

Cyclic voltammetry of volatile memristors in the Venus flytrap: short-term memory

Alexander G. Volkov^{A,C} and Leon Chua^B

^ADepartment of Chemistry, Oakwood University, Huntsville, AL 35896, USA.

^BDepartment of Electrical Engineering and Computer Sciences, University of California, Berkeley, CA 94720, USA.

^CCorresponding author. Email: agvolkov@yahoo.com

Abstract. Plants have sensory, short-term and long-term memory. Possible candidates for memory in plants are memristors; resistors with memory. Memristors have been found in seeds, plants, flowers and fruits. The electrostimulation of plants by bipolar periodic waves can induce electrical responses with fingerprints of volatile or non-volatile memristors. Here, we show that the electrostimulation of the Venus flytrap (*Dionaea muscipula* Ellis) by unipolar sinusoidal or triangular periodic electrical trains induces electrical responses in plants with fingerprints of volatile memristors. The discovery of volatile generic memristors in plants opens new directions in the modelling and understanding of electrical phenomena in the plant kingdom.

Keywords: *Dionaea muscipula* Ellis, ion channels, memristor, signal transduction, Venus flytrap, volatile memory.

Received 4 December 2020, accepted 15 December 2020, published online 11 January 2021

Introduction

Electrical processes play important roles in the electrophysiology of plants (Volkov 2012a, 2012b). Electrical forms of energy can be used to do work or make information transfer and analysis. These signals propagate along sophisticated electrical circuitry in plants consisting of many electrical components developed by nature. The standard electrical circuits comprise four basic elements: a resistor, a capacitor, an inductor and a memristors (Chua *et al.* 2012; Chua 2013). Memristors are memory circuit elements whose properties depend on the history and state of the system (Chua 2011, 2018). A memristor is a nano-scale memory device, which has huge potential technical applications. A memristor is a non-linear element because it does not obey the superposition principle and its current-voltage characteristics are similar to that of pinched Lissajous patterns observed from non-linear systems (Chua 1971). No combination of non-linear resistors, capacitors and inductors can reproduce this Lissajous behaviour of the memristors (Chua 2018). It is a fundamental two-terminal electrical circuit element described by a state-dependent Ohm's Law. A voltage-controlled memristor can be defined by

$$I = G(x_1, x_2 \dots x_n; V)V$$

$$\frac{dx_k}{dt} = f_k(x_1, x_2 \dots x_n; V), \quad k = 1, 2, \dots, n \quad (1)$$

where G is the memductance of the memristors (Chua 2013). The n state variables (x_1, x_2, \dots, x_n) depend on the internal state of the memristor (Chua 2013, 2018). A current-controlled memristor is defined by

$$V = M(x_1, x_2 \dots x_n; I)I$$

$$\frac{dx_k}{dt} = f_k(x_1, x_2 \dots x_n; I), \quad k = 1, 2, \dots, n \quad (2)$$

where M is the memristance of the memristor. The unit of the memristance is the Ohm. The unit of the memductance is the Siemens. Mathematically, memristance can be described by the equation:

$$M(q(t)) = \frac{d\varphi(q)}{dq} = \frac{\left(\frac{d\varphi}{dt}\right)}{\frac{dq}{dt}} = \frac{V(t)}{I(t)} \quad (3)$$

where φ and q denote the flux and charge, respectively.

When subject to a periodic stimulus, the pinched hysteresis loop of memory elements can either be self-crossing (type I memristor) or not (type II memristor). Recently, we found memristors of both types in imbibed seeds, plants, roots, flowers, and fruits (Volkov *et al.* 2014a, 2014b, 2014c, 2014d, 2015, 2016a, 2016b; Volkov 2017).

Chua (2013) presented theoretical proofs that the voltage-gated K^+ channel in neurons is a locally-active memristor. The K^+ channels in the giant squid axon studied by Hodgkin and Huxley are voltage-gated memristors (Chua *et al.* 2012; Chua 2013). Since plants and animals have similar voltage-gated K^+ channels, it will be interesting to investigate the existence of short or volatile memory in the Venus flytrap (*Dionaea muscipula* Ellis). Potassium channels in plants can be subdivided into two channel classes: non-voltage-gated and voltage-gated K^+ channels (Demidchik *et al.* 2003; MacKinnon 2003; Demidchik and Maathuis 2007; Dreyer and Uozumi 2011; Hedrich 2012). The genome *Arabidopsis*

thaliana L. contains 15 genes that encode subunits of potassium channels. The group of non-voltage-gated K^+ channels consists of six members. The family of voltage-gated Shaker-like K^+ channels consists of nine members in *A. thaliana*.

