature, most notably the sexual organs, is also of sufficient magnitude to enhance pollen capture from the air in wind-pollinated species (Erickson & Buchmann, 1983; Bowker & Crenshaw, 2007*a,b*). Thus, it has been proposed that many plants may have evolved more strongly protruding stigma in order to maximise electrostatic pollen capture (Armbruster, 2001; Vaknin *et al.*, 2001). Purportedly, some species of plant also produce seeds with notably strong electrostatic charges (Eddie, Cupido & Skvarla, 2010), which could be utilising electrostatic repulsion in order to enhance expulsion of seeds, increasing dispersal distances. However, the existence of such a mechanism remains to be empirically tested. It could additionally be possible that wind-dispersed seeds, such as those of dandelions, *Taraxacum* spp., slow their descents or even gain altitude, and thus increase dispersal range, through interactions with the APG. This would be supplementary to the aerodynamic forces recently described in detail (Cummins *et al.*, 2018). Similarly, the possibility of electrostatic adhesion of seeds to animal dispersal vectors should also be investigated. Electrostatics are further involved in pollination through the context of the sensory ecology of pollinators. Specifically, bumblebees, *Bombus terrestris*, and two species of hoverfly, *Eristalis tenax* and *Cheilosia albipila*, are capable of detecting electric fields of the strength found around flowers and may use this information to assess floral reward (Clarke *et al.*, 2013; Khan *et al.*, 2021). Similarly, the waggle dance performed by honeybees, *Apis mellifera*, in order to communicate the location of flowers and other foraging sites, contains information carried by the electric fields around dancing bees (Greggers *et al.*, 2013). Because these aspects of electrostatics in pollination pertain to the biological detection of electric fields, they are discussed in greater detail

in Section IV.3. Lastly, it has recently been demonstrated that flowers of the violet petunia, *Petunia integrifolia*, increase their emissions of volatile compounds known to attract pollinators when exposed to electrostatic charges comparable to those carried by bumblebees (Montgomery *et al.*, 2021). By releasing these attractive compounds in response to the electrical cues emitted by nearby bumblebees, it is suggested that these flowers may increase their chances of being pollinated. As the plant is arguably detecting an ecologically relevant external electric field, and responding to this stimulus physiologically, this phenomenon could be viewed as a case of electroreception in plants – the only known instance of this described to date.

(2) Electricity in predation and parasitism

(*a*) Electrostatics in terrestrial predation/parasitism

Electrostatics also play a role in predation. Specifically, it has been demonstrated that spider webs are electrostatically attracted to positively charged insects, deforming by a few millimetres towards them, and thus the prey-capture efficiency of the webs is likely enhanced (Ortega-Jimenez & Dudley, 2013). Because the webs consist of electrically conductive aqueous glue droplets distributed along comparatively insulating silk threads, it has been proposed that a charge separation is induced within the droplets when charged insects fly nearby, creating the attractive force between web and prey (Vollrath & Edmonds, 2013). If this inductive mechanism is true, then spider webs will also be attracted to negatively charged insects. In the related realm of parasitism, it has been proposed that the electrostatic charges found on honeybees and their parasitic mites, *Varroa destructor*, could be high enough to allow passive electrostatic attraction of the mites towards their host (Colin *et al.*, 1991). There is also evidence showing that the same parasitic mite species displays modified behaviour when exposed to electric fields of the magnitude present around honeybees, and that these changes in behaviour may increase the probability of encountering the host (Colin *et al.*, 1992). The possibility that electroreception is involved in this process is discussed further in Section IV.3.

(*b*) Electricity in aquatic predation

In the aquatic environment, electric fields also play distinct and crucial roles in predation. For example, the EODs produced by strongly electric fish are capable of facilitating prey capture, either through stunning of target animals (Bauer, 1979; Catania, 2014), or by startling hidden stationary prey, allowing their detection (Belbenoit *et al.*, 1979; Catania, 2014). In the electric eel, *Electrophorus electricus*, the temporal pattern of EODs when hunting appears to be optimised for triggering rapid and intense muscle activation in prey animals, resulting in either immobilisation of the target, or involuntary movements that reveal the prey animal's location (Catania, 2014). Behaviourally, electric eels will also alter the orientation of their bodies when tackling larger prey,

curling around targets so as to maximise the strength of electric shocks delivered, which subsequently fatigues the target through involuntary muscle contraction (Catania, 2015*a*). Furthermore, the EODs of strongly electric fish are widely believed to provide protection from predation by deterring or startling predators (Bennett, 1970, 1971*a*; Crampton, 2019), with strong behavioural evidence to support this (Catania, 2016) as well as territorial functions (Rankin & Moller, 1986). The lower magnitude electric fields produced by animals, both incidental from transmembrane and myogenic potentials, and intentional from the EODs of weakly electric fish, also play a huge role in predator–prey interactions in that they provide the source stimulus for aquatic electroreception. The mechanisms and ecology of this are discussed in detail in Sections IV.1 and IV.2.

(3) Electrostatics in animal dispersal and locomotion

Electric fields also make diverse contributions to the ability of several animals to traverse and disperse within their environments. After many early hypotheses (Murray, 1830; Darwin, 1860) and theoretical calculations (Gorham, 2013), it has recently been experimentally demonstrated that electrostatics facilitate ballooning in spiders (Morley & Robert, 2018; Morley & Gorham, 2020). Ballooning is a method of dispersal seen in spiders, spider mites and moth larvae, wherein strands of silk allow an individual to become airborne and subsequently be carried in the air over large distances (Bell *et al.*, 2005). Whilst wind and other air currents certainly contribute to this process (Humphrey, 1987; Weyman, 1993; Reynolds, Bohan & Bell, 2007), the APG alone provides a sufficient electric force under certain conditions to make linyphiid spiders airborne, and subsequently alter their altitude (Morley & Robert, 2018). It has been proposed that the silk strands carry a substantial negative charge, on the order of 1 nC, that results in the spider being dragged upwards in the atmosphere (Morley & Gorham, 2020). Behavioural experiments also demonstrated that the spiders can detect these atmospheric electric fields, and thus may use the strength of the local electric field to decide when to attempt ballooning (Morley & Robert, 2018). The detection of these electric fields by spiders is discussed in detail in Section IV.3.

In contrast to dispersal being aided by electrostatic forces, it was conversely hypothesised that the take-off of whiteflies, *Bemisia tabaci*, may be hindered by electrostatic attraction between the positively charged insects and the plants they inhabit, and that the observed jump away from the substrate prior to commencement of flight may be a strategy to mitigate this (Lapidot *et al.*, 2020). However, after the charge typically carried by these whiteflies was found to be in the region of 3.5 pC, theoretical calculations determined that it is unlikely that electrostatic forces play a significant role in whitefly take-off (Lapidot *et al.*, 2020).

In terms of the locomotion and dispersal of vertebrates, less has been demonstrated empirically. However, it has been

shown that, in addition to van der Waals forces (Autumn *et al.*, 2000, 2002) and capillary action (Huber *et al.*, 2005), electrostatic charging of the feet of geckos contributes to their remarkable adhesion to surfaces (Izadi *et al.*, 2014), enabling them to climb, hunt and rest on vertical and inverted surfaces of various materials.

(4) The ecology of lightning

(a) The direct ecological impact of lightning strikes

The most dramatic, macroscale manifestation of atmospheric electricity is undoubtedly lightning. Lightning occurs when atmospheric electric fields build up to sufficient magnitudes such that an electrical discharge can be generated through the air. Most lightning occurs between two points within or between clouds, but as humans have long witnessed, it can also occur between clouds and the ground (Dwyer & Uman, 2014). These cloud–ground discharges have many profound ecological and evolutionary impacts. Firstly, both plants and animals have been known to be struck by lightning, causing death or injury (Taylor, 1974; Gomes, 2012). Whilst lightning strikes on animals are probably relatively rare events, with megafauna fatalities likely numbering on the order of a few thousand per year, strikes on plants, in particular tall trees, are much more frequent events because protruding plants provide a notably more conductive path to ground than the surrounding air. When struck by lightning, a tree will often be destroyed or killed, along with many of the surrounding plants, and thus lightning is a major creator of clearings in forested areas (Anderson, 1964; Magnusson, Lima & de Lima, 1996; Sherman, Fahey & Battles, 2000; Yanoviak *et al.*, 2017). Furthermore, lightning-damaged trees are more susceptible to colonisation by beetles and fungi (Taylor, 1974; Parlato, Gora & Yanoviak, 2020). Because of these aspects, and the fact that emergent trees are more likely to be struck, lightning strikes can be seen as a significant source of disturbance in forests, and thus contribute heavily to the ecological dynamics of species composition and biomass distribution within these ecosystems (Gora *et al.*, 2020; Yanoviak *et al.*, 2020).

(b) Lightning and wildfire ecology

Further to this, at an even larger scale, lightning strikes are thought to be the most significant natural ignition source for wildfires (Amatulli, Peréz-Cabello & de la Riva, 2007; Krause *et al.*, 2014). Lightning-ignited wildfires can have catastrophic ecological impacts (Tedim *et al.*, 2018), and are increasing in frequency and severity (Veraverbeke *et al.*, 2017; Cattau *et al.*, 2020), in part due to climate change and its effect on lightning strike frequency (Williams, 2005; Krause *et al.*, 2014). Because of their tendency to create drastic disturbance over large spatial scales, wildfires have historically provided a potent source of natural selection, and as such, lightning has undoubtedly shaped the evolution and biogeography of many biomes and their constituent organisms (Bond, Woodward & Midgley, 2005). Indeed, many organisms have adapted to become fire-resistant or even rely upon fire to survive and reproduce (McGranahan & Wonkka, 2020).

(c) Lightning, horizontal gene transfer, and the origins of life

Lastly, lightning is thought to play an ecological role by facilitating horizontal gene transfer amongst prokaryotic communities. It has been suggested, with supporting experimental evidence, that the electrical currents generated within soil and water during cloud–ground lightning strikes are capable of inducing increases in cell membrane permeability and/or fusing prokaryotic cells together – both of these effects can generate pathways for horizontal gene transfer (Demanèche *et al.*, 2001; Kotnik, 2013), wherein genetic information is non-sexually transferred between different genomes. As such, it is possible that lightning contributes significantly to the genetic diversity of microbial communities, and furthermore, may have played a key role in the evolution of early life on Earth (Kotnik, 2013; Weaver, 2013). Further to this, it is thought by many that lightning may have provided the energy source behind the creation of key compounds required for the origin of life on Earth (Miller, 1953; Miller & Urey, 1959; Johnson *et al.*, 2008).

(5) Electrostatics in microbial ecology

(a) Electrostatic dispersal of microbes

Owing to their small size, it is expected that the influence of electric fields on microorganisms will be markedly higher in relation to other forces, as compared with macroscopic organisms. It is known that bacterial cells and their spores are generally negatively charged (Olitzki, 1932; Burke & Gibson, 1933), with measurements of airborne bacteria reaching up to around 1 fC (Mainelis *et al.*, 2001). It is also likely that even with no total net charge present, bacterial cells, as well as aerosols carrying viral particles, can be moved by electric fields *via* induction of a charge separation within the cell or the droplet of liquid containing the microorganisms. As such, it is possible that electric field sources contribute to the ability of aerial microorganisms to disperse, as the electrostatic force from the APG will typically act to increase their altitude. Furthermore, in the case of pathogenic microorganisms, electrostatic charge may facilitate transfer and adhesion to charged surfaces and hosts. Indeed, experiments in wind tunnels revealed that the quantity of bacteria and viruses deposited on flying honeybees correlated with the electrostatic charge on the individual bee (Lighthart *et al.*, 2000; Prier, Lighthart & Bromenshenk, 2001; Lighthart, Prier & Bromenshenk, 2005). As well as this, it has been demonstrated that bacterial pathogens adhere in greater numbers to surfaces such as personal protective equipment (PPE), when these surfaces are electrostatically charged (Cozanitis, Ojajärvi & Mäkelä, 1988; Becker, Kristjanson & Waller, 1996; Allen *et al.*, 2003; Allen, Close & Henshaw, 2006), as occurs triboelectrically through normal usage (Allen *et al.*, 2003, 2006). It has been suggested that this

contributes to an increase in pathogen mobility, and hence higher bacterial infection rates in the clinical environment (Cozanitis *et al.*, 1988; Becker *et al.*, 1996; Allen *et al.*, 2003, 2006).

