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PLANTS THAT LEARN: A REVIEW OF ADAPTIVE BEHAVIOR AND PLANT MEMORY

PLANTAS QUE APRENDEM: UMA REVISÃO SOBRE COMPORTAMENTO ADAPTATIVO E MEMÓRIA VEGETAL

PLANTAS QUE APRENDEN: UNA REVISIÓN DEL COMPORTAMIENTO ADAPTATIVO Y LA MEMORIA VEGETAL

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ABSTRACT
The survival in complex and unstable environments requires adaptive skills, including the ability to learn from experience, which allows organisms to adjust their behavior in response to specific cues, events, and circumstances. Although this ability has been extensively studied in animals, recent experimental evidence suggests that plants also exhibit associative learning. This discovery has significant implications for our understanding of plant biology as well as for the broader understanding of intelligence and behavior in living organisms. In this article, we review the current literature on memory and learning processes in plants, highlighting recent findings and discussing their relevance to science. Additionally, we explore the implications of these findings for plant biology and for research in sustainability and environmental conservation.

Keywords: Plant Intelligence. Associative Learning. Adaptive Behavior. Memory. Research Implications.

RESUMO
A sobrevivência em ambientes complexos e instáveis exige habilidades adaptativas, incluindo a capacidade de aprender com a experiência, o que permite aos organismos ajustar seu comportamento em resposta a sinais, eventos e circunstâncias específicos. Embora essa capacidade tenha sido amplamente estudada em animais, evidências experimentais recentes sugerem que as plantas também exibem aprendizagem associativa. Essa descoberta tem implicações significativas para nossa compreensão da biologia vegetal, bem como para a compreensão mais ampla da inteligência e do comportamento

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em organismos vivos. Neste artigo, revisamos a literatura atual sobre memória e processos de aprendizagem em plantas, destacando descobertas recentes e discutindo sua relevância para a ciência. Além disso, exploramos as implicações dessas descobertas para a biologia vegetal e para a pesquisa em sustentabilidade e conservação ambiental.

Palavras-chave: Inteligência Vegetal. Aprendizagem Associativa. Comportamento Adaptativo. Memória. Implicações para a Pesquisa.

RESUMEN
La supervivencia en entornos complejos e inestables requiere habilidades adaptativas, incluida la capacidad de aprender de la experiencia, lo que permite a los organismos ajustar su comportamiento en respuesta a señales, eventos y circunstancias específicas. Si bien esta capacidad se ha estudiado ampliamente en animales, evidencia experimental reciente sugiere que las plantas también exhiben aprendizaje asociativo. Este descubrimiento tiene implicaciones significativas para nuestra comprensión de la biología vegetal, así como para la comprensión más amplia de la inteligencia y el comportamiento en los organismos vivos. En este artículo, revisamos la literatura actual sobre los procesos de memoria y aprendizaje en plantas, destacando los hallazgos recientes y analizando su relevancia para la ciencia. Además, exploramos las implicaciones de estos hallazgos para la biología vegetal y para la investigación en sostenibilidad y conservación ambiental.

Palabras clave: Inteligencia Vegetal. Aprendizaje Asociativo. Comportamiento Adaptativo. Memoria. Implicaciones para la Investigación.

1 INTRODUCTION

Plants are living organisms that play a crucial role in maintaining life on Earth. They are capable of producing oxygen, purifying the air, and providing food and resources for humans and other animals. However, until recently, it was believed that plants were inert beings, without the ability to sense or respond to environmental stimuli. This has changed since the research of Jagadish Chandra Bose (1858-1937), who was a pioneer in outlining similarities between plant and animal responses (MINORSKY, 2020). Bose demonstrated that, like animals, excitability appears as a property of all plants and that electrical potentials (in plants) propagate over long distances through phloem cells - which he called "plant nerves". According to Baluška and Mancuso (2009), recent studies in plant neurobiology reveal that plants have structures and mechanisms that resemble animal neurons, including the presence of neurotransmitters such as dopamine and serotonin and the ability to form synapses to transmit electrical and chemical signals. Evidence of this kind has led to the establishment of a relationship between the concept of a neuron and studies in plant biology.

In animal organisms, the electrical properties of the nervous system are associated with intelligence, cognitive abilities, and the perception of endogenous and exogenous stimuli (Baluška & Mancuso, 2009). A consequence of the identification of electrical responses in plants was the emergence of a field of study that was then called plant neurobiology, described as a research area aimed at understanding how plants perceive the environment around them and how they respond to this environment in an integrated manner; taking into account molecular, chemical, and electrical components in intercellular signaling (BRENNER et al., 2006). In this sense, plant neurobiology proposes to integrate existing knowledge in neuroscience with existing understanding of plant cell properties to understand the mechanisms that regulate the individual and social behavior of plants.