The analysis of the presence of memristors in bio-tissue is based on cyclic voltammetric characteristics where the memristor, a resistor with memory, should manifest itself (Chua 2018; Volkov and Nyasani 2018). Tetraethylammonium chloride (TEACl), an inhibitor of K^+ channels, or 5-Nitro-2-(3-phenylpropylamino)benzoic acid (NPPB), a blocker of voltage-gated Cl^- and K^+ channels (Illek *et al.* 1992) transform a memristor into a resistor with a single-valued V-I curve in plant tissue (Volkov *et al.* 2014a, 2014b, 2014c, 2014d, 2015, 2016a, 2016b; Volkov 2017). This means that some of the voltage-gated potassium ion channels in plants, seeds, fruits and flowers can be memristors. However, TEACl is not specific and could block some non-selective cation channels.

Uncouplers carbonylcyanide-3-chlorophenylhydrazone (CCCP) and carbonylcyanide-4-trifluoromethoxy-phenyl hydrazone (FCCP) decrease the amplitude of electrical responses at low and high frequencies of bipolar periodic electro stimulating waves (Volkov *et al.* 2014a, 2014b, 2014c, 2014d, 2015, 2016a, 2016b; Volkov 2017).

Hodgkin and Huxley formulated a membrane model that accounts for K^+ , Na^+ and ion leakage channels in the squid giant axon. The membrane resting potential for each ion species is treated like a battery and the degree to which the channel is open is modelled by a variable resistor. According to Chua (2013), the Hodgkin–Huxley time-varying potassium conductance is a 1st-order memristor, and the Hodgkin–Huxley time-varying sodium conductance is a 2nd-order memristor. Nayak and Sikdar (2007) found time-dependent memory in a single voltage-gated sodium channel.

Memory is the ability to store the state of a system at a given time and access this information later (Trewavas 2014). Plants can sense and memorise changes in the environment, which allows them to control their life cycle. The general classification of memory in plants is based on the duration of memory retention and identifies three distinct types of memory: (1) sensory; (2) short-term and (3) long-term memory. Sensory memory corresponds approximately to the initial 0.1–3.0 s after an item is perceived. Short-term memory allows one to recall something from several seconds to a minute without rehearsal. The storage in sensory memory and short-term memory generally has a strictly limited capacity and duration, which means information is available for a certain period but is not retained indefinitely (Volkov *et al.* 2009a, b). Information memorised in a volatile memristor is lost after some time. Volatile memristors are usually locally active and are essential for other critical functions such as generating action potentials (Chua 2018). Long-term memory can store much larger quantities of information for a potentially unlimited duration including the entire life span of a plant. Electrical signalling and memory play fundamental roles in plant responses (Volkov *et al.* 2009a, 2009b; 2011). Examples of short-term (volatile)

and long-term (non-volatile) memory that have been observed in plants include storage and recall functions in seedlings (Thellier *et al.* 2000); chromatin remodelling in plant development (Goodrich and Tweedie 2002); transgenerational memory of stress (Molinier *et al.* 2006); immunological memory of tobacco (*Nicotiana tabacum* L.) plants (Baldwin and Schmelz 1996) and mountain birches (*Betula pubescens* subsp. *czerepanovii* (N. I. Orlova) Hämet-Ahti) (Ruuholta *et al.* 2007); vernalisation and epigenetic memory of winter (Amasino 2004); induced resistance and susceptibility to herbivores (Karban and Niiho 1995); memory response in ABA-entrained plants (Goh *et al.* 2003); photo-tropically induced memory in maize (*Zea mays* L.) (Nick *et al.* 1990); ozone sensitivity of grapevine (*Vitis vinifera* L.) as a memory effect in a perennial crop plant (Soja *et al.* 1997); memory of stimulus (Thellier and Lüttge 2013); systemic acquired resistance in plants exposed to a pathogen (Conrath 2006) and electrical short-term memory in the Venus flytrap (Volkov *et al.* 2009a, 2009b).

