

The potential of plant action potentials

Abstract

The mechanism underlying action potentials is routinely used to explicate the mechanistic model of explanation in the philosophy of science. However, characterisations of action potentials often fixate on neurons, mentioning plant cells in passing or ignoring them entirely. The plant sciences are also prone to neglecting non-neuronal action potentials and their role in plant biology. This oversight is significant because plant action potentials bear instructive similarities to those generated by neurons. This paper helps correct the imbalance in representations of action potentials by offering an overview of the mechanism for plant action potentials and highlighting their similarity to those in neurons. Furthermore, it affirms the role of plant action potentials in discovering the evolution and function of mechanisms of action potentials more broadly. We stress the potential of plants for producing generalisations about action potentials and the possible role of plants as experimental organisms.

Keywords

action potential; plant action potential; plant physiology; mechanism; mechanistic explanation; neuron; nervous system; generalisation; experimental organism

§1. Introduction

An action potential (AP) is a sudden transient rise and fall in the electrical potential of a cell membrane. Proponents of the mechanistic model of scientific explanation (Glennan, 2002; Bechtel & Abrahamsen, 2005; Glennan, 2017) have frequently used APs as an example to discuss form and effectiveness of mechanistic explanation (e.g. Craver, 2006; Kaplan & Bechtel, 2011; Levy, 2014; Hochstein, 2016). Not only is the mechanism for neuronal APs (those generated by neurons) well understood at multiple levels of organisation, but it also serves as an example of important aspects of scientific discovery, such as the value of interfield integration, and the role of mathematical models of causal processes (e.g., Craver, 2007).

Despite its prominence in the philosophical literature on mechanistic explanation, discussion of APs tends to single out APs in animals, especially neuronal APs, at the expense of other kingdoms, such as *Plantae* (e.g., Hedrich, 2012) and *Fungi* (e.g., Adamatzky, 2018). Non-animal APs are often mentioned either in passing—with exposition proceeding to detail neural-specific properties—or are ignored entirely (e.g., McCormick, 2014). However, besides being interesting in their own right, non-animal APs promise to inform our understanding of mechanisms for APs in general, given the conservation of APs across taxa and the corresponding variety of functions they play.

This paper provides an overview of the often-neglected mechanism for plant APs. We stress the importance of acknowledging both similarities and differences in mechanisms for APs across phyla for understanding their evolution and function. Moreover, we highlight the importance of considering plants in the context of APs more generally given their role as potential experimental organisms for guiding research in other taxa (Ankeny and Leonelli 2020)—offering, for instance, insight into the primary targets of anaesthetics— and in offering generalisations about the mechanisms for APs. Our aim is thus twofold: (1) to correct an imbalance in the philosophical (and scientific) literature on mechanisms for APs, by highlighting the existence of mechanisms for plant APs and their resemblance to mechanisms for neuronal APs, and (2) to demonstrate the potential of plant APs for scientific discovery.

The paper proceeds as follows. §2 outlines the mechanistic model of explanation using APs as a reference point. §3 introduces the phenomenon of APs in more detail and sketches the mechanism for the best-known case: neuronal APs. §4 provides an overview of plant APs, highlighting similarities and differences to neuronal APs, and offers the case study of APs in the Venus flytrap (*Dionaea muscipula*). §5 discusses the relevance of plant APs for important aspects of scientific discovery, in particular, their role as experimental organisms and in generalising the mechanisms for APs. This is illustrated through the example of work on anaesthesia in plants, which offers potentially critical clues about the primary targets of anaesthetics across taxa.

§2. Mechanistic explanation

'New mechanism' or simply 'mechanism' is a model of explanation in the sciences, particularly the biological and cognitive sciences. An heir to earlier causal-mechanical models of explanation that explain a phenomenon by citing its causes (e.g., Salmon, 1984), the mechanistic model promises an alternative to the once-dominant deductive-nomological or covering law model, according to which, explanations are arguments that demonstrate a phenomenon is necessary or expected given at least one general law and antecedent or background conditions (e.g., Nagel, 1961). According to the mechanistic model, a phenomenon is explained by uncovering its mechanism. A mechanism is a composite of parts, organised (spatially and temporarily) such that their properties and processes produce, maintain or underly a phenomenon. Several heterogeneous characterisations of mechanisms exist (in particular, see Glennan, 2002;

Bechtel & Abrahamsen, 2005). However, despite their differences, all proponents emphasise the importance of (i) target phenomena, (ii) parts, and (iii) organisation, each of which is exemplified by APs:

- (i) *Phenomena.* Mechanisms are necessarily mechanisms of some phenomenon (Glennan 2002). The action potential is a phenomenon realised by the mechanism of the action potential. What comprises the mechanism, therefore, is fixed by the phenomenon in question. Equivalently, a phenomenon is the behaviour of the associated mechanism as a whole, for instance, the total behaviour of the AP mechanism.
- (ii) *Parts.* A mechanism is a complex system constituted by more than one interacting component. Components consist of parts and their processes. Though exactly how to understand a part remains controversial, it is recognised among all proponents of the mechanistic model that mechanisms are constituted by distinctive physical entities that often play different causal roles within the system. Mechanisms are also characteristically decomposable, meaning we can identify a mechanism's organised components and the operations performed by those components, and in turn, we can identify *their* parts and operations and so on. Component parts of the mechanism of the action potential include ion channels, selectively semipermeable membranes that permit certain ions to pass through, but not others, transport pumps for the maintenance of resting potential, and the ionised atoms and protein molecules (as we shall see, *which* ions depend on the type of AP).
- (iii) *Organisation.* The organisation of components and their activities is crucial to how a mechanism realises a phenomenon. Organisation refers to the pattern of interactions between causally differentiated parts and processes. This contrasts mechanisms with mere aggregates as mechanisms are more than the sum of their parts. Components are arranged by their spatial, temporal and organisational properties. Investigating the location, size and orientation of components (spatial properties), as well as the order, rates and duration of their activities (temporal properties), in conjunction with any general organisational relations such as positive or negative feedback (organisational properties) is key to mechanistic explanation. The organisation of the mechanisms of the AP includes the relative duration and order of activation of ion channels.

We noted a mechanism may produce, maintain or underly a phenomenon. A production mechanism involves a causal sequence that results in some end product, such as the production of fuel ethanol from substrates. A maintenance mechanism involves the perpetuation of some state of affairs, such as homeostatic mechanisms for the maintenance of blood glucose levels. An underlying mechanism involves the realisation of the phenomenon through the behaviour of the mechanism as a whole. The mechanism of the action potential *underlies* or *constitutes* the action potential. To be exact, 'production', 'maintenance' and 'constitution' do not necessarily reflect separate kinds of relations but different spatiotemporal aspects of the same mechanism/phenomenon relation (cf. Kästner, 2021). For example, we may look at the underlying parts of a single step in a production mechanism or the sequence of steps leading to a product within a constitutive part. Whether constitution or production is more relevant depends on which aspect of a mechanism-phenomenon matters most given the epistemic context. In any case, we will be concerned with mechanisms for APs, a paradigmatic case of a constitutive mechanism.

As it happens, APs have been used in the case against the adequacy of the deductive-nomological model and the superiority of a mechanistic understanding of explanation in biology, cognitive science and beyond. For instance, the Hodgkin-Huxley (1952) model of the AP is a set of nonlinear differential equations that approximately describes AP activity. As a formal model, it has been leveraged to argue for how biological phenomena reduce to physical laws (M Weber 2005); but see (Marcel Weber 2008). In response, Craver (2006), argues that the model's efficacy can only be understood in relation to the concrete biological parts and processes the model describes, and which it abstracts over (cf. Levy, 2014). We return to this below.

In summary, APs have both been used to demonstrate the general need for mechanistic explanation, beyond the remit of the deductive-nomological model, and to highlight the essential features of mechanistic explanations—in particular, the phenomenon-to-be-explained, the constitutive nature of explanation, and the importance of considering a mechanism's organisation.

§3. Action potentials

With the mechanistic model of explanation established, we can now sketch the mechanism underlying action potentials. This section begins with an introduction to the generic structure of APs before detailing this broad picture using the mechanism for the most well-known case: APs generated by neurons. The following section will then turn to a more neglected case: APs generated by plant cells.

§3.1 A generic scheme for action potentials

In brief, APs involve the rapid reversal of a cell's membrane potential. Differences in electrical charge owe to groupings of ions on either side of the cell membrane; the ratio of differently charged ions is due to the permeability of each element, in conjunction with mechanisms for the inward and outward flow of ions, which determines the membrane potential at a given time. As will become clear, several features of electrical signals described as APs remain consistent across disparate cell types and kingdoms, despite varying molecular components. Specifically, all APs (1) are induced by voltage depolarisation, (2) follow an all-or-nothing kinetic principle, (3) possess a threshold potential and (4) travel at constant velocity and amplitude. In addition, most APs, including neuronal and plant APs, share the same threefold phase structure (Miguel-Tomé and Llinás 2021).