(b) Influence of atmospheric electricity on biogeochemistry

Independent of any electrostatic interactions directly with microorganisms themselves, electric fields also influence microbial ecology through modification of the chemical environment. For example, it has been shown that variations in the strength of the local APG result in alterations of the electrochemical conditions in soils and freshwater bodies (Hunting *et al.*, 2019). This most likely occurs through electrostatically induced migration of charge carriers in relation to the direction and strength of local electric field conditions, which will be largely influenced by the APG. This has ecological consequences because electrochemical conditions moderate the ability of microorganisms to undergo metabolic processes. Consequently, organisms incapable of significant movement may suffer or benefit physiologically depending on their location relative to these changes in electrochemical conditions, and mobile organisms may migrate to regions of more favourable electrochemical conditions (Hunting *et al.*, 2019). As such, the activity and behaviour of many microorganisms is likely tied to variations in the local APG. However, it has been suggested that trees and other vegetation, which can act as electrical shields, may protect the areas surrounding their canopies from significant variations in APG strength, and thus dampen the resultant biogeochemical changes (Hunting *et al.*, 2021b). Additionally, other recent findings have shown that many species of bacteria use electrochemical signalling to facilitate communication between individuals (Prindle *et al.*, 2015). *Via* release and detection of potassium ions, bacteria in biofilms are able to coordinate metabolic activity (Prindle *et al.*, 2015) as well as attract new individuals to the community (Humphries *et al.*, 2017). Because the potassium ions that mediate this signalling are charged, it is very possible that this communication system is supported, mitigated, or interfered with, by external modulations in the local electric field, such as those stemming from variations in the APG, although this remains to be tested.

(6) Electrostatics in olfaction

Whilst the detailed mechanisms of olfaction are still a matter of debate (Hoehn *et al.*, 2018; Liu, Fu & Li, 2020), electrostatics undoubtedly play some role at the molecular receptor level in terms of the substantial influence of electrostatics at this chemical scale. However, electrostatics may also impact the olfactory sense on a larger scale, by way of the interactions between the electrostatic charges carried by both the receptor organism and the odorant. For example, it has been shown that the placoid chemosensilla found on the antennae of honeybees hold a quasi-permanent electric charge (Erickson Jr., 1982), acting as electrets; the electric equivalent of a magnet. It was proposed that this electrical charge may function to attract odorant molecules and thus enhance the capture efficiency of the olfactory receptor organ, improving its sensitivity. Many other regions of the insect cuticle have similarly been found to exhibit electret properties (Callahan, 1967), which may likewise contribute to olfactory sensitivity (Callahan, 1975). It is not unreasonable to suggest either that the triboelectric charges exhibited on entire animals may also act to attract odorants and hence increase chemosensitivity. Indeed, it has been proposed that the electrostatic charge carried by mammalian species may alter their sensitivity to olfactory stimuli (Frey, 1968). Due to the electric fields found around plants, the same principle may also potentially apply to chemoreception in Plantae, which could, for example, enhance the efficiency of pheromonal and semio-chemical communication. Empirical testing is required to explore this potential role of surface charging in chemical signalling in plants.

(7) Avoidance of anthropogenic electric field sources

Many mammalian and avian taxa appear to avoid high-voltage power lines (Tyler *et al.*, 2014), most notably reindeer, *Rangifer tarandus* (Vistnes & Nellemann, 2001; Vistnes *et al.*, 2004; Vistnes & Nellemann, 2008) and the lesser prairie chicken, *Tympanuchus pallidicinctus* (Pruett, Patten & Wolfe, 2009). This avoidance behaviour has serious ecological and conservation implications because the widespread and interconnected distribution of power lines results in substantial habitat fragmentation, severing the migration routes of these threatened species (Vistnes *et al.*, 2004; Pruett *et al.*, 2009). The exact reason for these avoidance behaviours is not yet entirely known, however, it has been suggested that the animals may be perturbed by the ultraviolet (UV) light emitted from the power lines (Tyler *et al.*, 2014). These UV emissions are a direct result of the electric field strength around the cables of the power lines, which is high enough that the surrounding air is ionised, becoming a plasma. This is known as corona discharge. When the freed electrons recombine with the ionised gas molecules, photons are emitted, with wavelengths peaking at around 200–400 nm (Maruvada, 2000), firmly within the UV spectrum. Whilst humans cannot see these wavelengths, birds have specific UV receptors (Hart, 2001). Furthermore, unlike most mammals, the cornea and lens of reindeer are UV permissive, meaning that UV can still be detected by the retina with non-specialist receptors (Hogg *et al.*, 2011), despite the lack of a specific UV receptor (Bowmaker, 2008). Together, these visual characteristics mean that both birds and reindeer are most likely capable of seeing coronal discharge from powerlines. This coronal UV-mediated avoidance hypothesis is very plausible, however it remains to be tested behaviourally. Noteworthy also is the fact that UV sensitivity is generally believed be a conserved trait among the insects, including keystone bee species (Briscoe & Chittka, 2001; Skorupski & Chittka, 2010; van der Kooi *et al.*, 2021). Whether insects are affected by corona UV emissions is as yet unknown. It is also possible that the avoidance behaviours are in response to other

sensory cues, such as the audible humming produced by many power lines. Most pertinently here, these avoidance behaviours could result from direct detection of the electric fields around the power lines. Avoidance of strong electric fields, mediated by detection of the electric field itself, is well described in many other animals and so should not be discounted as a possibility in these cases; because this pertains to the sensing of electric fields, it is discussed fully in Section IV.3.

(8) Electrostatics in agricultural ecology

(a) Electroculture

Whilst arguably not an aspect of their natural ecology, many species' relationship with agriculture dominates their ecology in the Anthropocene, and therefore the involvement of electrostatics in this context should be discussed. The use of anthropogenic electric fields in agriculture began in the late 18th century with suggestions that exposure to strong electric fields or currents may increase the growth of plants, often referred to as electroculture (Pohl, 1977). Countless experimental studies over the next two centuries claimed to have demonstrated these improved growth rates, with some of the more well-controlled studies reporting increased crop yields of up to 50% from electric field strengths typically on the order of 10 kV m^{-1} or more (Blackman, 1924; Pohl, 1977; Ellis & Turner, 1978). However, it should be noted that other authors have actually reported that electric fields of this magnitude damage plants (Murr, 1963). It is important to note here that most of the studies on this topic suffer from methodological flaws to some degree (highlighted in Schmiedchen *et al.*, 2018). In terms of the mechanism behind electroculture, it has been proposed that the applied electric fields alter the concentrations of ion species around the plant (Pohl, 1977), which is known to have physiological consequences for many organisms, including plants (Krueger & Reed, 1976). Several other interactions between electric fields and biochemical or physiological processes are however also possible. Most notably, increased growth may be the result of electrotropism (also known as galvanotropism), a phenomenon in which some species of plant have been observed to grow towards sources of electric fields (Navez, 1927; Ellis & Turner, 1978), the mechanisms of which have only recently begun to be elucidated (Oliver *et al.*, 2020). Although the electric field strengths involved in electroculture are generally higher than those experienced by plants in nature, it is possible that the observed yield increases shown in electroculture experiments are simply exaggerations of smaller effects still present and functional in nature, that could be caused by the APG or other non-anthropogenic electric field sources. Investigations into this phenomenon are still ongoing, although scientific interest has decreased dramatically in recent decades due to the technique largely being labelled as impractical, or sometimes even pseudoscientific. Overall, whilst a plethora of early evidence does exist in support of the efficacy of electroculture, modern and suitably controlled experiments should be conducted to test the validity of the phenomenon conclusively, in light of recently acquired understanding of the ubiquity and influence of electric fields in the natural environment.

(b) Pest management

Electrostatics play further roles in agricultural ecology through their involvement in pest management. For example, in the case of nano-insecticides, an emerging agricultural technology (Kah *et al.*, 2018), adhesion of insecticidal nanoparticles to target pests is the result of electrostatic attraction between the negatively charged nanoparticles and positively charged insects (Stadler *et al.*, 2018). However, there are concerns that, because bees are also positively charged, there may be unintentional deposition and accumulation of these nano-insecticides on important pollinators, which could lead to dire ecological consequences (Hooven *et al.*, 2019). Similar electrostatic principles also apply to the attraction and adhesion of agrochemicals to plants, therefore agricultural sprays, including those used in artificial pollination, are often intentionally electrostatically charged (Matthews, 1989; Law, 2001). Electric fields can additionally be employed to physically exclude pests. For example, electrostatic precipitators have been designed to prevent fungal spores from reaching crops (Matsuda *et al.*, 2006; Shimizu *et al.*, 2007). It is suggested by the authors of these studies that these devices are capable of fungal spore capture because the strong electric field source induces a charge separation within the spore cells, subsequently attracting them towards the electric field source, upon which they can be collected (Moriura *et al.*, 2006*a,b*). Other authors have found that the conidia of some pathogenic fungi likely possess a net negative surface charge, which may further facilitate this process (Boucias, Pendland & Latge, 1988). Interestingly, by similar mechanisms in nature, it is very plausible that the electrostatic interactions of fungal spores with plants, animals, and the APG improve adhesion to hosts or increase spore dispersal efficacy. In addition, these electrostatic devices have been modified to exclude pest insects. By taking advantage of the electrostatic charges naturally occurring on insects, strong electric fields can similarly forcefully attract insects towards the voltage source, thus preventing them from reaching crops or stored produce (Tanaka *et al.*, 2008; Matsuda *et al.*, 2011, 2012; Kakutani *et al.*, 2012), or removing them from already infested plants (Takikawa *et al.*, 2015). The same methods have also been suggested as solutions for excluding mosquitos (Matsuda *et al.*, 2015), and pollen (Takikawa *et al.*, 2017), from houses, preventing malaria transmission and hay fever, respectively. As previously mentioned, there also exists an apparent behavioural avoidance of strong electric fields by many insect species, which could equally have agricultural applications in pest management. As this relies upon the insects sensing the electric field, it is discussed fully in Section IV.3.

IV. ELECTRORECEPTION

Electric fields permeate both the terrestrial and aquatic environment, and therefore, as with any physical stimulus that

has the potential to provide ecologically beneficial and/or behaviourally relevant cues, it is expected that organisms will have evolved systems to detect these electric fields. Electroreception is the ability of an organism to detect ecologically relevant electrical stimuli within its environment. Electroreception is thought to be an ancient sensory modality that may in fact be ancestral to all vertebrates (Bodznick & Northcutt, 1981; Bullock, Bodznick & Northcutt, 1983). Since then, it has been lost, and subsequently re-evolved, multiple times throughout evolutionary history across a diverse range of lineages (Bullock *et al.*, 1983; Baker, Modrell & Gillis, 2013; Crampton, 2019). Electroreception can be divided into two sub-types: passive and active. Passive electroreception is the detection of ecologically relevant electric fields that are already present within the environment, namely those originating from abiotic sources, or the incidental electric fields of other organisms. This contrasts with active electroreception in which an organism detects distortions of its own self-generated electric fields. These distortions are caused by the presence of nearby objects or organisms. The definition of active electroreception also extends to the detection of electric fields intentionally generated by other actively electroreceptive organisms in the pursuit of reciprocal communication, as is the case in the intra-specific communication of weakly electric fish. Due to the recent discovery of electroreception in terrestrial invertebrates (Clarke *et al.*, 2013), it may also be legitimate to divide electroreception in an alternative way; aquatic electroreception and aerial electroreception, as the evolution and ecology of these two sub-types are substantially different. The mechanisms and ecology of all four of these sub-types will be discussed herein.

(1) Passive aquatic electroreception

Passive aquatic electroreception allows an organism to detect ecologically relevant electrical stimuli present in the aquatic environment. In nature, these electric fields can be biotic in origin, such as the incidental electric fields produced by nearby prey items, predators, and conspecifics, or abiotic, in the case of inductive electric fields produced by the Earth's geomagnetic field. This sensory modality was first demonstrated in the cartilaginous fishes (Murray, 1960, 1962; Kalmijn, 1966, 1971) but has since been found to exist in a vast array of lineages of fishes (Bullock *et al.*, 1983; Crampton, 2019). It has also been shown in amphibians (Fritzsch, 1981*a*; Himstedt, Kopp & Schmidt, 1982), mammals (Scheich *et al.*, 1986; Gregory *et al.*, 1989; Czech-Damal *et al.*, 2012), and possibly aquatic invertebrates (Patullo & Macmillan, 2007, 2010; Steullet, Edwards & Derby, 2007).