Applying an electrical stimulus between a midrib (+) and a lobe (−) closes the upper leaf of the Venus flytrap upper leaf in 0.3 s without mechanical stimulation of trigger hairs. As soon as an 8- μ C charge (for a small trap) or a 9- μ C charge (for a large trap) is transmitted between a lobe and midrib, the trap starts to close at room temperature. The cumulative character of electrical stimuli points to the existence of short-term electrical memory in the Venus flytrap. The Venus flytrap can accumulate small charges and when the threshold value is reached, the trap closes (Volkov *et al.* 2009a, 2009b). A summation of stimuli was demonstrated through the repetitive application of smaller charges (Volkov *et al.* 2009a, 2009b). The cumulative character of electrical stimuli points to the existence of short-term electrical memory in the Venus flytrap. Action potentials can be measured at different points between the lobes and the midrib, but these electrical signals do not penetrate through power switches in the midrib to a petiole to protect other traps in the same plant from their closing. Some potassium AKT2-like channels display two current components with different voltage-dependent properties and can operate as power switches (Dreyer *et al.* 2001).

An inverted polarity pulse with a negative voltage applied to the midrib did not close the plant (Volkov *et al.* 2009a, 2009b). It was found that energy for trap closure is generated by ATP hydrolysis (Jaffe 1973). The concentration of ATP decreases from 950 μ M per midrib before mechanical stimulation to 650 μ M per midrib after stimulation and closure (Jaffe 1973). The equivalent electrical circuits for open trap have additional component consisting of H^+ -ATPase as a rechargeable battery and ATP molecules as a source of energy (Volkov *et al.* 2011).

The main goal of our brief communication is to explore the existence of volatile electrical memory in phyto-memristors of plants.

Materials and methods

Plants of *Dionaea muscipula* Ellis (Venus flytrap) were purchased from Fly-Trap Farm Supply (North Carolina, USA)

and grown in well drained peat moss in plastic pots at 22°C with 12/12-h light/dark photoperiod. We used plants grown from seeds alone. All these plants can be closed by a mechanical stimulation of trigger hairs in less than 1 s. We did not use plants grown using ‘cell culture’ methods, which usually have properties different from native plants in North and South Carolina. The average air humidity was 40% and the irradiance was 700–800 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ PAR at plant level. The source of light was Glixer Grow Light Full Spectrum LED.

Platinum electrodes were prepared from PFA (Perfluoroalkoxy Alkane Polymer)-coated platinum wires (99.99% purity; A-M Systems, Inc.) with a diameter of 0.076 mm. We allowed the plants to rest for 2 h after electrode insertion.

All measurements were conducted at constant room temperature of 22°C inside a Faraday cage, which was mounted on a vibration-stabilised table. High speed data acquisition of low-pass filtered signals was performed using a microcomputer NI-PXI-1042Q (National Instruments) with simultaneous multifunction I/O plug-in data acquisition board NI-PXI-6115 (National Instruments) interfaced through a NI SCB-68 shielded connector block to platinum electrodes (Fig. 1). The system integrated standard low-pass anti-aliasing filters at one-half of the sampling frequency. The function generator FG300 (Yokagawa) was interfaced to the NI-PXI-1042Q microcomputer (National Instruments) and used for electrostimulation of plants (Fig. 1). We selected a resistor (r) of 46 k Ω for measuring of voltage and V_R for estimation of electrical current I . All experiments were conducted during a day between 09:00 hours and 1600 hours.

All experimental results were reproduced at least 25 times using different plants. Software SigmaPlot 12 (Systat Software, Inc.) was used for statistical analysis of experimental data.

Results

Memristors in the trap (upper leaf) and in the lower leaf were found a few years ago (Volkov *et al.* 2014a). In both cases,

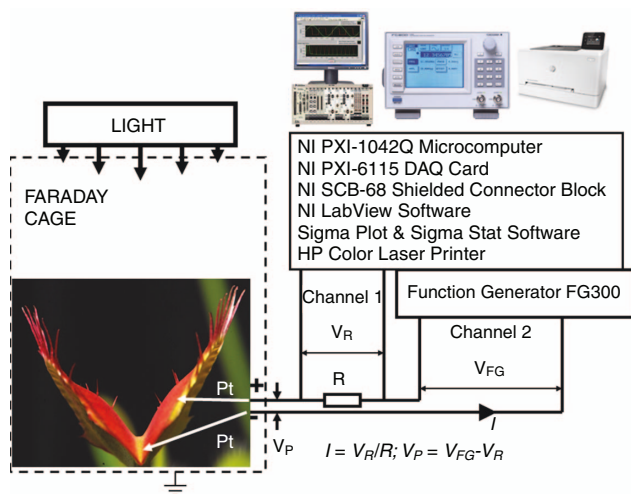


Fig. 1. Schematic diagram of the data acquisition and electrostimulation system.

pinched Lissajous patterns in the voltage-current plane were found. In this study, we only selected closed traps. The experimental setup is shown in Fig. 1.