In more detail, APs are electrical signals consisting of a transitory rise and fall in electrical potential across a cellular membrane (membrane potential) i.e., the difference in electrical charge between inside and outside the cell. In a cell's resting state (when it is not being stimulated), the membrane is polarised. This means the potential of the inside of the membrane is usually negatively charged relative to the outside, at a fixed voltage (equilibrium electrical, or resting potential); the inside of the cell is more negative than the outside. A stimulation of sufficient magnitude causes a cascade of ion channels to open, triggering the membrane to rapidly depolarise (the membrane potential rises). Repolarising then occurs due to an efflux of positive ions (the membrane potential drops towards its resting state), before returning to its resting state after a brief period of 'hyperpolarisation' during which the membrane potential is lower than the resting state. Within this process, typical APs possess three key phases: depolarisation or 'rising phase', repolarisation or 'falling phase', and after hyperpolarisation, that is, the period of relatively severe polarisation during which the membrane potential drops below its resting potential.

Across animal cell types, APs involve the same key components: (1) leak channels—that are always open and principally consist of potassium channels, alongside chloride

and sodium channels—(2) gated channels—that open in response to a stimulus; comprising both ligand- and voltage-gated ion channels, referring to whether ligand-binding or a voltage threshold is key—and (3) molecular pumps—transmembrane proteins that act as cellular ‘gateways’ between the inside and outside of the cell (e.g., Hill et al., 2004; Grider et al., 2022). These components are modulated by electrical potential and are affected by the strength of an incoming stimulus. Whereas leak channels remain constantly opened, gated channels only open following some stimulation. These channels are rapidly opened when the membrane is depolarised to the point of a ‘threshold’ voltage—a tipping point causing ion channels to open. Once open, additional, positively charged ions enter through the channel, resulting in further depolarisation, causing more channels to open, resulting in further depolarisation, and so on. The result of this cascading ion channel activation is a sudden, significant change in total membrane potential. Repolarisation occurs when positively charged ions can no longer cross the membrane and are actively pumped outwardly causing the membrane potential to drop. Typically, a period of repolarisation occurs in which positively charged ions are at a lower concentration than the resting state, meaning the membrane potential temporarily hyperpolarises i.e., the potential is lower than at rest. Once the ion groupings reset (due to the restoration of membrane permeability), the membrane potential returns to its resting state. The particular properties of the animal cell membrane, the ion channels and the molecular pumps involved determine the minutiae of the electrophysiological profile. A sketch of such an abstract profile, devoid of length and time scales is shown in figure 1.

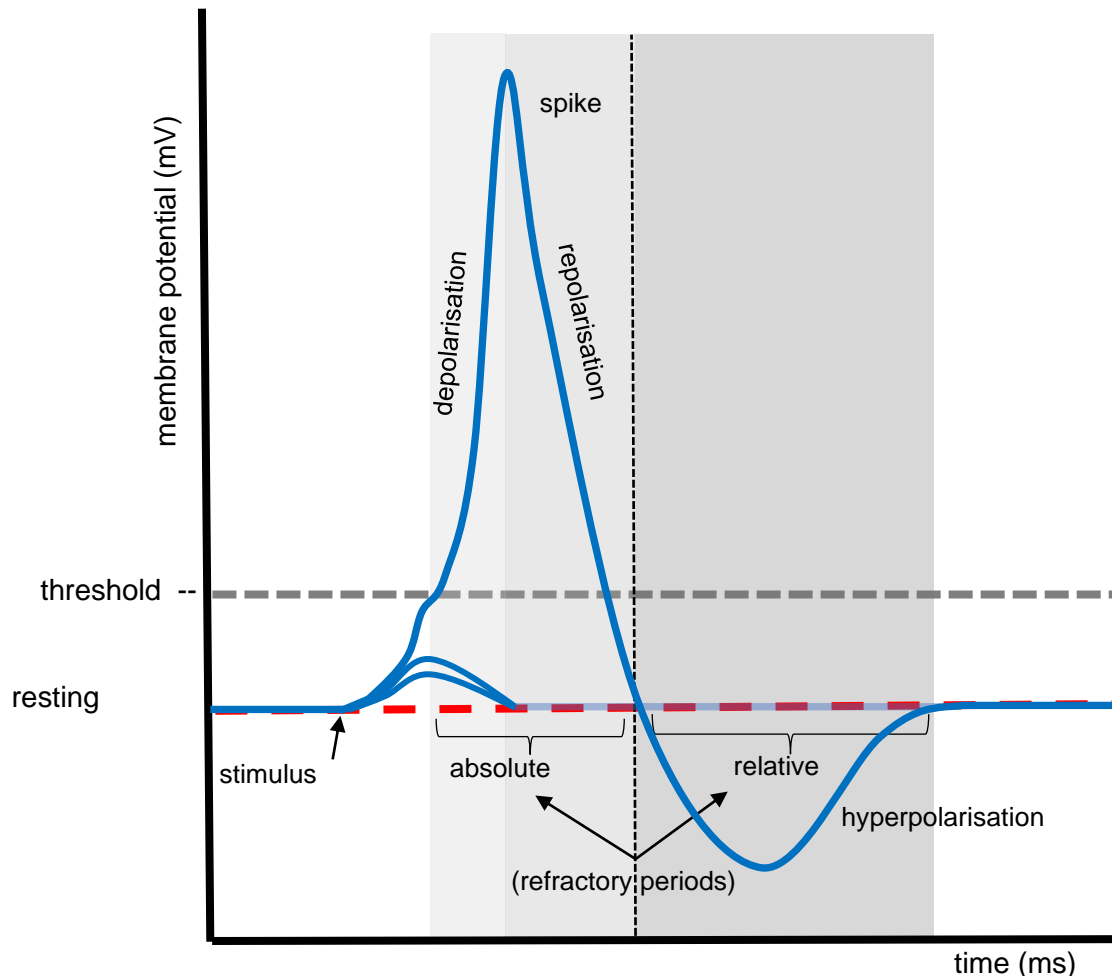


Fig 1. Schematic view of an AP three-fold phase of depolarisation-repolarisation-hyperpolarisation with subthreshold failed initiations, and refractory periods ('absolute': no stimulus can generate an AP; and 'relative': only large stimuli can generate an AP). See text for details.

§3.2 Neuronal action potentials

APs are most associated with electrical activity in and between neurons (e.g., Gazzaniga et al, 2014), as well as other parts of the animal body, such as some muscle cells. The membrane potential in neurons is determined by the ratio of sodium (Na^+), chloride (Cl^-) and potassium ions (K^+), among other charged organic ions. The resting potential (typically averaging around -60 to -70mV) is maintained via ion channels and the sodium-potassium pump. This latter mechanism is a transport protein that essentially pumps out three sodium ions whilst pumping in two potassium ions, retaining the concentration of negative to positive ions between the inside and outside of the cell. APs are transmitted when Na^+ enters the cell via open voltage-gated ion channels and the threshold potential is reached (typically around -55 mV).

Two activities assist the inflow of Na^+ , collectively known as driving force: (1) *diffusion* of sodium ions down the electrochemical gradient into the neuron due to increased permeability and lesser concentration of sodium inside the cell, and (2) *electrostatic attraction*, given the negative charge of the cell interior. The membrane potential of the neuron then rapidly rises, reversing its polarity until reaching its peak positive potential (typically around $+30\text{ mV}$ to $+40\text{mV}$). The membrane potential then depolarises due to the closing of sodium channels prohibiting the entry of positively charged sodium ions and the opening of potassium channels which let out positively charged potassium

ions. Hyperpolarisation occurs principally due to potassium efflux before enough potassium channels can close, temporarily causing a greater negative-to-positive ion ratio between the inside and outside of the membrane. The membrane thus overshoots its resting potential, typically around -90mV , before returning to its average resting potential of around -60mV to -70mV . The entire process takes approximately 5ms .