(a) Passive electroreception in fishes

Arguably the organisms most renowned for possessing electroreceptive abilities, fish have been the subject of the vast majority of electroreception research. After earlier suggestions based on electrophysiological evidence (Murray, 1960,

1962) passive aquatic electroreception was first confirmed behaviourally in the sharks and rays, in the context of prey detection (Kalmijn, 1966, 1971). Since then, it has been discovered to be a relatively widespread sensory modality in fishes, with an estimated 16% of fish species capable of passive aquatic electroreception (Crampton, 2019), and in many more ecological contexts. Whilst receptors capable of passive aquatic electroreception may have different evolutionary histories in different clades of fishes, a large degree of convergent evolution is evident, and thus some general overarching principles and adaptive constraints can be identified. Morphologically, these receptors exhibit similar designs, often referred to collectively as ampullary electroreceptors (see Fig. 2). Ampullary receptors, named for their ampulla-like shape, were first noted in the description of the 'ampullae of Lorenzini'; a term often reserved for the specific ampullary receptors found in elasmobranchs and other non-teleost fish, which were the first to be anatomically described (Lorenzini, 1678).

(i) General physiology. Ampullary electroreceptors are generally defined as consisting of a cutaneous pore leading to a canal filled with a jelly or mucus-like gel that is highly electrically conductive (Fig. 2A) (Jørgensen, 2005). The canal terminates at a blind-ending, with a layer of electrically excitable sensory cells. The walls of the ampullary canals are commonly composed of tightly packed cells that provide a high resistance barrier that prevents electrical leakage (Waltman, 1966; Bodznick & Montgomery, 2005). In the electrosensory cells themselves, the exact mechanisms of sensory transduction are still not completely elucidated, however it is generally accepted that the ampullary receptors as a whole are tonically active, with constant production of neurotransmitters causing continuous spontaneous firing of action potentials in the connected afferent nerve fibres. External electric stimuli will then increase or decrease (depending on the polarity of the stimulus) the potential difference across the membranes of the electrosensory cells, triggering the opening or closing of voltage-gated ion channels in the electrosensory cells. This in turn modulates the release of neurotransmitters, and thus the overall afferent nervous activity originating from the sensory organ. Teleost ampullary electroreceptors are all excited by anodal stimuli, meaning the external potential is positive relative to the internal tissue of the animal, whereas the ampullary electoreceptors of all other, non-teleost, fish are excited by cathodal stimuli, i.e. an external potential that is negative relative to the internal tissue of the animal (Bodznick & Montgomery, 2005; Baker *et al.*, 2013). The opposite stimulus polarities in each case respectively are inhibitory (Bodznick & Montgomery, 2005). The passive electroreceptors of lampreys are also often grouped with ampullary electroreceptors, however, the morphology of these sensory organs is significantly different from other ampullary electroreceptors (Fig. 2B). Instead of possessing a canal filled with conductive gel, lampreys have electrosensory cells protruding directly from the epidermis, in so called 'end-buds' (Jørgensen, 2005). Despite their morphological dissimilarity to typical ampullary electroreceptors, these end-bud
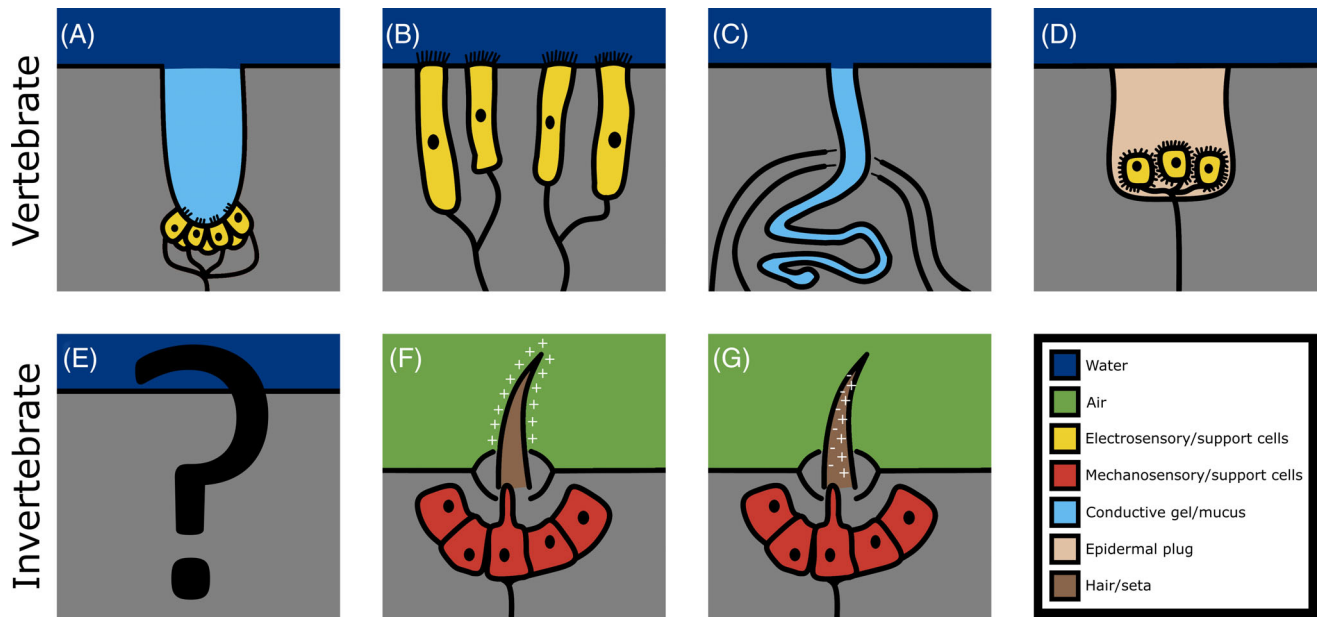
Fig. 2. Schematic depictions of the basic anatomy/morphology of the main types of electroreceptive organs (not to scale). (A) Ampullary organ typical of passive aquatic electroreception in fishes and amphibians. (B) End-bud receptors, used for passive aquatic electroreception in lampreys. (C) Mucous-gland electroreceptor with naked nerve endings, used for passive aquatic electroreception in monotremes. (D) Tuberous organ typical of active aquatic electroreception in fishes. (E) Yet to be identified electroreceptor utilised by aquatic invertebrates such as crayfish. (F) Mechanosensory hair with a quasi-fixed surface charge, used for electroreception by bumblebees and hoverflies. (G) Mechanosensory hair with an induced charge separation (polarisation), used for electroreception by spiders. Grey regions indicate miscellaneous tissues, black lines exiting at the bottom of each diagram represent afferent nerve fibres.

electroreceptors achieve similar sensitivities in magnitude and frequency to many ampullary systems (Bodznick & Northcutt, 1981), and it is under this criterion that they are sometimes grouped with the ampullary electroreceptors.

(ii) Maximising electrical sensitivity. It is apparent that maximising the change in potential difference across the membranes of the electrosensory cells for a given external stimulus will increase their sensitivity to that stimulus. This is likely achieved by the morphology, electrical properties, and physiology of the ampullary canals in several ways. Firstly, the high conductivity of the gel in the canal allows electric currents to travel through it almost unopposed, meaning that the electric potential at the base of the canal is largely equal to the potential at the opening to the external environment, i.e. there is a near-zero voltage drop along the length of the canal within the gel (Waltman, 1966; Kalmijn, 1974; Zakon, 1988). Thus, the ampullary electroreceptors essentially sample the electric potential at the opening of the canal, with reference to the potential of the tissue adjacent to the base of the canal. These potentials will henceforth be referred to as the stimulus potential and reference potential, respectively. Because the difference between these potentials is practically equal to the potential difference across the sensory cells, any increase in the difference between these two potentials will increase the electrical sensitivity of the organ. Unlike the highly conductive gel in the ampullary canal, the generic tissues found adjacent to the canal will have more significant resistivities, and thus a voltage drop,

increasing with depth, will be present between the external environment and any point within the tissue (Kalmijn, 1974). Therefore, the electric potential in the tissues adjacent to the sensory cells will decrease the deeper the ampullary canal extends into the tissue of the animal, i.e. the reference potential for the electrosensory cells decreases with depth. Ultimately, this means that the difference between the reference potential and stimulus potential is much greater than if the electrosensory cells were simply located on the surface of the animal, even though the stimulus potential would be essentially equal in both cases. Thus, a canal extending into the tissue of the animal, filled with a highly conductive substance, results in significantly greater electric field strengths across the electrosensory cells, increasing the sensitivity of the animal to electrical stimuli. It is important to note that this model for the role of the canal and gel has been challenged, with some experimental evidence and theoretical arguments suggesting that the gel in fact acts to create voltage differences along the length of the canal, similar to the functional principles of a radio antenna, instead of equalising to the potential at the pore (Brown, Hughes & Russo, 2005). Whilst this antenna model is enticing and offers other electrodynamic possibilities, the conventional model previously described is still the most widely accepted.

Another important way in which electrical sensitivity is thought to be increased is through the use of stochastic resonance. Stochastic resonance describes the observation that by adding noise to a signal, one can amplify the strength of

that signal. This happens because certain frequency components of the noise will resonate with the signal, thus amplifying it, whilst the remaining noise remains at the same amplitude. Interestingly, in some passive aquatic electroreception systems, such as in the paddlefish (*Polyodon spathula*), this stochastic resonance concept is proposed to be utilised to allow the detection of otherwise undetectable electrical signals from prey items (Russell, Wilkens & Moss, 1999; Freund *et al.*, 2002).

(iii) Comparisons between marine and limnic taxa. It is generally observed that marine fishes have considerably deeper ampullary canals than their freshwater counterparts (Jørgensen, 2005). This is largely due to the different conductive properties of their environments and of the fishes themselves. In freshwater fishes, the skin has a very high electrical resistance (Bennett, 1971*b*; Szabo *et al.*, 1972; Kalmijn, 1974); a by-product of the need to maintain homeostasis in an environment where they are highly hypertonic. The tissues beneath the skin, however, are by comparison relatively conductive. This means that when exposed to an external electric potential, the vast majority of the voltage drop inside the fish will occur within the skin (Szabo *et al.*, 1972; Zakon, 1988), and therefore, there is little benefit, in terms of sensitivity, in having canals that protrude further into the body tissues than the skin. On the other hand, the skin of marine fish species has a similar electrical resistance to the internal tissues underneath, and therefore when exposed to an external uniform or large-scale electric potential, significant voltage drops occur deep into the tissue (Kalmijn, 1974). Accordingly, it is evolutionarily adaptive for marine fishes to possess ampullary canals that protrude deep into the body tissue, sometimes as much as a third of the animal's body length (Bullock, 1973). It is worth noting briefly, however, that for a local dipole electric field source, such as that expected from a prey animal, most of the voltage drop will still occur within the skin, even for marine animals (Kalmijn, 1974). Because of this size disparity between the ampullary canals of marine and freshwater taxa, the term 'microampullary' is sometimes used to describe the passive electroreceptors of freshwater fishes (Szabo *et al.*, 1972; Kalmijn, 1974; Crampton, 2019).

(iv) The role of the ampullar gel. Beyond the basic biophysics outlined already, the exact function and mechanisms behind the conductive properties of the ampullar gel are an active topic of research (Josberger *et al.*, 2016). In some species the composition of the gel has been identified as a salty glycoprotein matrix (Brown *et al.*, 2002; Brown, 2003) that appears to be reasonably conductive in the ionic regime (Brown *et al.*, 2002), but remarkably so in the protonic regime, representing the highest protonic conductivity of any biological material identified so far (Josberger *et al.*, 2016). Being only 40 times less conductive in the protonic regime than current state-of-the-art artificial materials, the ampullar gel could be of great interest in the field of biomimetics. However, as stated above, the detailed functional role of the ampullar gel, as well as the precise mechanisms by which the electrosensory cells can detect such

low-magnitude electric fields, are currently not entirely clear or agreed upon (Brown *et al.*, 2005; Bellono, Leitch & Julius, 2017), and thus the complete pertinence of these conductivities cannot yet be fully assessed.