Bipolar or unipolar periodic electrical waves with amplitude V_{FG} were applied from a function generator. To measure the electrical current, we included in the circuit an additional ‘current sensing’ resistor R , so that electrical current was found as $I = V_R/R$. Potential difference, V , between Pt electrodes in plants is equal to $V_P = V_{FG} - V_R$ (Fig. 1).

We recorded the current flowing through the plant generated by unipolar sinusoidal or triangular waves with a frequency of 0.001 Hz for closed traps and obtained a pinched at the origin Lissajous pattern in the voltage-current plane (Fig. 2c). Increasing the bipolar triangular wave frequency to 1 Hz changes the shape of the line: it is still a loop but without a pinched point for both open and closed traps. Fig. 2 shows dependencies of electrical current between

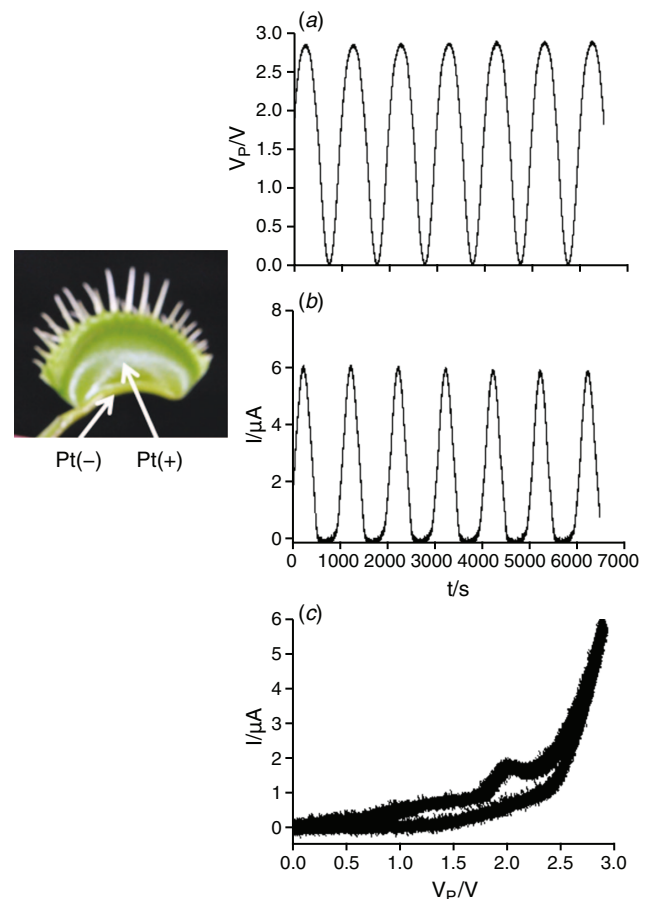


Fig. 2. (a) Electrostimulation of the Venus flytrap (*Dionaea muscipula* Ellis) by unipolar sinusoidal voltage wave (seven cycles). (b) Time dependence of electrical current I between Pt electrodes in the Venus flytrap. (c) Dependence of electrical current I in the Venus flytrap between Pt electrodes induced by unipolar sinusoidal voltage train V_P (seven cycles). Frequency of a sinusoidal unipolar voltage scanning wave was 0.001 Hz. Positions of Pt electrodes in the Venus flytrap are shown. The trap was closed after insertion of Pt electrodes. Note the I vs V_P loci consists of a single closed loop, which implies that the steady response $I(t)$ is a periodic waveform.

platinum electrodes (Fig. 2b) on time during 7-cycle electrostimulation of a closed trap between the midrib and the lobes. The electrostimulation of a trap by bipolar triangular or sinusoidal waves induces electrical responses in the closed Venus flytrap with fingerprints of memristors such as a hysteresis with a pinched point ($I = 0$ when $V_P = 0$). Electrical responses of the Venus flytrap during consecutive multiple application of a bipolar electrical train coincide (Fig. 2b, c). A pinched hysteresis loop measured from applying a periodic voltage with zero mean (Fig. 3) does not determine whether the device memory is *volatile*, or non-volatile.