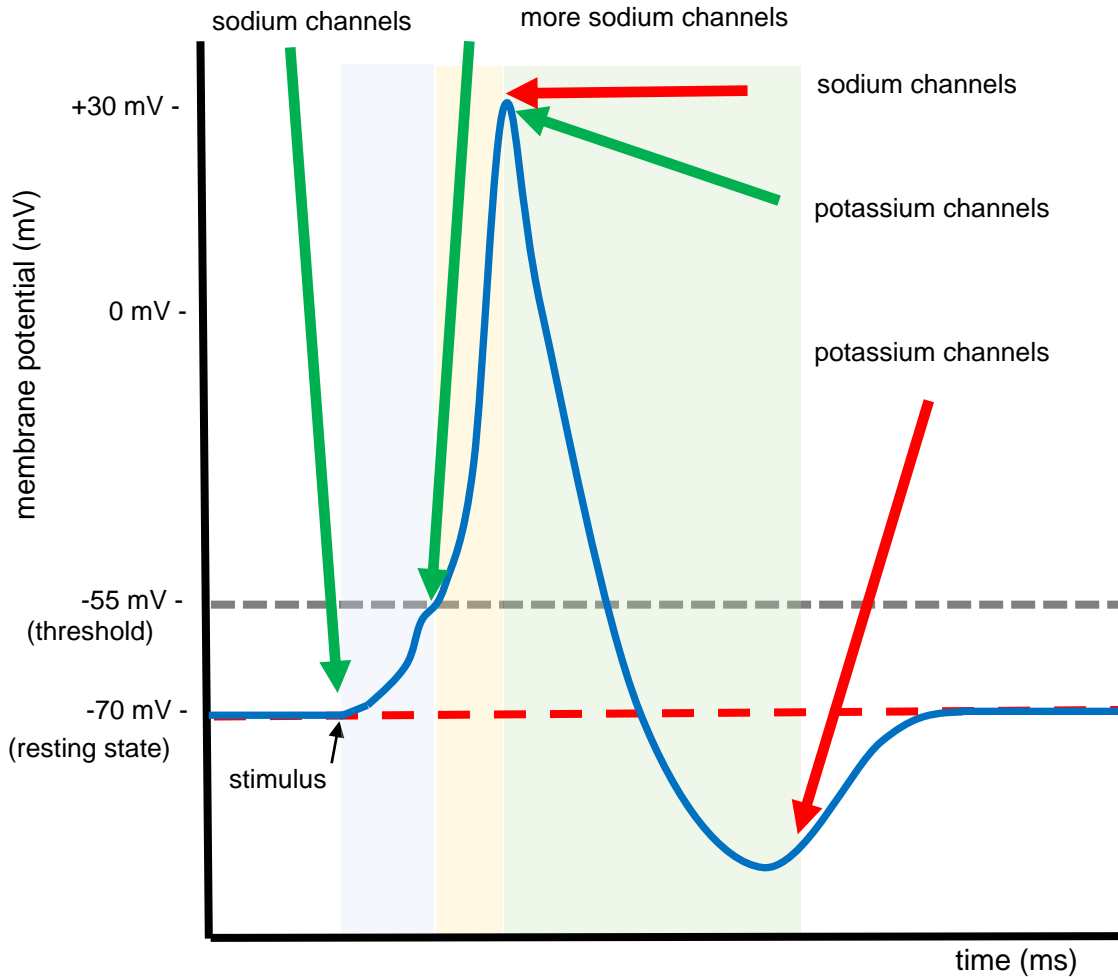


Fig. 2: Schematic view of the temporal opening (green arrows) and closing (red arrows) of sodium and potassium channels and resulting AP in neurons. See text for details.

Following an AP, neurons undergo a 'refractory period' during which a subsequent AP cannot be transmitted by the cell or its ability to do is reduced. An 'absolute refractory period' occurs because of the inactivation of sodium channels (regardless of input), meaning no APs can occur. A 'relative refractory period' occurs because many potassium channels remain open for a period, meaning depolarising in membrane potential remains more difficult. Figure 2 offers a schematic overview of key channels and timings involved in neuronal APs.

Neural signalling depends on APs which are propagated along the axon, a fibrous structure that projects from the cell and connects with other neurons via the synapse. In general, the electrical impulse from the AP generated by the signalling cell (the presynaptic neuron) at the 'synaptic terminal' leads to a process in which neurotransmitters are released and diffuse across a small gap (the synaptic cleft). These are bound by receptors at the receiving cell (the postsynaptic neuron). This alters the receiving cell's excitability, making it either more or less likely to fire an AP. Excitatory neurotransmitters further depolarise the postsynaptic membrane, increasing the likelihood that the threshold is reached, and an action potential will fire. Inhibitory neurotransmitters hyperpolarise the postsynaptic membrane, decreasing the likelihood that the threshold is reached, and an action potential will fire. Whether a cell fires an AP depends on 'summation', whereby the effect of neurotransmitters is aggregated, determining whether the threshold is reached. The total effect of the neurotransmitters results from the proportion of excitatory versus inhibitory neurotransmitters. Summation can either operate over the neurotransmitters released by many presynaptic neurons connecting to the same postsynaptic neuron, or the neurotransmitters of one presynaptic neuron that are released in rapid succession.

Neurons demonstrate two features of APs (e.g., Hill et al, 2004). First, APs are unidirectional, meaning they conduct in one direction. In the case of neurons, this is from the soma (cell body), along the axons, across the synapse, and to the postsynaptic receptor sites. This directionality is caused by the refractory period of the ion channels. Second, APs are 'all-or-nothing', meaning they do not vary their kinetics in magnitude or speed once the threshold is reached; additional changes in stimulus strength do not affect amplitude and shape. Moreover, they are discrete, meaning they do not overlap; APs either fire or they do not. The frequency of APs, however, can vary. How often a cell generates an AP is determined by the presence and magnitude of input stimulation, constrained by refractory periods. Thus, a stimulus of greater magnitude cannot cause a bigger AP, though it can cause APs to fire more frequently.

§3.3 Action potentials & mechanistic explanation

The mechanism for the action potential illustrates several aspects of mechanistic explanation (e.g., Craver, 2007). First, they are fixed by a target phenomenon, in this case, the sequence of events referred to as the action potential. Second, an explanation is often constitutive; the AP is explained in terms of component parts (e.g., ion channels and membranes) and processes (e.g., diffusion and neurotransmitter release) *of the action potential itself*. Third, components are organised: spatial organisation (e.g., the ion channels span the membrane) and temporal organisation (e.g., the relative duration and order of activation in Na⁺ and K⁺ channels) explain the phenomenon. Thus, APs demonstrate how mechanisms explain by showing how organised, constituent parts and processes exhibit the phenomenon to be explained.

Importantly, nothing about the mechanistic model of explanation eschews the importance of mathematical models. In fact, attention to mathematical models helps clarify mechanism's commitments. Take the Hodgkin-Huxley model of the action potential (Hodgkin and Huxley 1952). This incorporates general equations for the description of electrical currents (such as Ohm's law) and electrochemistry (such as the Nernst equation), and has since been expanded to form what is known as 'conductance-based modelling'. Drawing on a series of experiments on the squid giant axon (*Loligo pealii*), given the abnormally thick axons of the molluscs, Hodgkin & Huxley sketched a circuit model corresponding to how the squid axon fired an AP, consisting of a capacitor plus three parallel series of batteries and variable resistors. These stand in for (1) the flow of sodium and (2) the flow of potassium, as well as (3) the leakage current for additional charged particles (such as chloride). This circuit can be described using a formal model consisting of nonlinear differential equations that represent neuronal firing. Most generally, the total membrane current equation is:

$$I_{total} = C_m \frac{dV_m}{dt} + g_k(V_m - V_k) + g_{Na}(V_m - V_{Na}) + g_l(V_m - V_l)$$

The equation essentially states that the total current of the membrane (I_{total}) is the sum of four other currents in the membrane (capacitive current, K⁺ current, Na⁺ current and leakage current, respectively). Though diverse in its details, contemporary conductance-based modelling preserves the basic discrete gating picture (see below) and equations closely follow the Hodgkin-Huxley model (Levy 2014).

According to one interpretation, the apparent explanatory import of the Hodgkin-Huxley model indicates the power of the covering law model when it comes to APs because it combines antecedent conditions with an appeal to general laws such as Ohm's law and the Nernst equation. On the face of it, this might undermine the claim that APs are explained by mechanisms, and more generally the importance of mechanisms for explanation in biology and neuroscience, given the status of the model as a singular achievement in modern neurobiology (cf. Weber, 2008). There are two broad strategies available for those wishing to defend the claim that APs are explained by mechanisms. Which strategy is to be preferred hinges on whether molecular detail is crucial for explanation or whether abstraction over such detail is also explanatory in its own right.

The first strategy involves denying that the Hodgkin-Huxley model explains anything or much at all. For instance, as Craver (2006; 2009) argues, to *explain* the generation of APs, neuroscientists required biological details about the causal mechanisms the model describes (Hodgkin & Huxley knew little about the molecular structures and operations of neuronal APs). Accordingly, the model at best operates as a kind of sketch or partial outline of the phenomenon.¹ More specifically, Craver (2009) says the epistemic utility of the model rests in its role as a (i) data summary, (ii) characterisation of the phenomenon to be explained, (iii) set of temporal constraints on the mechanism, (iv) predictive tool, and (v) heuristic guide to future theorising (p. 1032). Rather than undermine the need for mechanisms to explain, the Hodgkin-Huxley model demonstrates their necessity; the model is impoverished, and knowledge of APs only matured alongside knowledge of ion channels and other structural details.