(v) Evolution and ecology. The ampullary receptors of fishes are deeply associated morphologically, developmentally and neurologically with the lateral line mechanosensory system (Bodznick, 1989; Modrell *et al.*, 2011; Gillis *et al.*, 2012; Baker *et al.*, 2013); a sensory modality present in almost all fish that allows for detection of small water movements (Montgomery, Bleckmann & Coombs, 2014). It is therefore widely accepted that the ampullary electroreceptors of fish evolved from modification of this lateral line system (Bodznick, 1989; Baker & Modrell, 2018).

Behaviourally, passive electroreception in fishes is most commonly associated with detection of the incidental electric fields produced by prey items (Kalmijn, 1971), especially those submerged in the benthic substrate. However, it has also been shown to play a role in mating interactions (Tricasa, Michael & Sisneros, 1995) and predator avoidance (Kempster, Hart & Collin, 2013). Furthermore, it is likely that ampullary electroreceptors are capable of detecting the low-frequency components of the EODs of electrogenic animals, thus potentially further facilitating predatory (Stoddard, 2002) and communicative (Bratton & Ayers, 1987; Crampton, 2019) functions. Intriguingly, passive electroreception has also long been suggested as a viable mechanism for the apparent magnetoreceptive abilities of elasmobranchs (Kalmijn, 1974, 1982; Paulin, 1995). It is thought that the ability to navigate using the Earth's geomagnetic field is a fairly ubiquitous trait in elasmobranchs (Meyer, Holland & Papastamatiou, 2005), and one hypothesised mechanism by which this is achieved suggests that ampullary electroreceptors are capable of detecting the electric fields induced within the water or fish as they move through the Earth's geomagnetic field (Kalmijn, 1974, 1982; Paulin, 1995). However, this mechanism of inductive indirect magnetoreception awaits experimental confirmation (Johnsen & Lohmann, 2005), and recent evidence suggests that the magnetoreceptive abilities of elasmobranchs are unlikely to be achieved by the electrosensory system alone (Anderson *et al.*, 2017). It is possible that these fish may use a combination of induced electric fields detected by electroreceptors, and magnetic fields detected by some as yet undetermined magnetoreceptor, in order to navigate using the Earth's geomagnetic field.

(vi) Behavioural thresholds. Due to the great diversity of fishes that display passive electroreception, there is also a fairly large variation in the minimum electric field strength detectable by a particular species. The highest degree of sensitivity is likely to be found in marine elasmobranchs, for which threshold sensitivities are widely accepted to be in the region of around 5 nV cm^{-1} (Kalmijn, 1982; Wilkens & Hofmann, 2005; Peters *et al.*, 2007), but may even be lower than 1 nV cm^{-1} (Kajiura & Holland, 2002; Kajiura, 2003). These thresholds have been demonstrated both physiologically and behaviourally. The sensitivity of freshwater organisms is believed to be comparatively diminished, with most studies presenting thresholds on the order of 1000 nV cm^{-1}

(Peters *et al.*, 2007). In terms of a frequency response, ampullary electroreceptors are generally regarded as being sensitive to electric fields from DC to around 50 Hz (Bodznick & Montgomery, 2005).

(b) Electroreception in amphibians

Electroreception in amphibians is similar to that of fishes. Amphibian electroreceptors are derived from the lateral line system and share morphological and developmental characteristics with the ampullary electroreceptors of fishes (Fritzsch, 1981*b*; Fritzsch & Wahnschaffe, 1983; Northcutt, Brändle & Fritzsch, 1995); therefore, it is likely that amphibian electroreception was inherited from the earliest tetrapod ancestor (Bullock *et al.*, 1983; Baker *et al.*, 2013). Ampullary electroreceptors and associated behaviours have been found in two of the three amphibian orders: Urodela (salamanders) (Fritzsch, 1981*a*; Himstedt *et al.*, 1982) and Apoda (caecilians) (Hetherington & Wake, 1979; Himstedt & Fritzsch, 1990). The remaining amphibian order, Anura (frogs), appears to be without an electroreceptive sense (Schlosser, 2002; Crampton, 2019), having presumably lost the capability as it diverged and progressed to a more terrestrial lifestyle. Detection thresholds of amphibian ampullary receptors have been found electrophysiologically to be approximately $100 \ \mu V \ cm^{-1}$ (Münz, Claas & Fritzsch, 1982; Schlegel & Roth, 1997). Feeding responses were elicited in 47% of tests at this field strength (Himstedt *et al.*, 1982), indicating that the behavioural threshold lies somewhere in this order of magnitude.

(c) Electroreception in mammals

Perhaps due to their generally terrestrial nature, studies on electroreception in mammals have been somewhat limited. However, passive aquatic electroreception has been shown in the extant clades of monotremes, namely the platypus, *Ornithorhynchus anatinus* (Scheich *et al.*, 1986; Gregory *et al.*, 1987; Manger & Pettigrew, 1995) and echidnas (Tachyglossidae) (Gregory *et al.*, 1989; Manger, Collins & Pettigrew, 1997), as well as a single species of placental mammal, the Guiana dolphin, *Sotalia guianensis* (Czech-Damal *et al.*, 2012).

(i) Electroreception in monotremes. The electrosensory structures in monotremes are analogous in many ways to the ampullary electroreceptors of fishes, but also possess a few distinctions (Fig. 2C). Monotreme electroreceptors are modified mucous or serous glands located on the bill, which are heavily innervated at their blind end (Gregory *et al.*, 1988). Unlike in fishes, these nerves possess naked endings, through which the external electrical stimuli can be detected, as opposed to utilising sensory cells (Manger *et al.*, 1995; Proske, Gregory & Iggo, 1998; Pettigrew, 1999). However, the exact mechanism by which external electric stimuli are transduced into afferent action potentials is still not known (Czech-Damal *et al.*, 2013).

In the platypus, behavioural thresholds for electroreception have been established as low as $20 \ \mu V \ cm^{-1}$ (Pettigrew, 1999) but through theoretical calculations of temporal integration, it may be as low as $10 \ \mu V \ cm^{-1}$ (Fjällbrant, Manger & Pettigrew, 1998). In nature, electroreception, combined with mechanoreception, appears to allow platypuses to achieve accurate detection of prey (primarily benthic invertebrates) despite hunting in dark, turbid water with their eyes, ears, and nostrils, closed (Scheich *et al.*, 1986; Manger & Pettigrew, 1995; Proske *et al.*, 1998).

In the case of the echidna, electroreception has only been investigated in two species (Czech-Damal *et al.*, 2013): the short-beaked echidna, *Tachyglossus aculeatus* (Gregory *et al.*, 1989), and the Western long-beaked echidna, *Zaglossus bruijnii* (Manger *et al.*, 1997). The only evidence for electroreception in the latter is based on histological examinations, however, it was found that *Z. bruijnii* has many more putative electroreceptive units than *T. aculeatus*, and is therefore probably more sensitive to electrical stimuli. Whilst they have not been explicitly assessed for electroreceptive abilities, the two remaining extant species of echidna currently described, *Zaglossus bartoni* and *Zaglossus attenboroughi*, most likely also possess electroreceptors. For *T. aculeatus*, minimum detectable electric field strength thresholds have been found electrophysiologically and through training experiments to be around $1.8 \ mV \ cm^{-1}$ (Gregory *et al.*, 1989), much higher than that found for the platypus. Albeit from a fully terrestrial animal, electroreception in the echidna is not an example of aerial electroreception, as the sense is only functional when the snout is submerged in moist soil or water. It is proposed that echidnas likely use electroreception to detect the bioelectric fields of prey items hidden in the soil, and it has been demonstrated in field studies that this may be the case (Proske *et al.*, 1998). However, due to the low sensitivity and a diminished number of electroreceptors on the snout of both echidna species investigated, as compared to the platypus (Manger *et al.*, 1997), it is also sometimes suggested that echidna electroreception may be a vestigial phenomenon that is in the process of being lost (Pettigrew, 1999).

(ii) Electroreception in placentals and marsupials. Electroreceptive abilities have also been demonstrated in one marine mammal, the Guiana dolphin (Czech-Damal *et al.*, 2012). In this study, behavioural psychophysical experiments were performed on a single captive dolphin, determining the detection threshold of electrical stimuli to be $4.6 \ \mu V \ cm^{-1}$. Histology was additionally performed on a different, deceased, Guiana dolphin to identify the vibrissal crypts of the dolphin as the electroreceptive organs. These vibrissal crypts are the location of vacated vibrissae; highly innervated whiskers used for detecting water movements in other aquatic mammals (Dehnhardt, Mauck & Bleckmann, 1998), but largely lost in adult toothed whales. Morphologically, these vibrissal crypts show a high degree of similarity to the ampullary structures of monotremes and fishes, including containing a glycoprotein-based gel that may improve conductivity within the crypt. Additionally, experimental covering of the vibrissal crypts with a plastic shell resulted in a loss of responsiveness

to electric stimuli (Czech-Damal *et al.*, 2012). Therefore, current evidence suggests that vibrissal crypts are the site of electroreception in Guiana dolphins (Czech-Damal *et al.*, 2012). However, as in monotremes, the exact mechanism of sensory transduction of external electric fields into activity of sensory neurons set into vibrissal crypts is yet to be determined. Overall, the arguments put forward by this study are strong, however, more experiments are likely needed with larger sample sizes to assess the efficacy and prevalence of this ability in the Guiana dolphin. It is also apparent that the psychophysical experiments do not carry clear ecological relevance to the dolphin's behaviour in nature. Whilst convincing hypotheses are presented to suggest that Guiana dolphins use electroreception, supplementary to echolocation, when feeding benthically (Czech-Damal *et al.*, 2012, 2013), these behaviours need to be tested explicitly.

Apart from in the Guiana dolphin, electroreception has not been confidently confirmed in any placental or marsupial. Some behavioural evidence has been put forward to suggest that the star-nosed mole, *Condylura cristata*, may possess aquatic electroreceptive abilities (Gould, McShea & Grand, 1993), however this evidence has been considered inconclusive (Bullock, 1999). A more recent study tested the possibility that the American water shrew, *Sorex palustris*, could use electroreception to locate prey underwater. This involved behavioural experiments in which shrews were exposed to DC and square-wave electrical stimuli with current strengths of 2–20 μA, as well as the use of scanning electron microscopy to search for candidate electroreceptive structures. However, these investigations yielded negative results (Catania, Hare & Campbell, 2008). It has additionally been hypothesised that because sperm whales, *Physeter macrocephalus*, have historically been known to become tangled in deep sea cables (Heezen, 1957), they may detect, and become confused, by the electric fields emitted (Dehnhardt *et al.*, 2020). It is argued that whale entanglements have since ceased following the inclusion of more efficient electrical shielding in modern sub-sea cables (Dehnhardt *et al.*, 2020). However, it has also been said that the reduction of entanglements is in fact simply due to changes in construction techniques (Wood & Carter, 2008). Most recently, it has been suggested that the bottlenose dolphin, *Tursiops truncatus*, possesses vibrissal crypts akin to those found in the Guiana dolphin, that may similarly be capable of electroreception (Dehnhardt *et al.*, 2020). Psychophysical experiments are reportedly ongoing to investigate this (Dehnhardt *et al.*, 2020).

(d) Electroreception in aquatic invertebrates

(i) Electroreception in aquatic arthropods and cephalopods. Research into the existence of electroreception in aquatic invertebrates has been particularly sparse (Bullock, 1999). No truly conclusive evidence has been presented to suggest that any invertebrate utilises aquatic electroreception in its natural sensory ecology, however some studies have shown that various crayfish species appear capable of reacting to electric fields. With the use of DC and sinusoidal voltage-driven dipole electrodes, it was shown that some feeding behaviours can be elicited in a freshwater crayfish, *Procambarus clarkii*, by electric fields of strengths greater than 20 mV cm^{-1} (Steullet *et al.*, 2007). Two other studies have similarly shown that the common yabby, *Cherax destructor*, and the Australian red claw crayfish, *Cherax quadricarinatus*, alter their walking behaviour when presented with DC and prey-imitating AC electric fields as low as 400 μV cm^{-1} (Patullo & Macmillan, 2007, 2010). These thresholds are low enough to reasonably suggest that crayfish may be able to detect the electric fields emitted by predators or prey items at very close range, especially if they are wounded, but not the induced electric fields from the Earth's geomagnetic field (Kalmijn, 1974; Patullo & Macmillan, 2010; see Fig. 3). No sensory mechanism was found or suggested by any of these studies (Fig. 2E). Due to this, and the fact that the electric field strengths required to elicit significant behavioural changes are higher than the thresholds of vertebrates, it is not yet certain whether or not electroreception is utilised by crayfish (or other aquatic arthropods) in nature.