Electrostimulation of a closed trap by unipolar sinusoidal or triangular voltage waves from a function generator (Figs 2a and 4a) induces periodic electrical responses in the Venus flytrap with constant amplitude (Figs 2b, c and 4b, c). Such periodic electrical responses are usual for memristors with a volatile memory according to literature (Chua 2018). Electrostimulation of a closed trap by unipolar sinusoidal voltage waves from a function generator also induces similar periodic electrical responses in the Venus flytrap with constant amplitude.

Discussion

There are slightly different definitions of memory in neurobiology, material science, plant physiology, microbiology, and computer science. In general, memory is the ability to store the state of a system at a given time and access this information at a later time. Plants can have three forms of memory, such as sensory, short, and long-term memory. Sensory memory is the ultra-shortest-term element of memory with the ability to retain impressions of sensory information after the original stimuli have ended. For example, trigger hairs with mechano-sensitive channels in the Venus flytrap have sensory memory. Short-term memory is the capacity for holding, but not manipulating, a small amount of information in an active, readily available state for a short period of time. For example, electrical memory in the Venus flytrap (Volkov *et al.* 2009a) is a short-term or volatile memory as it was also shown in the present work. The storage in short-term memory generally has a strictly limited capacity and duration, which means information is available for a certain period of time but is not retained indefinitely. Long-term or non-volatile memory is responsible for the storage of information for an extended period of time. Vernalisation is an example of a long-term memory process. Short-term and long-term memories are different processes, and plants do not have to pass through short-term memory in order to reach long-term memory.

Possible candidates for memory devices in plants are memristors, which are resistors with memory. Some K^+ -channels have memristive properties in germinated seeds, plants, flowers, and fruits (Volkov *et al.* 2014a, 2014b, 2014c, 2014d, 2015, 2016a, 2016b; Volkov 2017). The family of voltage-gated K^+ channels in plants subdivides into functional subgroups: inward-rectifying channels, silent weakly rectifying channels, and outward-rectifying channels. Some of these channels can have volatile or non-volatile memory.

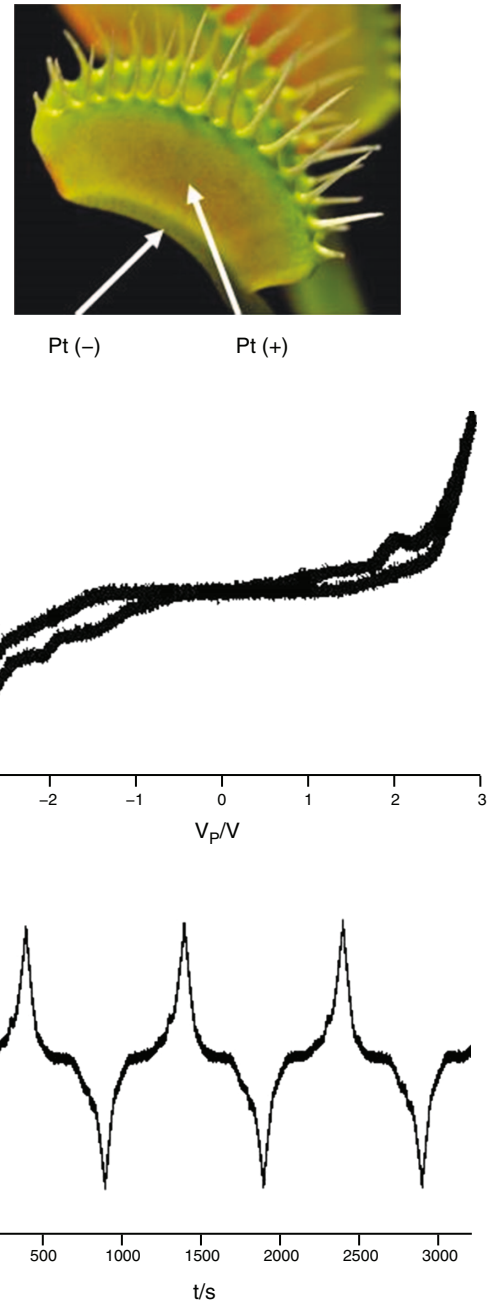


Fig. 3. (a) Electrical current I vs voltage V_P (b) and time dependence of electrical current I in the Venus flytrap between Pt electrodes in the Venus flytrap (*Dionaea muscipula* Ellis) induced by bipolar triangular voltage signal with zero mean (three cycles) from a function generator (a). Frequency of a triangular voltage scanning wave was 0.001 Hz. Data acquisition: 330 scans per s. Positions of Pt electrodes in the Venus flytrap are shown. The trap was closed after insertion of Pt electrodes.