The second strategy accepts that the Hodgkin-Huxley model does substantially explain and that the omission of structural details, such as those regarding ion channels, is a

¹ 'Mechanism sketches' have been elaborated by proponents of the mechanistic model (e.g., Craver 2007). The idea is that sketches of mechanisms are incomplete models that leave significant gaps. These are common prior to more complete explanations that fill in the structural and operational details.

feature, not a bug. The model intentionally abstracts over mechanistic details and gains its distinctive explanatory power by doing so. For instance, as Levy (2014) argues, the model offers a fruitful abstraction over the molecular details in order to show that the AP phenomenon was an ‘aggregate outcome’ of the activities of many underlying parts. As Levy argues, the notable feature of the Hodgkin-Huxley model is that it involves minimal commitments regarding underlying constituents, abstracting over concrete parts and processes to describe the overall properties of the whole system. Key to this story is that the Hodgkin-Huxley model answers the question of how lower-level events relate to macro-level changes. Briefly, the model does this by representing the ‘discrete gating’ nature of APs—the fact that the behaviour of the cell as a whole is an aggregate of discrete, independent events at a lower (molecular) level. This is because “molecules involved in ionic conductance are discrete, selective, independently acting gates: each one can be either open, in which case ions of a particular type may diffuse through it, or else closed” (Levy, 2014, p. 482). Whilst the Hodgkin-Huxley model abstracts from molecular specifics, it is explanatory *because of* and not *despite* this, intending to capture how cell-level currents are caused by underlying events. What remains unanswered is what parts and processes cause changes in conductance in the cell. This is provided by structural details, of the type Craver privileges (cf. Kaplan & Bechtel, 2011).

Both strategies stress the role of mechanisms in explaining APs whilst also accepting some role for mathematical modelling.² Despite agreement on the big picture, however, we emphasise the second strategy for two reasons. First, it reflects broader progress concerning the role of abstraction in mechanistic explanation (Levy & Bechtel, 2013; Boone & Piccinini, 2016; cf. Lyre, 2018). Second, it highlights one role for plant APs in understanding APs more generally (see next section). Specifically, the fact that formal models of plant APs resemble, with modification, the Hodgkin-Huxley model (Miguel-Tomé and Llinás 2021), despite molecular differences, reveals the shared organisation of mechanisms across otherwise disparate kingdoms. Correspondingly, the diversity of underlying molecular constituents for APs, as demonstrated by the existence of plant APs, reinforces the value of abstract models for capturing similarities in mechanisms across species. We return to this point below.

This section introduced neuronal APs. However, APs play a crucial role beyond neural signalling. Despite this well-established fact, expositions of APs often neglect plants, remaining focused on animal cells and especially neurons (e.g., Grider et al., 2022). Moreover, within the philosophical literature that treats APs as a paradigm case of mechanistic explanation, neuronal APs are taken as the default (e.g., Craver & Darden, 2013). Finally, even within the plant sciences, APs are often forgotten about or assumed to be unimportant. As Baluška & Levin (2016) observe, APs are not even mentioned in one of the most established plant physiology textbooks (Taiz and Zeiger 2010).

Plant APs are worthy of philosophical attention for at least two *prima facie* reasons. First, APs have been used as exemplar cases of mechanistic explanation. Therefore, the persistent neuronal bias with which APs are presented, and which has contributed to the overall neglect of plant APs across scientific and philosophical discourse, should be corrected (§4). Second, as we shall see, plant APs converge and diverge from neuronal APs in interesting respects, and in ways that allow us to make generalisations about APs, and support inferences about their evolution (§5). Moreover, whilst much research remains outstanding, there is support of the value of plant species as

² Incidentally, the debate over the explanatory role of the Hodgkin-Huxley model often displays a neuronal bias. Levy characterises APs, for example, as a rise in the electrical potential of an *axon* membrane (p. 471). Axons are not necessary for APs in plant cells.

experimental organisms for investigating APs more generally, evident in discoveries about the primary targets of anaesthetics from plant studies. Thus, plant APs bear on issues of scientific discovery. It is thus to plant APs that we now turn.

§4. Plant action potentials

Previous sections introduced the mechanistic model of explanation before presenting the generic profile of action potentials, particularised by the example of neuronal APs. In this next section, we provide an overview of plant APs, introducing their mechanism, highlighting similarities and differences to neuronal APs, and presenting the case study of APs in Venus flytrap (*Dionaea muscipula*). We will then be in a position in §5 to turn the impact of plant APs on issues concerning scientific discovery.

§4.1 The mechanism for plant action potentials

Plants exhibit activity that, though different in certain details, closely resembles those of action potentials in animals. In their discussion of the mechanism of APs, for instance, Craver & Darden write that “Action potentials are electrical signals in neurons” (p. 43). They go on to note that APs are “changes in *voltage* across a neuronal membrane [...] The charges, in this case, are borne by positively charged particles, known as *ions*. The movement of ions across the membrane constitutes the flow of an electrical *current*.” (p. 44, original emphasis). So long as we swap ‘neurons’ for ‘cells’ and drop the ‘neuronal’ from ‘neuronal membrane’, this description applies to activity found in plants and other parts of mammal physiology, for example, in skeletal muscle cells, or, more generally, in cells that possess gated channels for responding selectively to changes in membrane potential. For this reason, such non-neuronal activities, found in various taxa, are commonly classified as ‘action potentials’, capturing important properties that are conserved across kingdoms and cell types.³

Despite the mechanisms being less well understood than those underlying neuronal APs, and often ignored in scientific and philosophical literature, ‘plant action potentials’ have been known since the 19th century. Following correspondence with Darwin, Burdon-Sanderson (1873) conducted the first recording of plant APs on Venus flytrap (*Dionaea muscipula*), using an extracellular recording of the voltage difference between adaxial (upper) and abaxial (lower) surfaces of the trap whilst touching the sensitive hairs on its interior (Stahlberg, 2006a; Stahlberg, 2006b).⁴ As Stahlberg (2006a) notes, *Dionaea*—described by Darwin (1875) as “the most wonderful plant in the world”—has since acted as a model for the study of plant APs (see below for more on *Dionaea*). This is partially because APs demonstrably play a role in the rapid closure of the plant’s

³ In addition to transmitting APs, plants produce other forms of electrical signals: local electrical potentials, variation potentials, and system potentials (e.g., Debono & Souza, 2019). Moreover, in addition to APs generated by cell membranes, plants are capable of generating internal APs within their tonoplast—an intra-cellular membrane surrounding the vacuole (Shimmen et al. 1994). We touch on these phenomena below, but our focus remains on standard APs. Note that there is some variability in the literature on how plant electrical signals are taxonomized. For example, (Volkov and Shtessel 2020) group signals into: action potentials, electrotonic potentials, graded potentials, receptor potentials, and streaming potentials. For some mapping of features of these categories to the mainstream classification we adopt, see (Zimmermann et al. 2009).

⁴ There are broadly two ways of measuring plant electrical activity: extracellular and intracellular. The former are either surface recordings or measurements via inserted metal electrodes. The latter typically involves the insertion of glass microelectrodes into the cytoplasm or vacuole of the cell using micromanipulators. For an overview, see Fromm & Lautner (2007).

trap in response to mechanical stimulation (Shimmen et al. 1994), pointing to an analogous role in animal nerve-muscle responses (Simons 1981).⁵

The turn of the century saw debate over the mechanism for AP propagation. Haberlandt (1884) proposed (controversially at the time) that the phloem—bundles of vascular tissue—served as the conduit for propagation (for an overview of developments see Liesche, 2019; López-Salmerón et al., 2019). This hypothesis culminated in important work by Bose (1902; 1926; Bose & Guha, 1922) on the role of vascular bundles in enabling cell-to-cell propagation of electrical activity in plants, which Bose explicitly compared to nerves, and which has been confirmed by recent research (for an overview of Bose's work, see Calvo et al., 2017). Bose also (correctly) suggested that electrical signalling played a large part in plant physiology, beyond visible movement like trap closure in Venus flytraps, which garnered criticism from the wider scientific community (Shepherd 2012). Soon after, Umrath (1930) performed the first intracellular recording using microelectrodes, two decades before the first intracellular recording of an animal AP by Nastuk & Hodgkin in 1950 (Fromm & Lautner, 2007). In 1967, Spanswick and Costerton stimulated a cell in *Nitella* (a genus of green algae in the *Characeae* family), and traced the electrical current to another cell, demonstrating an electrical connection. Following Spanswick & Costerton (1967), the relatively large cells of *Characeae* algae have served as a model object in plant electrophysiology, akin to the squid giant axon in animal electrophysiology (Vodeneev et al., 2016). By the 1970s, it was widely known that most or all higher plants exploit electrical signals as part of a variety of functions (Pickard 1973). Today, plant physiologists are unearthing the molecular components of plant APs, as well as turning their attention to the part plant APs play in wider electrical signalling systems (e.g., Fromm & Lautner, 2007; Trebacz et al., 2006; Galle et al., 2014; Canales et al., 2018).