Currently, it is widely recognized that, just as in animal organisms, plants are also capable of perceiving and responding to environmental stimuli in an integrated manner (Ballaré & Casal, 2000). This process, which involves the detection of stimuli, interpretation, and production of appropriate responses, requires the coordinated action of various cells and tissues. In plants, this process was initially described as a complex signaling system, based on chemical and hydraulic components (KISS, 2018). However, the understanding of this process was expanded with the discovery not only of electrical signaling in plants but also with evidence of neurotransmitter signaling in plants (STRUIK et al., 2008). Studies indicate the existence of signaling by acetylcholine, dopamine, serotonin, adrenaline, noradrenaline, gamma-aminobutyric acid (GABA), and glutamate in plants. In addition, evidence points to the presence of neurotransmitter transporters in plants (Roshchina, 2001; Wipf et al., 2002). It has been demonstrated that polar transport of auxin in vesicles, according to Baluška et al. (2003), can be compared to the process of neurotransmitter release in the synaptic structures of the animal nervous system. In summary, the presence of electrical signals such as action potentials, as well as the identification of molecules that act as neurotransmitters, are strong evidence that justifies the use of the term plant neurobiology. This phenomenon also raises discussions about possible similarities between plants and animals regarding the process of detecting stimuli and producing coordinated responses, raising questions about plant behavior and their relationships.

As scientific literature attests (Thorndike, E. L., 1898; Samoilov, V.O., 2007; Watson, J.B., 1913), the study of animal behavior began (especially) during the 19th and 20th centuries. Ethologists and behaviorists have demonstrated in detail the behavioral nature of the interaction of animal organisms with their environment (Schneider, S.M., & Morris, E.K., 1987; Skinner, B.F., 2011; Fericean, M.L., Rada, O., & Badilita, M., 2015; Wheeler, W.M., 2015). The evidence indicates that the behavioral repertoire is partly constituted by hereditary responses and partly by learned responses. Interestingly, besides animal behavior, which was the focus of much of the research, plant behavior, as mentioned earlier, was also the subject of study (Mancuso, S., 2019). Considering that one of the first researchers to be interested in plant mimicry and behavior was Jean-Baptiste Pierre Antoine de Monet de Lamarck (1744-1829), considered by many as a pioneer of modern biology; it is important to highlight that Lamarck sketched a notable interest in the mechanism of leaf closure of Mimosa pudica (Mancuso, S., 2019), for which he devoted a long period of time in the search to understand how this mechanism could operate. This question remained devoid of a clear and consensual scientific explanation for decades. In addition to Lamarck, Charles Darwin was also interested in the behavior of Mimosa pudica, arguing that it was a plant that resembled animals (Darwin, C., 1875). Other pioneering cell biology scientists also dedicated themselves to describing the behavior of Mimosa pudica (Parise, A., 2017). These seminal studies already suggested that plants, like animals, have an innate behavioral repertoire. However, plant mimicry remained for a long time as a little-known dimension of the expression of life.

Only in more recent periods, studies have raised the question that plants, like animals, can learn through experience. For example, in his book "What a plant knows: A field guide to the senses", Chamovitz (2012) presents an overview of plant senses and behaviors, including the ability to learn through experience. Gagliano et al. (2014) reported a study in which plants demonstrated the ability to learn and remember important information for their survival. According to the authors, plants learn faster and forget more slowly in environments where this is essential. In another study, Gagliano et al. (2016) reported that plants demonstrated the ability to learn through association between stimuli. Although there are significant differences between organisms, there may be similar mechanisms between plants and animals that still need to be evidenced and understood (Baluska & Mancuso, 2013). Communication mechanisms, defense strategies, and other learned behaviors may present similarities between animals and plants. However, comparative works are recent and scarce. This problem, when addressed, may potentially enable a better understanding of the most elementary mechanisms of memory, learning, and adaptation. Considering that studies on plant mimicry point to the most elementary processes of mimicry, something that ultimately can broaden the current understanding of learning and memory, supports the understanding that learning exists a priori, as a skill expressed by living organisms (KARBAN, 2015). Based on the above, the objective of this work is to conduct a narrative review of the literature on the mechanisms of mimicry and plant behavior. We reviewed the current literature on memory and learning processes in plants, highlighting the latest findings and discussing their relevance to science.