If a memristor does not have non-volatile memory, it is possible to get only a single pinched hysteresis loop, when driven by a periodic input voltage with non-zero mean (Figs 2c, 4c). The Venus flytrap, which has volatile memristors, can accumulate small subthreshold charges during 30 s, and when the threshold value is reached, the

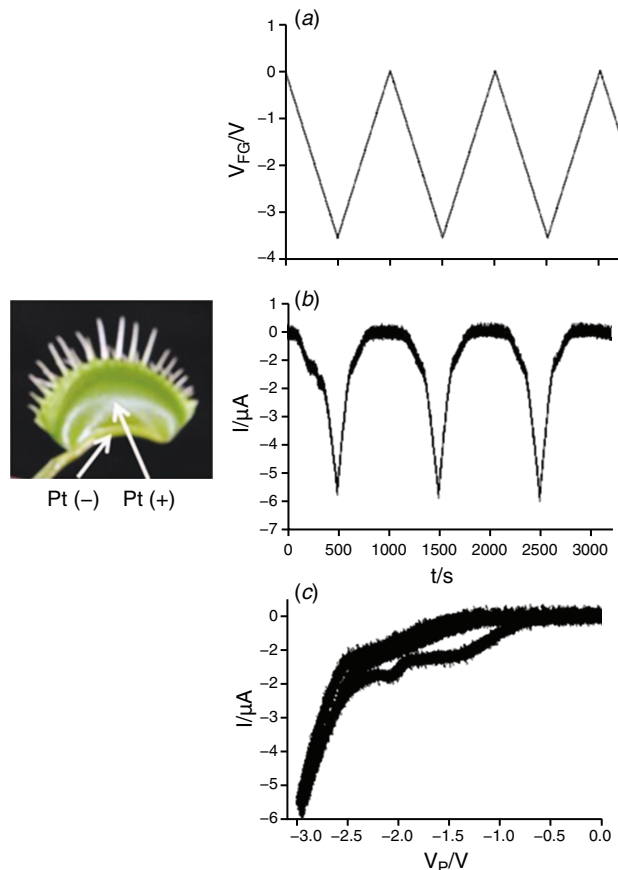


Fig. 4. Time dependence of electrical current I in the Venus flytrap (*Dionaea muscipula* Ellis) (b) and electrical current I v. voltage V_P between Pt-electrodes in the Venus flytrap (c) induced by negative unipolar triangular voltage train (three cycles) from a function generator (a). Frequency of a triangular unipolar voltage scanning wave was 0.001 Hz. Positions of Pt electrodes in the Venus flytrap are shown. The trap was closed after insertion of Pt electrodes. Note the I vs V_P loci consists of a single closed loop, which implies that the steady response $I(t)$ is a periodic waveform.

trap closes. The cumulative character of electrical stimuli points to the existence of short-term electrical memory in the Venus flytrap. Usually, sensory and short-term memories in the Venus flytrap are caused by electrical phenomena (Volkov *et al.* 2009a, 2009b). Short-term memories can be considered as *volatile* memories in the Venus flytrap. The discovery of volatile and non-volatile memristors in plants can be a starting point for understanding the mechanisms of memory, learning, circadian rhythms, and biological clocks.

Conclusion

The presence of memristors with *volatile* memory in the Venus flytrap was found. When driven by a *bipolar* periodic sinusoidal or triangular voltage train, plants exhibit a pinched hysteresis loop in the voltage-current plane (Fig. 3a). Application of unipolar triangular or sinusoidal electrical waves to a plant tissue can be used for evaluation of volatile or non-volatile memories associated with ion

channels. Memristors are essential model building blocks in electrical networks in the plant kingdom.

Conflicts of interest

The authors declare no conflicts of interest.

Acknowledgements

This work is supported by the NSF EPSCoR RII-Track-1 Cooperative Agreement OIA1655280.