In keeping with our introductory sketch of APs in the previous section, there are several characteristic features of APs that do not depend on the unique properties of neurons or any other cell type: APs are transitory and propagating changes in the resting membrane potential of a cell that (1) are induced by voltage depolarisation, (2) follow an all-or-nothing principle, (3) possess a threshold potential, and (4) travel at constant velocity and amplitude (Trebacz, Dziubinska, and Krol 2006). There are no plant neurons and no plant neuronal membranes, nor are there plant axons and synapses connecting any type of specialised nerve-like cells (but see Baluška, 2010, for similarities between axon extension and plant cell tip growth). Some plant cells are nevertheless capable of generating an electrical signal following contact with moderate non-damaging stimuli (typically; cooling, touch, changes in light conditions or electrical stimulation) that meet the four aforementioned criteria. Moreover, they follow the same three-fold structure as neuronal APs, introduced above, and their behaviour can be described using similar formalisms to the Hodgkin-Huxley model (Sukhova, Akinchits, and Sukhov 2017).⁶

⁵ The paradigmatic model organism in the plant science *Arabidopsis thaliana* has also characteristically yielded information on APs and signalling more generally. For an overview of *Arabidopsis* as a model organism, see (Krämer 2015) (Woodward and Bartel 2018). For sample discussion on APs in *Arabidopsis*, see (Favre and Agosti 2007); (O'Neal et al. 2012).

⁶ Variation potentials also result from damaging stimuli but produce graded signals (Vodeneev et al., 2015).

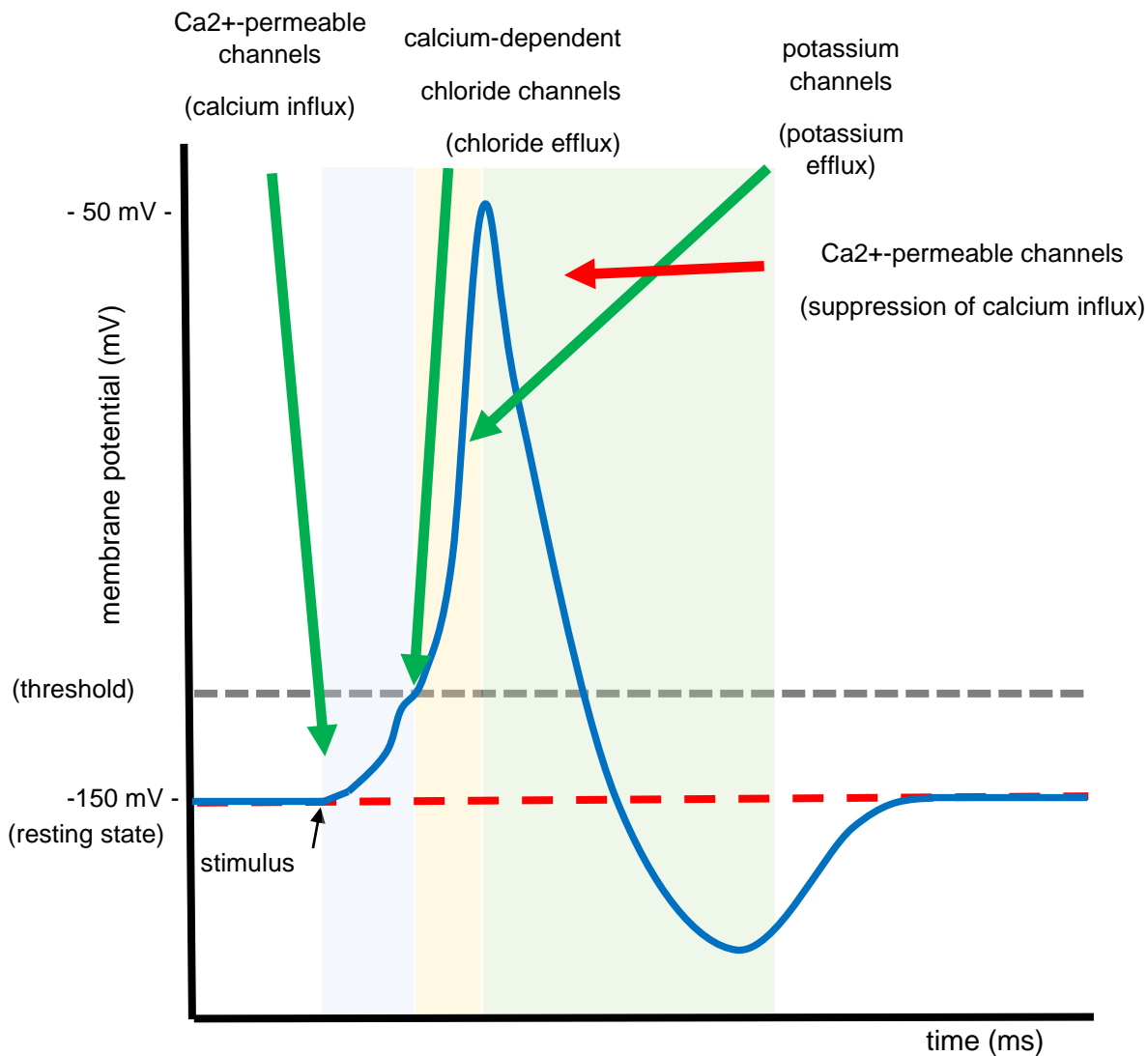


Fig. 3: Schematic view of a plant AP and temporal sequence of an influx of ions into the cytosol and related efflux. A resting cell with Ca^{2+} and Cl^- kept apart from the electrochemical equilibrium is stimulated (non-damaging stimulation). As a result of excitation, depolarisation of the membrane is initiated with the influx of calcium into the cytosol (through the activation of Ca^{2+} -dependent permeable anion channels). This in turn activates Cl^- channels, with the subsequent efflux of Cl^- down their electrochemical potential gradient. As a result, the concentration of calcium ions in the cytoplasm increases, resulting in the depolarisation of the resting potential. Voltage-dependent K^+ channels and anion channels activate resulting in an efflux of K^+ . Repolarisation starts with the plasma membrane returning gradually to its resting potential. Reduction of membrane depolarisation takes place by the suppression of Ca^{2+} influx and promotion of Ca^{2+} resequestration. This cancels stimulation for Cl^- flux and also triggers K^+ efflux through the activation of (outward-rectifying) voltage-gated K^+ channels (from Fromm & Lautner 2007; Klejchova et al., 2021; Li et al., 2021; Trebacz, 2006; and Sukhova et al., 2017).

As with neurons, the resting potential of plant cells is reversed during the firing of an AP, owing to the rapid reversal of polarisation between the interior and exterior of the cell membrane, after a set potential threshold is exceeded. This is facilitated by voltage-dependent ion channels within the plasma membrane. Figure 3 provides an outline of the ions and channels involved.

The AP is thereafter transmitted with a fixed amplitude and propagation speed (e.g., Galle et al., 2014). In higher plants, this electrical signal is then propagated short

distances by direct electrical coupling between cells via plasmodesmata (membranous channels that traverse plant cell walls) and long distances via the phloem (Yan et al., 2009; Choi et al., 2017). Plasmodesmata provide uninterrupted cytoplasmic contact between neighbouring cells, suggesting a continuous propagation of the signal between cells (Kitagawa and Jackson 2017). Thus, whilst plants lack gap junctions (pervasive intercellular channels coupling animal cell cytoplasm), plasmodesmata serve as functional analogues, facilitating direct symplasmic connection between adjacent cells (Lucas, Ham, and Kim 2009). These plant APs are implicated in several crucial functions in higher plants, including but not limited to photosynthesis, respiration, and organ movements, such as the trap closure of the Venus flytrap (*Dionaea muscipula*) or the leaf folding of the sensitive plant (*Mimosa pudica*) (see below). This indicates an analogous role to neuronal APs, serving to connect stimuli and bodily movement in response to stimuli.

Turning to how plant APs are embedded in plant signalling systems, much of the wiring for electrical signalling in plants, and its functional divergence from animal signalling, is still unknown (as is its interdependencies with chemical signalling systems). This itself points to the need for further research. However, as noted above, it is known that electrical propagation in plants involves direct cellular coupling through plasmodesmata and conductive bundles of fibre in the phloem. Such direct coupling allows, in a sense, to bypass the need for synapses (cf. Kitagawa & Jackson, 2017). It has been suggested that the phloem serves as a single conducting 'green cable' for the long-distance transmission of APs in plants; Hedrich et al., 2016). To enter and exit the phloem, however, electrical signals must transition through the cortex (Canales, Henriquez-Valencia, and Brauchi 2018)—the tissue situated between the epidermis and vascular tissues of stems and roots in higher plants. This is possibly achieved via the unique extracellular space between cell walls, called the 'apoplast', in conjunction with the plasmodesmata. Regardless, the plant electrical/chemical connection in particular requires further investigation.