In addition, some studies have characterised a startle response in various shrimp species that can be elicited by exposure to electric fields (Kessler, 1965; Polet, Delanghe & Verschoore, 2005). Both the Northern pink shrimp, *Farfantepenaeus duorarum* (Kessler, 1965) and the brown shrimp, *Crangon crangon* (Polet *et al.*, 2005) display a 'tail-flip' or 'scare hop' response when subjected to relatively strong voltages, wherein the animal suddenly launches vertically and contracts its abdomen. These studies were conducted with the aim of assessing the ability of electric fields to improve efficiency and reduce by-catch in shrimp fishing, because this startle response can be utilised to make shrimp selectively more vulnerable to net capture. Consequently, the electric field strengths used are considerable, estimated to be at least 40 mV cm^{-1} across the length of the shrimp, and therefore the behaviours exhibited are most likely due to involuntary muscular contractions caused by electrification of the animal. Therefore, these studies in shrimp cannot be considered as evidence of electroreception, as the stimuli presented are very unlikely to be ecologically relevant. Concurrent experiments also found that the swimming crab, *Liocarcinus holsatus*, and the shore crab, *Carcinus maenas*, display agitated behaviours when exposed to similarly strong electric fields (Polet *et al.*, 2005), but again, the magnitudes of these stimuli are most likely too high to be considered ecologically relevant. Outside of the Arthropoda, preliminary electrophysiological experiments have been carried out to assess the possibility of electroreception in the cuttlefish, *Sepia* sp., but these yielded negative results (Bullock, 1999).

(ii) Electrotaxis as electroreception?. In addition to these findings on macroinvertebrates, several studies on the model organism, *Caenorhabditis elegans* (Sukul & Croll, 1978; Gabel *et al.*, 2007; Rezai *et al.*, 2010), as well as nematodes in general (Sukul, Das & Ghosh, 1975), have revealed electrotactic behaviours which may by some definitions be regarded as aquatic electroreception. These studies show that when exposed to electric fields in an aqueous environment, many
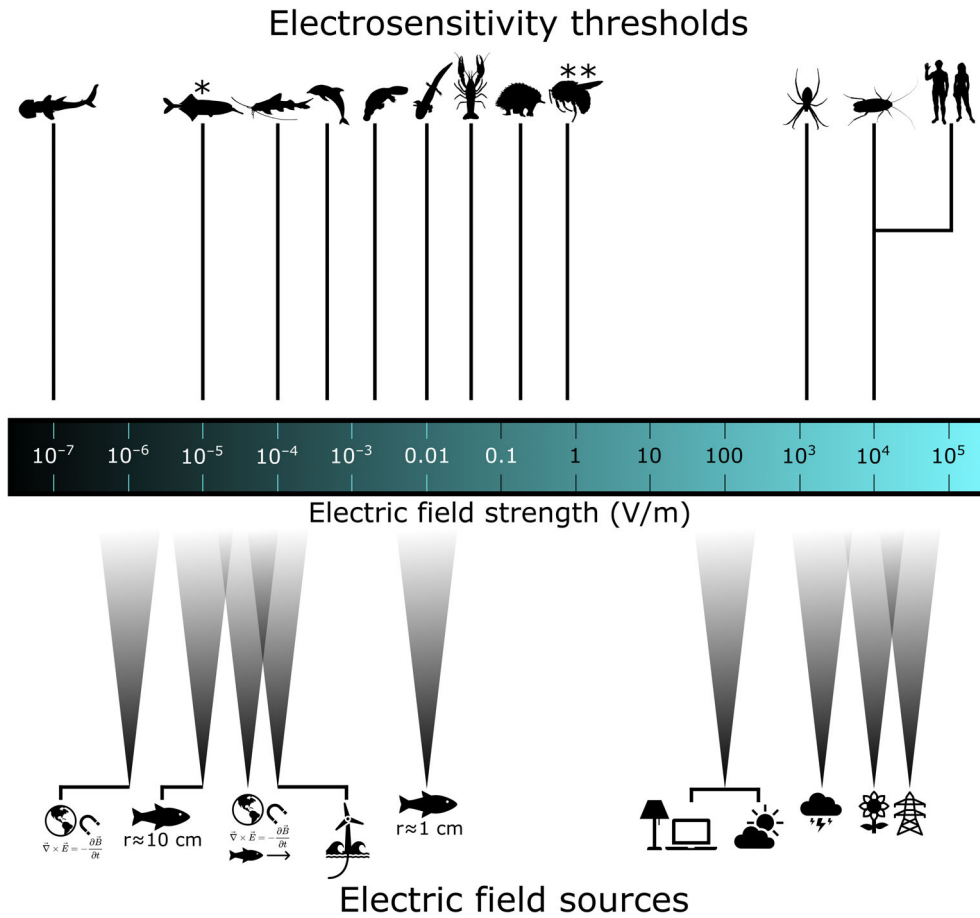
Electrosensitivity thresholds

Fig. 3. Minimum behavioural thresholds of electric field detection for various taxa representative of the main groupings of electroreceptive or electrosensitive animals, alongside typical electric field strengths of important environmental stimuli at relevant distances from source. Animals from left to right: marine passive electroreceptors (Kajiura & Holland, 2002; Kajiura, 2003), active aquatic electroreceptors (Nelson, 2005), limnic passive electroreceptors (Peters *et al.*, 2007), dolphins (Czech-Damal *et al.*, 2012), platypuses (Pettigrew, 1999), amphibians (Himstedt *et al.*, 1982), crayfish (Patullo & Macmillan, 2010), echidnas (Gregory *et al.*, 1989), bees (Sutton *et al.*, 2016), spiders (Morley & Robert, 2018), cockroaches (Newland *et al.*, 2008), and humans (Blondin *et al.*, 1996; Petri *et al.*, 2017). Electric field sources from left to right: electric fields induced by water movement through, and/or changes in, the Earth's geomagnetic field (Kalmijn, 1974), aquatic animal transmembrane electric fields at ≈ 10 cm (Kalmijn, 1974), electric fields induced by fish moving at 1 m/s through Earth's geomagnetic field (Kalmijn, 1974), magnetically induced electric fields from subsea power cables (Gill *et al.*, 2012), aquatic animal transmembrane electric fields at ≈ 10 cm (Kalmijn, 1974), household electronics (Repacholi & Greenebaum, 1999), fair-weather atmospheric potential gradient (Wilson, 1903), storm atmospheric potential gradient (Bennett & Harrison, 2007), floral electric field within centimetres of plant surface (Bowker & Crenshaw, 2007*b*), and overhead powerlines at ground level (Repacholi & Greenebaum, 1999). *active aquatic electroreception thresholds are not directly comparable to their passive counterparts because they are not sensitive to the DC and low-frequency electric fields produced by most environmental stimuli. **behavioural thresholds for bees are not yet known, therefore the mechanical threshold of bumblebee electroreception is given instead. Equation present in some icons is the Maxwell–Faraday equation, representing Faraday's law of induction, where $\vec{E}$ is the electric field and $\vec{B}$ is the magnetic field.

nematodes appear to move with a directionality related to the polarity and magnitude of that field. Typically, this involves moving towards the cathode in a dipole electrode arrangement, although this directionality seems to be dependent on the electric field strength (Sukul & Croll, 1978). It is believed that electrotaxis (also referred to as galvanotaxis) in nematodes is mediated by sensory neurons in the amphids (innervated invaginations of the cuticle) (Gabel *et al.*, 2007) and that this may be related to detection of ions by these

structures. Minimum behavioural thresholds of electric field strength appear to be in the region of 2 V cm^{-1} for adult *C. elegans*, with an upper bound of 4 V cm^{-1} (Rezai *et al.*, 2010) at which point paralysis is induced. Larval *C. elegans* require slightly stronger electric fields to elicit a behavioural response (Rezai *et al.*, 2010) however these are still of roughly the same order of magnitude. It has been suggested that the function of nematode electrotaxis is for locating food sources or potential hosts (in the case of parasitic

species) that produce electric fields or currents, for example by modification of the local redox potential (Bird, 1959). However, it has not been well established whether electric fields of the magnitudes discussed are ecologically relevant to nematodes in nature. Here, ecological relevance is especially questionable considering that the behavioural thresholds lie in the same order of magnitude as the field strengths capable of causing paralysis. Similar electrotactic behaviours have also been observed in larvae of the mosquito, *Aedes aegypti* (Riordan, 1971), however, as with the studies on nematodes, the electric field strengths presented in these experiments are most likely too high to be of ecological relevance.

(2) Active aquatic electroreception

Active aquatic electroreception is the ability of an organism to produce an electric field and subsequently detect distortions of said field that are caused by nearby objects or animals. Despite its arguably more complex mechanism, active aquatic electroreception, or electrolocation, was actually discovered before its passive counterpart. This is most likely due to the added conspicuousness introduced by an animal producing its own electric fields. Most obvious are the strongly electric fish, as introduced in Sections II.4 and III.2. The strongly electric fish have been noted since ancient times, due to their observable ability to stun other animals, as well as cause pain to humans, but it was only realised that the source of these abilities was electric field production in the late 18th century (Piccolino & Bresadola, 2002). In the 19th century, it was discovered that some fish produce electric fields too low in magnitude to stun other animals successfully; these are now known as the weakly electric fish – the animals capable of active aquatic electroreception (Zupanc & Bullock, 2005).

(a) The electric organ

The biological production of an electric field, electrogenesis, is performed in both strongly and weakly electric fish by modified muscle and nerve tissues, known as the electric organ, that generate EODs (Bennett, 1971a; Crampton, 2019). Electric organs were discussed by Darwin, as he viewed their evolution as one of the biggest challenges for natural selection to explain. In his words, "The electric organs of fishes offer another case of special difficulty; for it is impossible to conceive by what steps these wondrous organs have been produced. But this is not surprising, for we do not even know of what use they are" (Darwin, 1859, p. 192). His difficulty in comprehending the evolution of the electric organ stemmed from an ignorance within the scientific community at the time as to the function of EODs in weakly electric fish. Whilst people were aware that these fish had electric organs similar to those found in strongly electric fish, it was assumed that these organs were not functional in the ecology of the animal. Therefore, Darwin struggled to imagine how the electric organs of the strongly electric fish evolved, given that

there were no conceivable selective advantages to being capable of weaker discharges, which is presumed as the most rational evolutionary stepping-stone to strong electric discharges. It was not until the 1950s that definitive evidence was presented as to the function of the electric organ of weakly electric fish, with a series of studies demonstrating that the electric organ facilitates an active mechanism of electrolocation (Lissmann, 1951, 1958; Lissmann & Machin, 1958). Active electroreception has since been confirmed to exist in two families of teleost fishes (the African Mormyridae and the American Gymnotiformes), both of which live in fresh water, and have evolved the ability independently and convergently (Crampton, 2019).

(b) Electrolocation and electrocommunication

The basic mechanism utilised by weakly electric fish for electrolocation is that the animal generates an electric field with an EOD, which then polarises objects in the near vicinity. The resultant polarisation of a particular object will be dependent on the electrical impedance of that object, and thus if the object differs in impedance from the surrounding water, discrepancies will exist in the local electric field as compared to the field expected in the absence of an object. The local electric field is then detected by electroreceptors, and these discrepancies can be deduced. Research in this area has revealed active electroreception to be a remarkably detailed, intricate, and highly proficient sensory modality. Weakly electric fish are capable of detecting differences in the resistive and capacitive components of the impedance of nearby objects independently (von der Emde, 1999; Budelli & Caputi, 2000), as well as the distance to them (von der Emde *et al.*, 1998). The ability to distinguish the resistive and capacitive components separately allows for remarkably specific object type recognition, irrespective of size or distance, that may be functionally akin to colour vision both in terms of reliability and as a concept underlying sensory perception (Gottwald *et al.*, 2018). The discriminations possible include not only differentiating between alive and inanimate objects but even specific prey types (Gottwald *et al.*, 2018). The range of active electrolocation in the weakly electric fish is approximately one body length of the electrolocating animal (von der Emde, 1999). Generally, active aquatic electroreception is thought to be used by fish to detect the presence of other organisms, such as prey, predators, or conspecifics, as well as navigating their environment by detection of physical structures. In addition to electrolocation, it has also been shown that many weakly electric fish use their EODs and electroreceptors for species recognition and intra-specific communication, facilitating a plethora of social functions (Zupanc & Bullock, 2005; Crampton, 2019). These include group cohesion (Khait *et al.*, 2009) and coordination of pack hunting (Arnegard & Carlson, 2005), as well as communication and recognition of species, sex, and potentially even individual identity (Hopkins, 1972; Hopkins & Bass, 1981; Moller & Serrier, 1986; Crampton, 2019). Electrolocating fish are also known to adjust the frequency of

their own EOD if a nearby fish is producing EODs at a similar frequency to avoid jamming of each other's signals (Watanabe & Takeda, 1963; Heiligenberg, 1977). Whilst active electroreception was thought to be exclusively associated with the low-amplitude EODs of weakly electric fish, recent evidence has been put forth to suggest that the electric eel, which is both strongly and weakly electric, can use both strong and weak EODs to electrolocate prey (Catania, 2015*b*). It is suggested that utilisation of strong EODs allows for a greater range of detection (Catania, 2015*b*).