References

- Amasino R (2004) Vernalization, competence, and the epigenic memory of winter. *The Plant Cell* **16**, 2553–2559. doi:10.1105/tpc.104.161070
- Baldwin IT, Schmelz EA (1996) Immunological “memory” in the induced accumulation of nicotine in wild tobacco. *Ecology* **77**, 236–246. doi:10.2307/2265673
- Chua L (1971) Memristor – The missing circuit element. *IEEE Transactions on Circuit Theory* **18**, 507–519. doi:10.1109/TCT.1971.1083337
- Chua L (2011) Resistance switching memories are memristors. *Applied Physics. A, Materials Science & Processing* **102**, 765–783. doi:10.1007/s00339-011-6264-9
- Chua L (2013) Memristor, Hodgkin-Huxley, and edge of chaos. *Nanotechnology* **24**, 383001. doi:10.1088/0957-4484/24/38/383001
- Chua L (2018) Five non-volatile memristors enigmas solved. *Applied Physics. A, Materials Science & Processing* **124**, 563. doi:10.1007/s00339-018-1971-0
- Chua L, Sbitnev V, Kim H (2012) Hodgkin-Huxley axon is made of memristors. *International Journal of Bifurcation and Chaos* **22**, 1230011. doi:10.1142/S021812741230011X
- Conrath U (2006) Systemic acquired resistance. *Plant Signaling & Behavior* **1**, 179–184. doi:10.4161/psb.1.4.3221
- Demidchik V, Maathuis FJM (2007) Physiological roles of nonselective cation channels in plants: from salt stress to signaling and development. *New Phytologist* **175**, 387–404. doi:10.1111/j.1469-8137.2007.02128.x
- Demidchik V, Shabala SN, Coutts KB, Tester MA, Davies JA (2003) Free oxygen radicals regulate plasma membrane Ca^{2+} - and K^{+} -permeable channels in plant root cells. *Journal of Cell Science* **116**, 81–88. doi:10.1242/jcs.00201
- Dreyer I, Uozumi N (2011) Potassium channels in plant cells. *The FEBS Journal* **278**, 4293–4303. doi:10.1111/j.1742-4658.2011.08371.x
- Dreyer I, Michard E, Lacombe B, Thibaud JB (2001) A plant Shaker-like K^{+} channel switches between two distinct gating modes resulting in either inward-rectifying or ‘leak’ current. *FEBS Letters* **505**, 233–239. doi:10.1016/S0014-5793(01)02832-0
- Goh CH, Nam HG, Park YS (2003) Stress memory in plants: a negative regulation of stomatal response and transient induction of *rd22* gene to light in abscisic acid-entrained Arabidopsis plants. *The Plant Journal* **36**, 240–255. doi:10.1046/j.1365-3113X.2003.01872.x
- Goodrich J, Tweedie S (2002) Remembrance of things past: chromatin remodeling in plant development. *Annual Review of Cell and Developmental Biology* **18**, 707–746. doi:10.1146/annurev.cellbio.18.040202.114836
- Hedrich R (2012) Ion channels in plants. *Physiological Reviews* **92**, 1777–1811. doi:10.1152/physrev.00038.2011
- Illek B, Fischer H, Kreusel KM, Hegel U, Claus W (1992) Volume-sensitive basolateral K^{+} channels in HT-29/B6 cells: block by lidocaine, quinidine, NPPB, and Ba^{2+} . *The American Journal of Physiology* **263**, C674–C683. doi:10.1152/ajpcell.1992.263.3.C674
- Jaffe MJ (1973) The role of ATP in mechanically stimulated rapid closure of the Venus’s flytrap. *Plant Physiology* **51**, 17–18. doi:10.1104/pp.51.1.17