§4.2 Plant cells vs neurons: similarities & differences

There are at least five major differences between plant and neuronal APs:

- I. **Molecular components.** The mechanism for plant and neuronal APs differ in the underlying molecular components for depolarisation. The ions and channels responsible for plant APs remain uncertain (Miguel-Tomé and Llinás 2021). However, depolarisation is thought to occur primarily due to the outflow of negatively charged chloride ions (Cl^-) and inflow of positively charged calcium (Ca^{2+}) into the cytosol—the intracellular water-based solution—following the stimulus-triggered opening of Ca^{2+} channels (Tester, 1990; Galle et al., 2014) alongside potassium (K^+) and hydrogen (H^+) ions. Ionic differences with animal APs likely owe at least partially to the toxicity of sodium for plants (Canales et al., 2018).
- II. **Falling and hyperpolarisation phases.** In plants, the falling and afterhyperpolarisation phases of the AP rely on the outward transportation of potassium ions. Moreover, repolarisation in higher plants involves utilising energy to release hydrogen via transporter protein (H^+ -ATPase) in contrast with Na^+/K^+ -ATPases in animal cells (Vodeneev et al., 2015).
- III. **Resting potential.** The average resting potential of a plant cell membrane also differs from that of a neuron. For example, the Venus flytrap cell rests on average at approximately -120 mV (in contrast to the average -60 mV to -70mV of animal APs), eliciting an AP at the threshold of approximately -100

mV, and reaching a peak of approximately -20 mV (Hedrich and Neher 2018).

- IV. **Speed of propagation.** A fourth difference is the speed of propagation: plant APs are typically slower compared to most (but not all) animal APs, with varying speeds that can range from mm s⁻¹ to cm s⁻¹ (Huber & Bauerle, 2016; Choi et al., 2017). For instance, APs in the leaf pinna of *Mimosa* are around 20–30 mm s⁻¹ (Fromm and Lautner 2007). In the Venus flytrap, APs are propagated at approximately 5–25 cm· s⁻¹ in contrast to nerves where APs propagate at approximately 0.1–100 m· s⁻¹ (Hedrich and Neher 2018). However, APs have been reported to reach up to 105.5 m· s⁻¹ in the stem in soybeans (*Glycine Max*) following flame to damage to leaves (Choi et al. 2017). Exceptions aside, the comparative slowness of plant AP propagation is likely due to several properties of the phloem which acts as a propagation channel, namely: (1) greater activation threshold of chloride channels, (2) lower density of ion channels, (3) differences in intrinsic activation kinetics, (4) the need for the signal to traverse cell-to-cell junctions, and (5) the absence of myelination found in nerves (Hedrich and Neher 2018).⁷
- V. **Duration of refractory periods.** The duration of the refractory period diverges across cell types. As Fromm & Lautner (2007) note in their review, for instance, absolute refractory periods last 2-4 mins. in *Conocephalum* (a genus of liverwort) compared with 0.0005 s. in mammals, whilst relative refractory periods last 6–8 min in *Conocephalum* compared with 0.001–0.01 in mammals (following Dziubińska et al., 1989).

These differences can be loosely grouped into two classes: differences in molecular components [(I) and (II)], and differences in the electrical and signalling properties within and between cells [(III), (IV) and (V)].

To recap, despite differences in molecular components and electrical signalling properties, plant APs preserve four cell-neutral features of all APs: they are induced by voltage depolarisation, follow an all-or-nothing principle, possess a threshold potential, and travel at constant velocity and amplitude (Zawadzki et al. 1991). They also follow the three-fold structure of neuronal APs. Moreover, plant APs exhibit absolute and relative refractory periods post-firing. Following Miguel-Tomé & Llinás (2021), similarities extend to the mathematical modelling of plant APs that transpire to be modifications of the Hodgkin-Huxley model (cf. Sukhova et al., 2017; on the need for further development of the model, see Yan et al., 2009).⁸ For a summary, see Table 1.

⁷ Plant AP speeds are adequate given that plants are autotrophic (they produce their own food), and modular (constituted by repeated root, leaf and bud structures with massive redundancy built into their bodily integrity). This means that plants need not respond to environmental contingencies at the same timescales as, say, non-sessile animals.

⁸ Baluska & Mancuso (2009) observe that neurons and plant cells share other curious commonalities. Neurons are the only animal cells that, like plant cells, lack centrioles and are not bathed directly in blood.

Characteristic	Plant AP
Voltage threshold	Yes
All-or-nothing principle	Yes
Constant velocity and amplitude	Yes
Absolute and relative refractory periods	Yes
Three-fold structure	Yes
Typical duration	3-20s
Typical amplitude	120-150mV
Mechanism	Ion channel activation
Voltage direction	Depolarisation
Dominant ions	Cl ⁻ , Ca ²⁺ , K ⁺

Table 1. Selective characteristics of plant action potentials.

Beyond the mechanism for plant APs itself, there is evidence of similarities in the wider signalling system in which they are situated. Chemicals that function as neurotransmitters and neuromodulators in animals also interact with electrical signalling in plants, especially gamma-aminobutyric acid (GABA) and glutamate (which diffuse across the plant in extracellular space, analogously to the transmission through diffusion of neuromodulators in animals). For example, as Miguel-Tomé & Llinás (2021) report, following Toyota et al. (2018), when glutamate is detected it plays a role in increasing calcium ion concentration, assisting in the propagation of the electrical signal throughout the plant after wounding. Moreover, as Bouché et al. (2003) and Bouché & Fromm (2004) note, GABA is no longer viewed as a mere metabolite (a substance produced during metabolism) but as a plant signalling molecule involved in, among other things, plant development and stress response (cf. Žárský, 2015; Ramesh et al., 2017). Such clues have consequences for our understanding of the phylogenetic development of neurotransmitters. For instance, some have suggested that signalling cascades via GABA are likely a “phylogenetically conserved ubiquitous mechanism” (Bouché et al., 2003, p. 609). Others have questioned whether the spread of glutamate receptors indicates “high incidence of independent convergent evolution”, implying, “molecular constraints on the evolution of the coupling between basal metabolism and intercellular signalling in multicellular eukaryotes” (Žárský, 2015, p. 2). Cellular messengers, such as calmodulin, and cellular motility mechanisms incorporating myosin and actin, are also found in plants, begging for further investigation (Ma and Yen 1989); Fromm, 2006; Fromm & Lautner, 2007, following Baluška et al., 2006; Murch, 2006).⁹ Considering the possession of these key chemical components of nervous systems, Fromm (2012) suggests that “Plants possess most of the chemistry of the neuromotoric system in animals” (p. 269).

In short, plant APs exhibit the core functional features of neuronal APs, and appear embedded in wider signalling mechanisms that share important properties of those in animals (e.g., Bouché et al., 2003). We return to the significance of this below.

§4.3 The curious case of the carnivorous plant

APs play a crucial role in two of the most well-known movements in the plant kingdom: the rapid folding of the sensitive plant (*Mimosa pudica*) and the snapping of the Venus flytrap (*Dionaea muscipula*).¹⁰ The physiological consequences of plant APs have been

⁹ (Karkan 2008) notes the apparent lack of ubiquitous actin/myosin-based processes in plants, which are characteristic of animals. However, in *Chara corallina*, APs appear to play a vital role in disrupting interaction between myosin and actin, resulting from increased levels of Ca²⁺. This is an important function in wound healing ((Johnson et al. 2002). Actin-myosin interaction is also thought to play a role in the organ-level movement of pea tendrils (Ma and Yen 1989).

¹⁰ These are not the only rapid movements found in the plant kingdom. Others include the activities of Bladderworts, Telegraph plants and sundews. However, these plants depend on forms of mechanical pressure for their movement, not electrical stimulation.

best studied in *Dionaea*, have often served as a model for APs in other plants, and serve as a colourful illustration of the role of APs in plant behaviour (for sample discussion of the role of APs in the rapid movement of *Mimosa*, and its interaction with other forms of signalling, see (Shepherd 2012); (Hagihara et al. 2022).

Like most plant electrical signalling, there are many gaps in our knowledge of APs in insectivorous plants (despite interest stretching back to Darwin, 1875). Nonetheless, the basic process is understood. Flytraps utilise APs to operate their traps—a kind of modified leaf—in order to catch prey, typically insects and arachnids. Thus, these plants exploit electrical signalling for organ closure. This trap allows *Dionaea* to supplement their diet within their naturally nutrient-depleted environments (subtropical wetlands of North America), which lack significant levels of nitrogen, phosphate, sulphur and minerals that are normally absorbed from soil (Hedrich 2015).

The titular trap of *Dionaea* consists of a bilobed snap trap, with each lobe interior containing three 'trigger' or sensory hairs. These hairs consist of a 'lever' adjoined to a basal podium containing the receptor site (S. Scherzer et al. 2019). Prey are lured to the trap because (1) the inner part of the trap is coloured bright red, and (2) the plant releases a scent containing more than 60 volatile organic compounds (VOCs), most of which are possessed by ordinary fruit and flower scents (Hedrich and Neher 2018). Both are attractive to many insects. Once on the trap, the prey risk stimulating trigger hairs.