(*c*) Physiology of tuberous electroreceptors

The electroreceptors involved in active electroreception are known collectively as tuberous receptors and are distinct from the ampullary receptors used in passive electroreception. Tuberous receptors, like their ampullary counterparts, exhibit a great amount of variation between species, and even within a single individual (Szabo, 1974; Jørgensen, 2005), however some general characteristics can be broadly ascribed to them (Fig. 2D). Tuberous receptors are sensitive to electric fields with frequencies of a few tens of Hz up to and often exceeding 1 kHz (Kawasaki, 2005). Tuberous receptors are so named due to the tuber-shaped capsule within which each is contained. This capsule is formed from an invagination of the epidermis and is generally plugged at its open end by loosely packed epidermal cells (Szabo, 1965, 1974; Jørgensen, 2005; Kawasaki, 2005). At the base of the capsule lie innervated electrosensitive sensory cells, which are structurally and functionally different from those found in ampullary receptors (Szabo, 1965). These sensory cells typically possess a great number of microvilli on their outer surface, which likely act as a coupling capacitor, and thus provide the high-pass filter required by the system to ignore the DC and low-frequency electric fields picked up by ampullary receptors (Kawasaki, 2005). The sub-types of tuberous receptor include the knollenorgan and mormyromast of the mormyrid fishes (Derbin & Szabo, 1968; Szabo & Wersäll, 1970), the gymnomast of the gymnotids (Szabo, 1965), and the gymnarchomast of the gymnarchids (Szabo, 1974; Jørgensen, 2005). Each of these vary from each other in both the gross morphology of the organ, and the design of the electrosensory cells contained within (Szabo, 1974; Jørgensen, 2005). Tuberous organs have also been found in a single species of silurid, *Pseudocetopsis* sp. (Andres, von Düring & Petrasch, 1988). This sub-type is referred to as the siluromast (Jørgensen, 2005), however, the exact function of these tuberous receptors is not known because these catfish are not apparently capable of active electroreception, being thought to lack an electric organ (Andres *et al.*, 1988). It has been hypothesised instead that this catfish species may use its tuberous receptors to eavesdrop on the electrolocation and electrocommunication of other species truly capable of active electroreception, in order to prey upon them (Andres *et al.*, 1988). If true, this could in fact be considered an example of passive electroreception, because the detecting organism is not producing the EODs itself.

(*d*) Behavioural thresholds

In terms of sensitivity, it is difficult to compare detection thresholds of active electroreceptive systems with passive systems because of their fundamentally different mechanisms, however behavioural detection thresholds for active electroreceptive systems are believed to be approximately $0.1 \ \mu\text{V cm}^{-1}$ in the water surrounding the fish (Nelson, 2005). This is estimated from an observed minimum detectable root mean square change in transdermal potential of about $0.1 \ \mu\text{V}$ (Rasnow, 1996).

(3) Aerial electroreception

Historically, electroreception was thought to be a sensory modality exclusively confined to aquatic or amphibious fauna. This was due to the perceived requirement of a conductive medium to exist between the stimulus source and the electroreceptor, as aquatic electroreception functions *via* electrical conduction of the signal from source to receptor. Because air has a significantly diminished electrical conductivity as compared to water, the possibility of aerial electroreception was therefore not considered by most. However, this determination ignored the fact that electric fields can act at a distance regardless of the presence of a propagation medium, conductive or not. Any electrically charged object will produce electric fields that can propagate, even through a vacuum, and apply forces to other electrically charged objects (Coulomb, 1785). As discussed extensively in Section II.3, insects and many other terrestrial animals commonly carry electrostatic charge and will therefore experience electrostatic forces from electric field sources in their environment, as well as exert electrostatic forces on other charged objects. Thus, electric fields could be detected in air by mechanosensory structures because if charge is carried on a mechanoreceptive sensillum, an electric field may be capable of actuating it, triggering nervous activity. This is the fundamental principle behind our current understanding of aerial electroreception. Indeed, even before the discovery of aerial electroreception, electric fields had been used many times as a convenient method of actuation when studying arthropod mechanoreceptors (Hoffmann, 1967; Albert, Nadrowski & Göpfert, 2007; Nadrowski, Albert & Göpfert, 2008; Effertz *et al.*, 2012). The following subsections aim to comprehensively outline our contemporary understanding and knowledge of aerial electroreception and similar phenomena.

(*a*) Effects of strong electric fields on insects

Earlier studies found evidence that changes in local electric field strength and polarity can induce alterations of behaviour in insects, generally indicated by avoidance, stalling, or a reduction of activity. Most of these studies concerned strong electric fields, defined here as fields of magnitudes at the upper limit or exceeding those found in nature. These early studies found such effects of strong electric fields in a parasitoid wasp, *Itoplectis conquisitor* (Maw, 1961*a*), the fruit fly, *Drosophila melanogaster* (Edwards, 1960*b*), housefly, *Musca*

domestica (Perumpral, Earp & Stanley, 1978) and the honeybee (Warnke, 1976; Bindokas, Gauger & Greenberg, 1989), among others (Orlov, 1990). Relatedly, a negatively charged insect trap reportedly captured significantly fewer hymenopterans than an uncharged trap (Maw, 1964), indicating that the charged trap may have been behaviourally avoided. In other early studies, exposure to strong electric fields was reported to increase levels of aggression in honeybees (Schuà, 1952; Warnke, 1976), influence pupation duration and/or fecundity of the phantom hemlock looper moth, *Nepytia phantasmaria* (Edwards, 1961), the parasitoid wasp, *Scambus buolianae* (Maw, 1961b), and *D. melanogaster* (Levengood & Shinkle, 1960), as well as alter the wingbeat frequency of cabbage looper moths, *Trichoplusia ni* (Perumpral *et al.*, 1978).

Research into the behavioural effects of strong electric fields has been continued more recently, with a collection of studies on American cockroaches, *Periplaneta americana*, in which triboelectrically charged dielectrics (Hunt, Jackson & Newland, 2005) and voltage-driven electrodes (Newland *et al.*, 2008) were avoided by cockroaches in a Y-tube choice behavioural experiment. Here, the lowest electric field strength given that induced statistically significant avoidance behaviour was approximately 8–10 kV m^{-1} (Newland *et al.*, 2008). Ablation of the antennae removed this avoidance behaviour and therefore, with the support of electrophysiological data, it was concluded that electrostatic deflection of the antennae, transduced by mechanoreceptors, is the mechanism by which the cockroaches detected the electric fields. In addition, cockroach locomotory behaviour has been found to be altered by very strong ($\geq$70 kV m^{-1}) electric fields in an open arena experiment (Jackson *et al.*, 2011). It was similarly shown that fruit flies avoid electric fields (Newland *et al.*, 2015). Ablation experiments and photographic measurements of displacement were used to suggest electrostatic deflection of the wings as the mechanism of electric field detection in these flies, with deflection visible under electric field strengths of 28 kV m^{-1}. A separate group of studies has similarly shown that rice weevils, *Sitophilus oryzae*, and cigarette beetles, *Lasioderma serricorne* (Matsuda *et al.*, 2011, 2020), as well as potentially a great diversity of other terrestrial arthropods (Matsuda *et al.*, 2015), avoid strong electric fields produced by high-voltage sources. The antennae are again proposed by these authors as the site of electric field detection, however little evidence is given in support of this hypothesis. In direct contrast to these examples of electric field avoidance in insects, at least 10 species of ant (Formicidae) appear to be attracted to electric fields, both AC and DC, at strengths found around household electrical equipment (MacKay *et al.*, 1992). Similar attraction to electric fields has also been reported in various other insect orders (Wijenberg *et al.*, 2013).

Whilst all of these studies certainly demonstrate a behavioural influence of aerial electric fields on insects, the ecological relevance of these behaviours and field strengths is not yet completely clear, as it is unlikely that most insects would encounter electric fields of these magnitudes in their natural ecological contexts. However, it is very possible that the behaviours observed in these studies are in fact derivative of ecologically relevant electroreceptive abilities, such as avoidance of predators or hazardous meteorological conditions. Indeed, it has long been speculated that weather-associated fluctuations in atmospheric electricity may influence the behaviour of insects (Uvarov, 1931; Wellington, 1957; Helson & Penman, 1970). It could certainly be the case that the excessive behavioural thresholds recorded are the result of a lack of stimulus specificity to those encountered in the natural ecology of the animal, particularly in terms of temporal components such as the frequency and envelope modulations of the electrical signal. It should also be considered that most insects cultured in laboratories, or collected in cities, are likely to have been exposed to, and possibly habituated to, a high level of background anthropogenic electric fields for much of their lives, and therefore their behavioural responses to such stimuli may be dampened. However, because this explanation remains to be empirically examined, it is still uncertain whether these behavioural effects of strong electric fields on insects bear adaptive evolutionary significance, and therefore more experimentation is needed before they can be considered as examples of aerial electroreception.

(b) Electroreception in bumblebees

(i) Behavioural evidence. Whilst some suggestions that aerial electric field detection may be utilised by bees in nature have been made in the past (Eskov & Sapozhnikov, 1976; Warnke, 1976; Eskov, 2013), it was not until 2013 that strong behavioural evidence was presented to indicate that an animal is capable of aerial electroreception in an ecologically relevant context (Clarke *et al.*, 2013). This study presented evidence suggesting that bumblebees, *Bombus terrestris*, may use floral electric fields (described in Section II.2) as a foraging cue (Clarke *et al.*, 2013). Because bumblebees typically possess an electric charge (Clarke *et al.*, 2013; Montgomery *et al.*, 2019), some induction of current in the stems of flowers is expected to take place as bees approach them. This was confirmed experimentally by measuring the floral stem potential of *Petunia* plants, demonstrating an average stem potential peak of 25 $\pm$ 3 mV induced by individual free-flying bumblebee visits. Notably, these bee-induced variations of stem potential outlasted the presence of the bee on the flower, for up to *ca.* 100 s. This timescale is likely sufficient for subsequently arriving bees to be exposed to the altered floral electric field, and thus potentially to use it as a foraging cue indicative of recent bee visitation, and consequent likely diminished nectar levels. This hypothesis was then tested behaviourally. Bumblebees were allowed to fly freely within an arena populated with artificial flowers held at different electric potentials. A sucrose reward was placed inside flowers held at a potential of 30 V (an estimation of the floral potential of a 30 cm tall flower in open ground within the fair-weather atmospheric potential gradient) and an aversive quinine solution was placed in grounded (0 V) flowers. Within this paradigm, the bumblebees were successfully trained to discriminate between the rewarding and aversive

flowers held at different potentials. Importantly, once learning was complete and discrimination achieved, the removal of electric cues immediately impaired the ability of the same bumblebee sample to determine the rewarding flowers reliably, and they failed to subsequently re-learn the task. This strongly indicates that the experimental conditions did not provide the bees with confounding cues that could have been learned instead of the electric potential. Similar learning curves could not be produced when the rewarding flowers were placed at 10 V and the aversive flowers at 0 V, suggesting that the behavioural detection threshold lies somewhere between the electric field strengths associated with these voltages (10–30 V). It was also shown that the presence of differently structured electric fields decreased the amount of time taken by bumblebees to learn to discriminate between two similar hues of green. This indicates that bumblebees are able to integrate electrical information into multimodal assessments of sensory information. Together, these findings strongly suggest that bumblebees are capable of aerial electroreception at ecologically relevant field strengths, and indicate that they may use this ability to make foraging decisions in nature. It has also been suggested that recognition of important landmarks, such as the nest, may be similarly facilitated by detection of the associated electric fields (Lihoreau & Raine, 2013), although this hypothesis remains to be tested.