- Karban R, Niiho C (1995) Induced resistance and susceptibility to herbivory: plant memory and altered plant development. *Ecology* **76**, 1220–1225. doi:10.2307/1940928
- MacKinnon R (2003) Potassium channels. *FEBS Letters* **555**, 62–65. doi:10.1016/S0014-5793(03)01104-9
- Molinier J, Ries G, Zipfel C, Hohn B (2006) Transgeneration memory of stress in plants. *Nature* **442**, 1046–1049. doi:10.1038/nature05022
- Nayak TK, Sikdar SK (2007) Time-dependent molecular memory in single voltage-gated sodium channel. *The Journal of Membrane Biology* **219**, 19–36. doi:10.1007/s00232-007-9058-4
- Nick P, Sailer K, Schafer E (1990) On the relation between photo- and gravitropically induced spatial memory in maize coleoptiles. *Planta* **181**, 385–392. doi:10.1007/BF00195892
- Ruuhola T, Salminen JP, Haviola S, Yang S, Rantala MJ (2007) Immunological memory of mountain birches: effects of phenolics on performance of the autumnal moth depend on herbivory history of trees. *Journal of Chemical Ecology* **33**, 1160–1176. doi:10.1007/s10886-007-9308-z
- Soja G, Eid M, Gangl H, Redl H (1997) Ozone sensitivity of grapevine (*Vitis vinifera* L.): evidence for a memory effect in a perennial crop plant? *Phyton* **37**, 265–270.
- Thellier M, Lüttge U (2013) Plant memory: a tentative model. *Plant Biology* **15**, 1–12. doi:10.1111/j.1438-8677.2012.00674.x
- Thellier M, Sceller LL, Norris V, Verdus MC, Ripoll C (2000) Long-distance transport, storage and recall of morphogenetic information in plants. The existence of a sort of primitive plant “memory.” *Comptes rendus de l'Académie des Sciences* **323**, 81–91. doi:10.1016/S0764-4469(00)00108-6
- Trewavas A (2014) ‘Plant Behavior and Intelligence.’ (Oxford University Press: Oxford, UK.)
- Volkov AG (2012a) ‘Plant Electrophysiology. Methods and Cell Electrophysiology.’ (Springer: Berlin, Germany.)
- Volkov AG (2012b) ‘Plant Electrophysiology. Signaling and Responses.’ (Springer: Berlin, Germany.)
- Volkov AG (2017) Biosensors, memristors and actuators in electrical networks of plants, *International Journal of Parallel Emergent and Distributed Systems* **32**, 44–55. doi:10.1080/17445760.2016.1141209
- Volkov AG, Nyasani EK (2018) Sunpatis compact hot coral: memristors in flowers. *Functional Plant Biology* **45**, 222–227. doi:10.1071/FP16326
- Volkov AG, Carrell H, Baldwin A, Markin VS (2009a) Electrical memory in Venus flytrap. *Bioelectrochemistry (Amsterdam, Netherlands)* **75**, 142–147. doi:10.1016/j.bioelechem.2009.03.005
- Volkov AG, Carrell H, Markin VS (2009b) Biologically closed electrical circuits in Venus flytrap. *Plant Physiology* **149**, 1661–1667. doi:10.1104/pp.108.134536
- Volkov AG, Pinnock MR, Lowe DC, Gay MS, Markin VS (2011) Complete hunting cycle of *Dionaea muscipula*: consecutive steps and their electrical properties. *Journal of Plant Physiology* **168**, 109–120. doi:10.1016/j.jplph.2010.06.007
- Volkov AG, Forde-Tucket V, Reedus J, Mitchell CM, Volkova MI, Markin VS, Chua L (2014a) Memristor in the Venus flytrap. *Plant Signaling & Behavior* **9**, e29204. doi:10.4161/psb.29204
- Volkov AG, Reedus J, Mitchell CM, Tucket C, Forde-Tucket V, Volkova MI, Markin VS, Chua L (2014b) Memristor in the electrical network of *Aloe vera* L. *Plant Signaling & Behavior* **9**, e29056. doi:10.4161/psb.29056
- Volkov AG, Reedus J, Mitchell CM, Tuckett C, Volkova MI, Markin VS, Chua L (2014c) Memory elements in the electrical network of *Mimosa pudica* L. *Plant Signaling and Behavior* **9**, e982029. doi:10.4161/15592324.2014.982029
- Volkov AG, Tucket C, Reedus J, Volkova MI, Markin VS, Chua L (2014d) Memristors in plants. *Plant Signaling & Behavior* **9**, e28152. doi:10.4161/psb.28152
- Volkov AG, Nyasani EK, Blockmon AL, Volkova MI (2015) Memristors: memory elements in potato tubers. *Plant Signaling and Behavior* **10**, e1071750. doi:10.1080/15592324.2015.1071750
- Volkov AG, Nyasani EK, Tuckett C, Blackmon AL, Reedus J, Volkova MI (2016a) Cyclic voltammetry of apple fruits: memristors *in vivo*. *Bioelectrochemistry (Amsterdam, Netherlands)* **112**, 9–15. doi:10.1016/j.bioelechem.2016.07.001
- Volkov AG, Nyasani EK, Tuckett C, Greeman EA, Markin VS (2016b) Electrophysiology of pumpkin seeds: memristors *in vivo*. *Plant Signaling & Behavior* **11**, e1151600. doi:10.1080/15592324.2016.1151600

Handling Editor: Vadim Demidchik