Mechanical pressure on the trigger hairs leads to an influx of calcium in the cytosol of mechano-receptor sensor cells which then generate an initial AP that spreads across the trap surface at a velocity of approximately 10cm s^{-1} (Trebacz et al., 2006). If a second trigger hair is stimulated within approximately 20-40s after the initial stimulation, a second AP fires. The second AP travels at a greater velocity, approximately 25cm s^{-1} . This generates a signal that propagates across the lobes of the trap, stimulating the midrib area between them and causing the trap to close. Thus, two APs are typically required for trap closure (Böhm et al., 2016). One reason the trap may require a second AP is that the first results in an insufficient rise in cytoplasmic calcium ions (Ca^{2+}). The second AP causes a sufficient influx of calcium (Ca^{2+}) and the efflux of chlorine and potassium (Cl^- and K^+) within a certain period (Trebacz, Dziubinska, and Krol 2006). Closing and opening the trap is energetically costly. Avoiding false positives is therefore important. Hence, the requirement of two APs guards against unnecessary energy expenditure (but see Burri et al., 2020).

Once the trap is closed, the prey continues to activate the trigger hairs, stimulating electrical stimulation for often several hours (Böhm et al. 2016). The digestion process only begins after a further three stimulations to the hairs by the struggling prey. The hormone jasmonate causes growth reactions that further force the lobes together, hermetically sealing the trap and beginning the release of digesting enzymes within a temporary 'plant stomach' (Hedrich & Neher, 2018). The hard chitin shell of insect prey is degraded by the hydrolytic enzymes which allow for the degradation of the polymer coat into the macronutrients needed by the plant.

Given the need for two stimulations of the trigger hairs within a certain period for trap closure, and the requirement of five stimulations of the trigger hairs before the digestive process begins, Venus flytraps are often described as relying on the ability to 'count' prey contacts via APs (e.g., Böhm et al., 2016). Flytraps are thus sometimes attributed a form of short-term memory (e.g., Volkov, 2017) because they must track the number of triggers. What is clear is that APs facilitate a form of temporary bioelectrical information storage, and that plants are capable of discriminating between numbers of stored signals (Hedrich, 2012; Böhm et al., 2016; Hedrich et al., 2016; Calvo et al.,

2017). Thus, despite otherwise very different mechanisms, APs underlie different kinds of memory-like phenomena across the plant and animal kingdoms.

APs play a part in the charismatic movements of *Dionaea* and *Mimosa*, bioelectrically regulating rapid leaf movements that are perceivable to the human eye. However, it is important to remember that they also play a role in physiological processes in other higher plants (cf. Vodeneev et al., 2016). Again, the details of the mechanism of plant APs, and their precise function, are less well-known than in animals (Hedrich et al., 2016). This itself is worth acknowledging insofar as it reflects a historical bias toward studying electrical signalling in animals. However, some general comments on the wider role of APs are possible. APs are costly to generate, and so are not (as some have indicated) likely to be an evolutionary accident (for discussion, see Baluška & Mancuso, 2009). Indeed, there is evidence that electrical signals are crucial for regulating physiological functions in all higher plants (Pickard 1973), with evidence that APs play a role in respiration, gas exchange, phloem translocation, opening/closing of stoma, osmotic adjustment and nycinastic movements (circadian response to diurnal light and temperature patterns) (e.g., Klejchova et al., 2021; Li et al. 2021). Electrical signalling in plants likely serves as a ‘high-speed’ communication channel between different parts of the organism, facilitating a relatively rapid response to stimuli and across longer distances than is possible with hormones or other chemical signals (Fromm and Lautner 2007).¹¹ According to Volkov (2017), the ubiquitous phenomenon of plant sensing and response can be represented by a general schema consisting of three stages: (1) the perception of a stimulus via a ‘phytosensor’, (2) the transmission of a signal via an electrical network, and (3) decision making process culminating in responses via ‘phytoactuators’. APs play a key role in the signalling stage.

In summary, it is now widely recognised that electrical signalling in general and action potentials, in particular, play a crucial role in transducing environmental signals and coordinating behaviour across the whole plant, by facilitating long-distance communication (Canales, Henriquez-Valencia, and Brauchi 2018).¹² In the following section, we turn to the importance of plant APs in understanding APs more generally, and their demonstration of key facets of scientific discovery.

§5. Plant action potentials & scientific discovery

Mechanistic models are often characterised as targeting particular realisers of a particular phenomenon in particular species. However, mechanistic explanation also allows for generalisation. One form of generalisation is in the explication of the same or similar mechanisms for the same or similar phenomenon across species, resulting from convergent evolution or descent from a common ancestor (Bechtel 2009).¹³

¹¹ The role of plant APs in long-distance communication has been questioned until comparatively recently. For instance, see Goldsworthy (1983)

¹² Davies (2004) implies at least two historical causes for the neglect of plant electrical signalling. The first was the focus on chemical signalling in plants—ironically, identified by Darwin who also evidenced electrical signals in insectivorous plants—which led to an attractive (but false) individuation of two essential types of signalling: chemical (in plants) and electrical (in animals). The second was the popularity of the pseudoscientific book ‘*The secret life of plants*’ (Tompkins and Bird 1973) which undermined the scientific credentials of those studying plant behaviour and communication via “animal-like” mechanisms. For the most recent book-length treatment that aims to set the scientific record straight, and away from the pseudosciences, see Calvo & Lawrence’s *Planta Sapiens* (2022).

¹³ Some discussion of generalisation in mechanistic models focuses on conservation at the expense of convergence (e.g., Bechtel, 2009). Though APs are an instance of conservation, we think plants provide a strong case for considering convergence in generalising about

Mechanisms are conserved in descendent species or result from convergence due to sufficient parallels in selection pressures. Hence biologists seek resemblance in parts and processes across phyla—a kind of generalisation. At the same time, speciation is expected to lead to differences in similar mechanisms, so biologists seek variation in parts and processes. Indeed, appeals to conservation and convergence seem especially informative when two similar mechanisms for a phenomenon are largely conserved but with some small but significant differences (Bechtel 2009). Plant action potentials serve as an exemplary case of generalisation of this form.

As we have seen, despite several important differences in the cellular/subcellular makeup of plant and animal APs, alongside divergences in electrical signalling properties, APs in both kingdoms share the same functional profile. This demonstrates the flexibility of components for APs at one organisational level without compromising the essential functions associated with APs. Supporting this is the fact that mathematical models of plant APs closely match those of the Hodgkin-Huxley model (Miguel-Tomé and Llinás 2021), formally demonstrating how lower-level events relate to macro-level changes is largely preserved across the plant and animal kingdoms, and that the characteristically 'discrete gating' nature of APs is maintained.

Similarities extend beyond the mechanisms for APs themselves and into the wider signalling systems of which they are a part. The efficacy of anaesthesia on plants provides an illustrative example of how similar principles of electrical signalling (and their cessation) are pivotal across kingdoms. For instance, studies show the trap-shutting of *Dionaea* and the leaf folding of *Mimosa* are inhibited by the application of general anaesthesia (Yokawa et al. 2018). One plausible explanation is that, as with animals, anaesthesia disrupts the firing of APs; specifically, anaesthesia affects glutamate and gamma-aminobutyric acid (GABA) that assist in the production of APs, and which function as neurotransmitters in animals (see below for further discussion). This again raises questions regarding phylogeny. As Baluška & Mancuso (2009) write—in noting the power of anaesthetics to interrupt motor responses in animals, tactile plants and ciliated protists alike—it may be that sensitivity to anaesthetics “arose already in unicellular organisms as an adaptation to boundary membrane homeostasis and ion channels activities to changing environmental conditions” (p. 62). In turn, this indicates the possibility of, and the need to investigate further, endogenous anaesthetic-like substances in plants, with ethylene as a prime candidate.

The persistent cross-kingdom properties of APs raises the possibility of plant species as experimental organisms for investigating APs in other taxa.¹⁴ By analogy, consider Bechtel's (2009) illustration of the part that *Drosophila* played as an experimental organism, paired with the assumption of conservation, in the discovery of mechanisms underlying circadian rhythms in mammals (and vice versa). The assumption that the mechanism for circadian rhythm first identified in an insect species would be conserved in mammals acted as a fruitful heuristic in the search for the latter. This then fed back into further investigation of mechanisms in *Drosophila*. For starters, the discovery of a crucial gene (*per*) in *Drosophila* led to the search for and discovery of mammalian homologs, whilst subsequent work on mammals led to uncovering further components (*Clock* and *Bmal1*) which instigated the search for and discovery of homologs in *Drosophila*. Moreover, the differences between species were crucial in discovery; for instance, the search for a mammalian homolog for a crucial cryptochrome gene (CRY) in *Drosophila* revealed a different role for a similar gene in mammalian circadian

mechanisms as some similar traits in plants and animals result from convergent evolution (for a list of candidate traits, see Baluška & Mancuso, 2009).

¹⁴ By 'experimental organism' we refer to the use of particular species to guide research into and form generalisations about mechanisms in other species (possibly in other phyla), with fewer assumptions about established techniques and protocols than is implied by 'model organism'.

rhythms, leading to further investigation of the similar gene in *Drosophila*. There was thus a back-and-forth process of uncovering the mechanisms for circadian rhythms in *Drosophila* and mammals. The lesson here is that the search for conserved mechanisms led to a form of generalisation that at the same time served as a discovery heuristic.