(ii) Sensory mechanism. A subsequent study (Sutton *et al.*, 2016) aimed to identify the mechanism by which bumblebees detect electric fields. Laser Doppler vibrometry (LDV) and electrophysiology were used to compare the mechanical and neuronal responses of bumblebee mechanosensory hairs and antennae to electric fields. It was shown that the mechanosensory hairs are far more sensitive to electric field stimuli than the antennae, and thus electrostatic deflection of these hairs is likely the primary mechanism of electroreception in bumblebees (Fig. 2F). Mechanical responses in the hairs could be elicited by electric field strengths as low as 0.77 V m^{-1} meaning that the detection threshold probably lies somewhere above this value. However, it should be noted that the detection thresholds of individual bees will likely be intrinsically tied to the charge carried by each of their mechanosensory hairs, and so thresholds will most probably vary and correlate with the gross electric charge of the bumblebee. Indeed, the electromechanical sensitivity of individual hairs has been found to be proportional to the net charge on the bee (Sutton *et al.*, 2016; Koh *et al.*, 2019).

Because of their mechanoreceptive nature, it is valid to question whether or not the detection of electrical cues by these mechanosensory hairs is in direct competition with the detection of mechanical cues such as airflow. This question is made even more pertinent in light of the experimental finding that electric stimuli can be placed in opposition to acoustic stimuli, in order to cancel out any net actuation of an individual mechanosensory hair (Koh *et al.*, 2019). However, theoretical and modelling approaches suggest that the mechanosensory hairs of bumblebees have distinct modes

of actuation elicited by electrical stimuli, as compared to a typical acoustic stimulus, such as the wingbeats of a flying insect (Koh & Robert, 2020). This suggests that bumblebees may not have their electrical sense overwhelmed by acoustic noise; either self-generated or from other nearby sources, and that these mechanosensory hairs could be capable of acting as bimodal sensory structures (Koh & Robert, 2020). The same methods were used to show that ecologically relevant electric field strengths are capable of actuating mechanosensory hairs by magnitudes similar to those generated by typical acoustic stimuli. Notably, the electrosensitivity of a mechanosensory hair is significantly influenced by its morphology, in particular by its surface area (Koh & Robert, 2020). Furthermore, the mechanical properties of filiform mechanosensory systems have been predicted mathematically to play a significant role in determining their relative sensitivities to electrical and aerodynamic stimuli (Palmer, Chenchiah & Robert, 2021). By examining example systems of spider trichobothria and cricket cercal hairs, it was hypothesised that at least two distinct types of filiform mechanosensory system exist: those that are tuned for detection of either aerodynamic stimuli or electrical stimuli, and those tuned for bimodality – effective detection of both aerodynamic and electrical stimuli (Palmer *et al.*, 2021). The distribution of sensilla lengths within a particular mechanosensory system, as well as their individual mechanical properties, will determine which of these types it falls into.

It should also be noted that there is some possibility that magnetic stimuli are involved in electroreception by bumblebees. Because a moving charge creates a magnetic field, and in the reference frame of a bee approaching a flower, the flower is a moving charge, there will be some magnetic field associated with the bee–flower interaction. Bees have previously been shown to be capable of detecting magnetic fields (Hsu & Li, 1994; Wajnberg *et al.*, 2010), and so it is possible that they are using this magnetoreceptive system to detect floral electric fields indirectly. However, it is unlikely that magnetoreceptive systems are capable of instantaneously acquiring magnetic information, instead relying upon longer scale time-averaged sampling methods (Johnsen, Lohmann & Warrant, 2020), and therefore the time course of the bee–flower interaction is probably too short to be detectable by magnetic means. Furthermore, the magnitude of the magnetic field created by the bee–flower interaction is likely to be several orders of magnitude lower than the Earth's geomagnetic field and variations thereof, making it even more doubtful, albeit not impossible, that magnetoreception could be playing a role in this situation.

(c) Electroreception in honeybees

(i) Behavioural evidence. Aerial electroreception has also been shown in honeybees (Greggers *et al.*, 2013). In support of earlier hypotheses (Eskov & Sapozhnikov, 1976; Warnke, 1976), this study provides strong evidence to suggest that honeybees are capable of detecting the modulated electric fields emitted by conspecifics performing the waggle

dance – a series of movements used to communicate the location of foraging sites (von Frisch, 1967). It appears that electric field information contributes to a multimodal (Michelsen *et al.*, 1989; Kirchner & Sommer, 1992; Tautz & Rohrseitz, 1998; Rohrseitz & Tautz, 1999; Thom *et al.*, 2007) transfer of knowledge from bee to bee. Greggers *et al.* (2013) measured the electric fields emanating from dancing honeybees, showing that the electric field is modulated in a significant way at frequencies corresponding to the movements of the abdomen and wings. Proboscis extension reflex (PER) conditioning was then used to demonstrate that honeybees can learn to associate constant and modulated electric fields with a sucrose reward. The presented electric fields were of comparable magnitude and frequency to those emitted by dancing bees. In addition to this, general behavioural observations were made of honeybees walking on floating ball treadmills whilst being intermittently exposed to electric fields of various modulations. The electric field stimuli most similar to those produced by honeybees elicited significantly higher behavioural responses compared to a signal of supposed abiotic character.

(ii) Sensory mechanism. Laser Doppler vibrometry, electrophysiology, and ablation experiments were used to attempt to identify the mechanism of electroreception in honeybees. These techniques pointed to electrostatically evoked mechanical deflection of the antennae, detected by the Johnston's organ, as the electroreceptive mechanism in honeybees. It was also proposed that other mechanoreceptors could also contribute to the electroreceptive abilities of honeybees, but that they are less sensitive than the antennal mechanism (Greggers *et al.*, 2013). The LDV measurements also indicated that the antennae are more sensitive to the electric fields produced by flapping honeybee wings than to the associated air movements. Together the results of this study demonstrate that honeybees are capable of detecting ecologically relevant electric fields, particularly those produced by conspecifics in a communicative context. One might view the finding of the antennae as the primary electroreceptive structure to be in conflict with the identification of mechanosensory hairs as the primary electroreceptor in bumblebees. However, these two views are not necessarily mutually exclusive, as the studies did investigate two different species that may simply favour different mechanisms. Evidence is not currently sufficient to draw conclusions on exclusive or common mechanisms for the detection of electric fields across honeybees and bumblebees. Therefore, it is possible that in fact both antennae and mechanosensory hairs contribute to electroreception in both species.

As with bumblebees approaching flowers, it is possible that magnetic fields generated by the moving charges of the dancing honeybees could play a role in this communication system, however, for the reasons discussed in Section IV.3*b*, detecting magnetic fields on this timescale, and of such low magnitude, is probably not feasible for the magnetoreceptive system of bees. However, this cannot be said with certainty until the capabilities of the magnetoreceptive sense in bees are characterised more fully.

(d) Electroreception in spiders

(i) Behavioural evidence. Spiders have recently been shown to utilise electric fields and electroreception in the context of ballooning (Morley & Robert, 2018). As discussed in Section III.3, ballooning is a method of dispersal used by many species of spiders wherein strands of silk are utilised to carry individuals in the air over large distances (Bell *et al.*, 2005); and it has recently been shown that atmospheric electricity can supply a sufficient lifting force to facilitate this process (Morley & Robert, 2018; Morley & Gorham, 2020). Perhaps most intriguingly, evidence was also presented that indicates that spiders can detect local electric field conditions and may use this information to inform decisions on whether and when to balloon. The primary support for this theory was found in behavioural experiments. Adult linyphiid spiders (*Erigone* spp.) were placed on a platform and exposed to various vertical electric field strengths, comparable to those found in the atmosphere in differing meteorological conditions. It was shown that behaviours indicative of intention to balloon could be elicited by these naturally occurring atmospheric electric field strengths. Tiptoeing, when the spider lifts its opisthosoma and extrudes silk into the air above, significantly increased when the electric field was held at 6.25 kV m^{-1} compared to 0 kV m^{-1}. The dropping of a silk dragline, another proxy for ballooning intention, was also increased significantly by electric field strengths of 6.25 kV m^{-1} compared to 0 kV m^{-1}, but also by fields of 1.25 kV m^{-1} compared with 0 kV m^{-1}. Once airborne, the spider's altitude could be controlled by varying the electric field strength. Together, these findings strongly suggest that ballooning spiders are able to detect electric fields at strengths generated by the atmospheric potential gradient. Furthermore, they may use this information to decide to balloon in meteorological conditions most optimal for effective dispersal.

(ii) Sensory mechanism. Laser Doppler vibrometry was used to identify the mechanism of electroreception in these spiders. Trichobothria, highly sensitive mechanosensory hairs primarily utilised for sensing air movements (Barth, 2002), were determined to be the most likely candidates, as they were considerably more responsive to electric fields than another candidate tested, the metatarsal spines. In addition, the responses of the trichobothria to electric fields and air flow were compared. This revealed that there are distinct differences in the way trichobothria react to each stimulus type. Specifically, air flow causes a tonic response where the hair is bent and held statically at that position until the stimulus has ceased. In comparison, electric fields elicit a phasic response, wherein a peak displacement is produced instantaneously upon stimulus onset, that then decays over the time course of the stimulus. This indicates that air flow and electric field stimuli may be distinguishable from each other by the spider, and that the two functions do not necessarily need to be exclusive. Interestingly, the displacement direction of the trichobothria was independent of the electric field polarity, always being attractive, meaning that inductive

polarisation of the hairs is likely taking place (Fig. 2G). This is an exciting discovery because it differs from the static charging of hairs measured in bees and indicates that a quasi-fixed charge may not be a requirement for aerially electroreceptive structures.

(e) Electroreception in hoverflies

(i) Behavioural evidence. Using a similar learning experiment to that previously presented to bumblebees (Clarke *et al.*, 2013), it has recently been shown that two species of hoverfly, *Eristalis tenax* and *Cheilosia albipila*, are also capable of detecting floral electric fields and may similarly use these as a foraging cue (Khan *et al.*, 2021). Both hoverfly species were successfully trained to associate an ecologically relevant 30 V voltage with rewarding artificial flowers, but could not repeat this when the rewarding flowers were held at 0 V.

(ii) Sensory mechanism. It was shown that hoverflies carry net charges comparable to those of bumblebees, and therefore it is likely that they also utilise mechanosensory hairs with quasi-fixed charges upon them to detect electric fields. Indeed, Laser Doppler vibrometry on charged dead hoverflies of both species showed that thoracic mechanosensory hairs are physically deflected by external electric fields. Furthermore, electrophysiological data show that the fire rate of nerves associated with these mechanosensory hairs increases when the animal is presented with electrical stimuli, whereas the fire rate of antennae-associated nerves does not. Together, these observations strongly indicate that aerial electroreception in hoverflies is facilitated by electrostatic deflection of mechanosensory hairs carrying a quasi-fixed charge, as is the case in bumblebees.

(f) Electroreception in parasitic mites

As briefly mentioned in Section III.2. some evidence and arguments have also been put forward that suggest that a honeybee parasitic mite, *Varroa destructor*, may also be capable of detecting ecologically relevant electric fields (Colin *et al.*, 1992). This study placed adult mites in an arena with a conducting cylinder, held at voltages of various magnitudes and polarities, at its centre. It was observed that the behaviour of these mites was significantly affected by the polarity of the voltage held on the cylinder. The affected behavioural characteristics were the immobility, velocity, and turning angle characteristics of the mites' movements. Colin *et al.* (1992) proposed that such alterations in the locomotion of mites may act to increase the probability of a mite encountering a host, and that this is triggered by detection of the electric fields around honeybees. However, the efficacy of these changes in locomotory behaviour to improve host encounter rates has not been demonstrated. It is also intriguing that this study found no significant differences in behaviour caused by changes in the intensity of the field. This may suggest that mites only rely upon some minimum electric field strength threshold to begin responding behaviourally, and that all of the voltages presented in this study fell

above this value and were thus perceived categorically in the same way. Another surprising finding of this study is that negative voltages incited the strongest behavioural responses. This is unexpected because the majority of honeybees will carry a positive charge. In conclusion, the results of this study indicate that it is plausible that this parasitic mite species is capable of aerial electroreception. However, the exact relevance of the behaviours witnessed, as well as the unexpected influence of negative voltages, and lack thereof in terms of electric field intensity, imply that this system if far from being fully understood. Further work with these animals, utilising more refined behavioural assays, is needed before electroreception can confidently be confirmed in parasitic mites.