Bechtel's (2009) examination of the role of *Drosophila* in discovering the mechanisms underlying cross-species circadian rhythms incidentally contains a piece of trivia that bears on the possibility of conserved mechanisms across plants and animals: identifying photoreceptors in *Drosophila* that are conserved from cryptochromes (flavin-containing blue light photoreceptors) in plants aided the discovery of the mechanism for entrainment (resetting circadian rhythms in response to light exposure). Thus, plants too played a role in uncovering animal mechanisms. More generally, research has begun to reveal the dependence of similar molecular networks for circadian rhythms between animals and plants (Cashmore 2003), indicating conserved mechanisms and the potential for plants as experimental organisms (cf. Más, 2008).

Though our knowledge of plant APs is still relatively impoverished compared to neuronal APs (Klejchova et al. 2021), we know they play a part in multiple plant behaviours (Baluška & Yokawa, 2021). Given this, we should remain open to the possibility that plants may serve as experimental organisms for investigating phenomena involving APs in other kingdoms. From the perspective of cognitive science, for example, there is growing attention to the value of unorthodox model and experimental organisms for the study of cognitive capacities like decision-making. As Huang et al. (2021) argue, studying non-neural organisms like bacteria has illuminated some fundamentals of decision-making—such as the importance across the tree of life of heterarchically organised control mechanisms that gather and evaluate information, and select between alternative courses of action (cf. Bechtel & Bich, 2021). Indeed, decision-making is an active area of research, as noted by Huang et al. (2021), and some emerging models of plant decision-making implicate action potentials as a crucial element in the electrical signalling component of plant decision-making (e.g., Volkov, 2017). The takeaway lesson is that acknowledging plant APs motivates an appeal to consider plants as experimental organisms.

Research into the effect of anaesthetics on plants (introduced above) points to an instance of this. Knowledge of the effect of anaesthetics in animals, and that disruption of APs is involved, combined with knowledge of APs in plants, served to guide further research into anaesthetic effects in plants. However, in the process of investigation, evidence has accumulated in favour of a theory of the primary targets of anaesthetics—a notoriously unsettled issue—that applies to animals (for discussion, see Baluška & Yokawa, 2021; Jakšová et al., 2021; Scherzer et al., 2022). Briefly, there are two main contenders in theorising about how anaesthetics works: lipid (membrane) theory, whereby the anaesthetic dissolves in the lipid bilayer altering key membrane properties, and protein (receptor) theory, according to which anaesthetic-induced membrane alterations interfere with receptor proteins in critical ways (Pawson & Forsyth, 2008). Research in plants has suggested that plasma membrane integrity is the primary target of anaesthetics, i.e., it supports lipid (membrane) theory. Consequently, plants have been suggested as appropriate test systems for anaesthesia intended for animal use. Plants serve as experimental organisms, in part, because their electrical activity is easier to measure than that of most animals (subjects are also easy to acquire and may be less prone to ethical considerations). In short, investigating the mechanisms for anaesthetic effects in plants, initiated partially because of known parallels between plants and animals, has led to evidence for a theory of anaesthetic effects that encompasses animals.

Generalising the mechanisms for APs, and using plants as experimental organisms, may also affect our conception of how fields interrelate. For instance, there is ongoing controversy over the nascent field of 'plant neurobiology' (Brenner et al., 2006). Some have argued that as plants lack neurons and synapses, studying the so-called 'neurobiology' of plants speaks to conceptual confusion or will result in an empirical dead-end (Alpi et al. 2007). We will not weigh in on whether 'neurobiology' is the most appropriate term for the study of plant signalling (for discussion, see Calvo & Lawrence, 2022). However, we note that the debate must at least acknowledge mechanistic models of plant APs and the resemblances to animal electrical signalling they reveal (Brenner et al., 2007;). Mechanistic modelling of plant signalling that falls under the rubric of 'plant neurobiology' (whether appropriate or not) is clearly of interest, and comparisons to neuronal biology are wise given the considerations set out above. Following Miguel-Tomé & Llinás (2021), we may also wish to consider the mechanisms for plant APs, and their role within plant signalling, when considering whether to broaden the definition of 'nervous system' to encompass plants (for some etymological considerations, see Mehta et al., 2020).

The effects of maintaining a dialogue between the study of plant and animal APs on the relationship between different disciplines can be further clarified by considering 'interfield integration'. Proponents of the mechanistic model of explanation have explored how it informs our understanding of integration in science. This has tended to focus on interfield integration. Craver & Darden (2013) identify several types:

- (i) *simple mechanistic integration*: different fields study different stages or entities within a mechanism, e.g., different stages of protein synthesis, the results of which can be brought together for a complete understanding
- (ii) *interlevel integration*: different fields study different organisational levels, different spatial and temporal scales, e.g., organisms vs genes, the results of which can be brought together for a more complete understanding
- (iii) *intertemporal organisation*: different fields study different aspects of temporal organisation, e.g., different mechanisms of heredity at different stages.

We suggest, however, that comparing mechanisms for animal APs from the purview of the cognitive sciences with mechanisms for plant APs from the purview of the plant sciences may also achieve a different form of integration. This is because the above forms of interfield integration chiefly concern knowledge of how a mechanism works relative to its role within a particular type of system (e.g., the stages and organisation of neuronal APs in animal brains), whereas attention to APs across scientific fields can provide an understanding of the distribution and degrees of similarities between members of a mechanism type across taxa.

To clarify, we have hinted at the possibility of plants serving as experimental organisms for the study of APs in other kingdoms (and vice versa). Hence, the study of APs in one taxon *may* lead to discoveries about the stages and organisation of a mechanism in another. If correct, then using plants as experimental organisms for the study of, say, neuronal APs may indeed serve as a heuristic for investigations leading to the type of interfield integration targeted by Craver & Darden. Beyond playing this widely recognised role in interfield integration, however, what we acquire when comparing plant and other APs is knowledge of (1) how generalised the broad mechanism type is across evolutionary distant organisms, including how similar formal models apply; (2) the diversity of functions these mechanisms may play in the tree of life; and (3) the timeline for their evolutionary emergence. In short, comparing plant and animal APs may facilitate a form of integration across scientific practice without necessarily

contributing to the type of interfield integration identified by Craver & Darden—though it may do this too.

In addition to studying similarities in APs across plants and other taxa, and using plants as experimental organisms, we should also recognise their idiosyncrasies. Plants are unique in using APs to signal between underground and aboveground organs and for interplant and communication with fungi. They are also capable of generating APs *within* the cell via their tonoplasts (Shimmen et al. 1994).¹⁵ Furthermore, whilst this paper has focused on plant action potentials, plant electrophysiology involves novel types of electric potential, namely ‘local electrical potentials’ (LEPs), ‘variational potentials’ (VPs) (e.g., Yan et al., 2009; Choi et al., 2017; Gilroy et al., 2016; Vodeneev et al., 2016; Debono & Souza, 2019) and system potentials’ (SPs) (Maischak et al., 2010; Zimmermann et al., 2016). Local electrical potentials are only locally generated but play an important part in plant physiology. VPs are induced by wounding and transmitted across the plant but possess several significant dissimilarities to APs, generating graded signals of variable size (contravening the all-or-nothing principle), moving at a slower speed, regulating via hydraulic pressure, and transmitting via the xylem. VPs also appear to play a role in triggering APs. SPs are long-distance hyperpolarisation (rather than depolarisation) events that can propagate, for instance, from leaf to leaf. Understanding the potential of plant action potentials will ultimately require contextualising them within a broader, idiosyncratic electrical signalling system.

§6. Conclusion

Action potentials are crucial for “explaining the brain” (Craver, 2007); they are also crucial for explaining plant behaviour. Plant and animal APs possess some differences in their molecular basis. However, all the key characteristics of APs can be found in plants. Plant APs also exhibit similarities in their sensitivity to substances that function as neurotransmitters in neuronal APs. Though not as well understood as those in animals, plant APs appear to serve crucial functions, including those particular to plants (such as regulation of photosynthesis and transpiration through the opening and closing of stomata) as well as those with some resemblance to functions in animals (namely, organ-level movements such as the foliar nyctinasties, or drooping of leaves, characteristic of legumes in response to day/night cycles and changes in temperature and light intensity, among other environmental stimuli).

Presentations of AP mechanisms often assume a neuronal bias. This should be corrected by taking account of plant APs, as well as APs and AP-like activities in other branches of the tree of life such as Fungi (Slayman et al., 1976; Olsson & Hansson, 1995). We should also recognise that plants help to produce generalisations about the mechanisms for APs, given their structural and organisational similarities to neuronal and other APs. Given apparent convergences in electrophysiology, we should remain open to the possibility of plants serving as experimental organisms whilst simultaneously using what we know from the animal kingdom to guide research into plants.

¹⁵ Our thanks go to František Baluška for drawing our attention to these features.

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