(g) Is aerial electroreception passive or active?

Because it stands as the primary division between the different types of aquatic electroreception, it is a natural progression to question whether aerial electroreception is passive or active in its mechanism. This is seemingly a simple question, however, it may not be as trivial to answer. Whilst the mechanosensory structures involved in aerial electroreception are generally thought to be passive in function, it is also true that the sensitivity of these mechanosensory structures to electrical stimuli will be generally dependent on the charge deposited on the structure. Indeed, the electrosensitivity of bumblebees appears to be largely dictated by the magnitude of charge held by the bee (Sutton *et al.*, 2016). It stands to reason then, that aerial electroreception in bees could be considered an active mechanism, because the charge on the bee is likely produced predominantly by the movements of the bee itself; which requires metabolic input. However, this same line of reasoning does not apply to spiders. Current knowledge indicates that the electroreceptive structures of spiders, the trichobothria, react in an inductive manner (Morley & Robert, 2018). This suggests that the influence of charges deposited on the surface of the trichobothrium is minimal compared to the influence of induced polarisations within the hair itself. In this example, it is clear to state that aerial electroreception relies upon passive mechanisms, assuming that trichobothrial mechanoreception is mechanically passive in itself. Altogether, it is therefore evident that aerial electroreception can be considered to be both passive and active, depending on the specific example and definitions used. As further research is conducted into the mechanisms of aerial electroreception, a more robust answer to this question will likely emerge.

(h) Future directions of aerial electroreception research

As previously stated, every instance of aerial electroreception discovered so far has been in different species, with most using this ability for different ecological functions. Because of this, it seems increasingly likely that there are many more species capable of aerial electroreception, and many more electric ecologies yet to be identified. As a sensory modality discovered so recently, there are countless research avenues

ready to be explored. In particular, field studies need to be performed on wild animals to validate the existence of aerial electroreception in their own natural sensory ecology. Minimum detection thresholds should also be defined, as this will guide behavioural studies in the future and build a more certain picture of the electrostatic interactions relevant in the environment. As with any sensory modality, the potential impact of anthropogenic noise within that sensory channel should also be investigated, for example power lines or other man-made electric field sources, as well as anthropogenic processes likely to modify ecologically important electric fields. One example of such an anthropogenic process is the application of agrochemicals to plants and the resultant effects on the local electric ecology (Hunting *et al.*, 2021a). Another aspect that should be considered within any sensory modality is camouflage; the possibility of electrostatic crypsis or mimicry should be explored, especially because bioelectric crypsis has already been shown in the aquatic environment (Kempster *et al.*, 2013; Bedore, Kajiura & Johnsen, 2015).

More importantly, and perhaps most excitingly, more species and more behaviours need to be studied in the context of aerial electroreception. This will allow us to begin to grasp the potential phylogenetic, evolutionary, and ecological diversity of this newly unveiled sense. The physical principles behind aerial electroreception are ubiquitous, and likewise mechanosensory hairs are not unique to bees, hoverflies and spiders, therefore there is almost certainly a wealth of species waiting to be identified as electroreceptive in the terrestrial environment. Of particular interest would be the possible role of aerial electroreception in predator–prey interactions: it is highly likely that predators could in some circumstances detect their prey items by the electric field emitted from them, and *vice versa*.

Whilst other arthropods are certainly very strong candidates for utilising aerial electroreception, the possibility should not be ruled out that some vertebrates may also be capable. In terms of aerial electroreception in vertebrates, little to no research has been conducted. Claims have been made suggesting that rattlesnakes have the ability to detect electric fields in air (Vonstille & Stille III, 1994). Through largely inductive reasoning, it was suggested that because rattlesnakes accumulate charge when moving and rattling their tail, they may be able to detect local variations in electric field strength *via* electrostatic deflection of their tongue. These local electric field variations, for example, could be indicative of humidity sources such as shelter or prey items. Whilst an exciting suggestion, very little evidence was provided to support these claims, and many of the arguments were seen as fundamentally flawed (Schwenk & Greene, 1995). It therefore seems fair to discount this hypothesis until further evidence is presented. In addition to this, purportedly, evidence has also been gathered demonstrating that the golden hamster (*Mesocricetus auratus*) will relocate its nest away from electrodes producing fluctuating electric fields comparable to those experienced during thunderstorms (Schuà, 1954, cited in Wellington, 1957), although the validity of these observations could not be assessed as these data appear

no longer to be available. It should also be noted that humans and some other vertebrates are already known to perceive electric fields of very high magnitude (Petri *et al.*, 2017). For humans, the typical detection threshold appears to be around $40\,kV\,m^{-1}$, although some individuals have been reported to be sensitive to fields below $10\,kV\,m^{-1}$ (Blondin *et al.*, 1996; Petri *et al.*, 2017). However, these thresholds are likely too high to suggest that humans use or used electroreception in their natural ecology, especially as no adaptive function for this ability has been suggested.

In light of current evidence, future research on aerial electroreception in vertebrates should likely focus on two main study systems; pollinators and small insectivorous mammals. Vertebrate pollinators such as hummingbirds provide a convenient experimental paradigm in that the behavioural experiments already performed on bumblebees and hoverflies could largely be reproduced with hummingbirds substituted in as the study organism. Indeed, it has already been demonstrated that flying hummingbirds accumulate positive charges of up to 800 pC (Badger *et al.*, 2015), and as such may detect electric fields *via* electrostatic deflection of mechanosensory structures in the same ways as arthropods, or even by the modulation of their own wingbeat imposed as their charged wings move through an electric field. Furthermore, as birds, hummingbirds may also be capable of magnetoreception (Falkenberg *et al.*, 2010), which could provide an alternative, indirect, mechanism of electroreception through detection of the magnetic fields induced as the charged flower moves within the reference frame of the hummingbird, although as previously stated for bees, this magnetic mechanism is less likely. Small insectivorous mammals, in particular those who hunt nocturnally such as shrews, also offer an enticing research direction because their vibrissal mechanoreceptive systems may be capable of detecting the electric fields from charged arthropod prey, in lieu of a strong visual system.

(4) Anthropogenic noise in electroreception

(a) Anthropogenic noise in aquatic electroreception

As with any sensory modality, in the modern day, it is important to consider the potential impact of human activity on the quality of sensory information available to organisms within that modality. It is surprising therefore, that very little work has been done to investigate how anthropogenic electric fields may impact electroreceptive animals. As discussed in Section II.5, it is known that subsea cables are a source of anthropogenic electric fields in the surrounding water. The possibility that these fields may interfere with the electrosensory systems of nearby animals has long been hypothesised (Gill *et al.*, 2012; Taormina *et al.*, 2018; Newton, Gill & Kajiura, 2019), however, detailed experimental evidence has only recently begun to be presented (Hutchison *et al.*, 2020). In this specific study, it was shown that the behaviour of the little skate, *Leucoraja erinacea*, is significantly altered when exposed to electric fields imitating those emitted by subsea power transmission cables. Most notably, these skates travelled further distances when exposed to the treatment

electric fields, possibly indicative of an increased desire to forage. As such, it is likely that subsea power cables result in unnecessary energy expenditure by electroreceptive organisms that may be confused by the emitted anthropogenic electric fields. Exact reactions to subsea cables are likely to be species specific, and therefore many other negative consequences for electroreceptive animals are conceivable, such as increased levels of stress, reduced food intake, and subsequent poor health.

(b) Anthropogenic noise in aerial electroreception

In the field of aerial electroreception, even less is known about the impact of anthropogenic noise. However, recent findings are beginning to suggest that the application of agrochemicals may be a source of anthropogenic noise for electroreceptive bumblebees (Hunting *et al.*, 2021a). The spray application of fertilisers and pesticides modifies the strength and structure of the floral electric field, and behavioural experiments appear to demonstrate that these modifications result in reduced bee visitation (Hunting *et al.*, 2021a). This indicates that the agrochemical-induced modifications to the floral electric field may be misleading bees into interpreting those flowers as being undesirable.

In addition to this, the fact that many terrestrial arthropods have been shown to avoid strong electric fields could well mean that exposure of aerially electroreceptive animals to the electric fields around man-made structures, in particular overhead power lines, results in avoidance behaviours. This warrants immediate investigation because any anthropogenically induced modification of the behaviour of key pollinators, namely bees, could have significant ecological consequences. Indeed, it has already been shown that honeybee colonies situated underneath power lines suffer adverse effects, including significantly reduced survival (Greenberg *et al.*, 1981a; Greenberg, Bindokas & Gauger, 1981b). Whether or not these effects are the result of detection of the anthropogenic electric fields is not yet known, however, as honeybees have been shown to utilise electroreception in their communication (Greggers *et al.*, 2013), it is very plausible that the strong electric fields under power lines are interfering negatively with this system. However, evidence also points to electric shock from induced currents in the hive substrate as the primary cause of the observed adverse effects on honeybees (Bindokas, Gauger & Greenberg, 1988a,b; Bindokas *et al.*, 1989). Overall, it is clear that many common anthropogenic sources of electric field exist at magnitudes detectable by the animals demonstrated to be electroreceptive thus far (Fig. 3), and as such the potential impacts of human electrical activity on these ecological interactions should be addressed with urgency.

(5) Common trends and comparisons in electroreception

Despite their very disparate evolution, mechanisms and ecologies, both aquatic and aerial electroreception do share commonalities, as well as differences. It becomes apparent that mechanisms for aerial or aquatic electroreception have repeatedly evolved by specialisation or co-option of mechanosensory structures. It therefore seems reasonable to suggest that a mechanosensory structure could be a required precursor for the evolution of an electrosensory system.

One fundamental difference between aquatic and aerial electroreception is the physical context in which they evolved and now operate. This is most apparent when considering the behavioural thresholds of animals that use electroreception in air as compared to water (Fig. 3). Minimum detectable electric field strengths are much higher in aerially electroreceptive species than in those that utilise aquatic electroreception. From this, it may be easy to conclude that electroreception in air is less sensitive than electroreception in water. However, this suggestion requires refinement as it ignores the differences in transmission properties of the respective media. In water, very weak source electric fields can produce currents of a notable magnitude, whereas the lower conductivity of air prevents this, meaning that the electric field must be detected directly *via* electrostatics. As such, the source electric field must be necessarily higher. This is somewhat analogous to concluding that an organism living in turbid water must be less sensitive to light, as compared to a terrestrial organism with an identical visual system, because the terrestrial organism will be able to detect dimmer light sources (as measured at the source). It is not the sensitivity of the receptor that causes this disparity, but instead the difference in the transmission efficiency of the animal's environment for that stimulus. If instead we consider the energy input, or some other similar parameter, at the point of the electroreceptor, then it is possible that aerial and aquatic electrosensory systems may in fact be more comparable in terms of sensitivity.

Lastly, it is also worth noting that the vast majority of organisms capable of aquatic electroreception are vertebrates, whereas conversely, every example of aerial electroreception demonstrated so far has been in invertebrates. It certainly seems that the biophysical properties of each of these groups does lend itself more to electroreception in those respective environments, however, it can be expected that as further research is conducted with novel study organisms, these phylogenetic disparities will rebalance somewhat.

V. CONCLUSIONS

(1) Research into the role of electricity in ecology has been long-standing, but is characterised by punctuated, largely isolated, islands of research.

(2) This review provides the first collation and synthesis of these studies, and in so doing demonstrates the importance of considering electric phenomena when investigating ecological interactions. Together, the studies published to date make clear the prevalence of electrical interactions within ecological systems, but there are large gaps in our current knowledge.

(3) As an acknowledgment and understanding of the ubiquity of electric fields within the natural environment begins to grow within the scientific community, it is anticipated that many more aspects of electric ecology are soon to be uncovered.

(4) The recently discovered sense of aerial electroreception provides an exciting and promising new field of research, with a plethora of species and ecologies awaiting investigation.

(5) The electric field should be viewed and appreciated as a major driver of evolutionary adaptation within biological systems, not only at the atomic, molecular, or cellular levels, but also at the organism and ecological scales too.

VI. ACKNOWLEDGEMENTS

VII. REFERENCES

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