2 ELECTRICAL SIGNALING IN PLANT CELLS

Burdon and Sanderson (1873), based on studies by Charles Darwin (1875) with carnivorous plants, described the existence of action potentials following stimulation of Dionaea sp. leaves, indicating that electrical signals do not belong exclusively to the animal kingdom (Williams & Pickard, 1980). A few years later, in 1926, Bose used isolated vascular bundles from a plant embryo to demonstrate that excitation can be transmitted as an electrical impulse, suggesting that this phenomenon could be controlled by physiological events similar to those that occur in animal nerves (BOSE, 1927). In 1930, action potentials (APs) were recorded with microelectrodes inserted into cells of Nitella sp. (Umrath, 1930). Bose (1927) was a pioneer in considering electrical signaling between plant cells in the coordination of a type of innate responsive behavior. Bose demonstrated that the movements in Mimosa and Desmodium leaves were stimulated by electrical signaling. Currently, four types of electrical potentials have been described in plants, which can mediate responsive

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behavior in plants, namely action potentials (APs), variation potentials (VPs) or slow wave potentials (SWPs), wound potentials (WPs), and systemic potentials (SPs). In 1984, voltage-dependent ion channels were discovered in plants, which are the basis for action potentials (SCHROEDER et al., 1984). Since then, one of the most important questions has been whether excitability in animals and plants has a similar set of ion channels as its basis.

According to Volkov et al. (2008), the induction of non-excitability after excitation and the summing of subliminal irritations were developed in protoplasmic structures in the plant and animal kingdoms before the morphological differentiation of nervous tissues. These protoplasmic structures fused into the organs of a nervous system and adjusted the interface of the organism with the environment. Some neuromotor components include acetylcholine neurotransmitters, the cellular messenger calmodulin, cellular motors actin and myosin, voltage-dependent ion channels, and sensors for touch, light, gravity, and temperature (Taiz & Zeiger, 2017). As in animal nerves, a simple neural network was formed within the plasma membrane of a phloem or plasmodesmata, allowing it to communicate efficiently over long distances. The reason why plants developed pathways for the transmission of electrical signals is likely due to the need to respond rapidly to environmental stress factors (BALUSKA et al., 2006). Different environmental stimuli evoke specific responses in living cells, which have the ability to transmit a signal to the response region. In contrast to chemical signals, such as hormones, electrical signals are capable of rapidly transmitting information over long distances. Electrical potentials have been measured at the tissue and whole-plant levels.

3 PLANT MEMORY AND ITS MECHANISMS

Memory is a fundamental capacity that allows organisms to store information about the state of the environment at a given moment and access it later. Plants, like animals, are capable of forming and maintaining memories, and these memories can influence their future behavior. Studies on plants have demonstrated memory storage and retrieval functions, indicating that memory plays an important role in plant behavior (Biju Kumar, 2016). Plants have biological clocks and circadian rhythms that involve electrical elements of memory (Dodd & Webb, 2019). The circadian clock in plants is light-sensitive, while circadian rhythms respond to electrical stimulation, which resets every phase of the light-dark cycle (Tamaoki & Karahara, 2018). Leaf opening and closing in many plants follow a circadian rhythm of approximately 24 hours (Tamaoki & Karahara, 2018). Studies on Mimosa pudica have demonstrated that this plant is capable of memorizing the time intervals separating day and night (ADAMEC, 1998). After a learning period, the circadian rhythm of Mimosa pudica was observed even when kept in continuous darkness (Adamec, 1998). Additionally, leaf closure after physical stimuli in Mimosa pudica is regulated by electrical signals, and the mechanics of the movements are regulated by the pulvinus, an organ located at the base of the leaf responsible for its motility (Volkov, Carrell, Adesina, Markin, & Jovanov, 2013).

It has been demonstrated that if a persistent stimulus occurs, i.e., if the plant is repeatedly touched shortly after the leaves open, it stops the response of closing the leaves (VOLKOV et al., 2013). This characteristic was initially related to a process of exhaustion (PARISE, 2017). However, another hypothesis emerged, indicating a memory process related to the behavior of closing and opening the leaves (ABRAMSON; CHICAS-MOSIER, 2016). This type of learning-mediated adaptation has led to the search for the underlying mechanisms of learning in plants. It has been suggested that memory resistors and capacitors could be a starting point for understanding memory mechanisms, learning, circadian rhythms, and biological clocks in plants (VOLKOV, Alexander G. et al., 2014). Memristors are memory circuit elements whose properties depend on the system's history and state (CHUA, Leon; SBITNEV, Valery; KIM, Hyongsuk., 2012). Evidence indicates that plant tissue has the ability to form different types of memory, including sensory memory, short-term memory, and long-term memory (VOLKOV, Alexander G. et al., 2008). In animal tissues, there are fundamental differences in the mechanisms related to different types of memory. Long-term memory, unlike short-term memory, involves gene transcription, synaptic strengthening, and dendrite growth. This raises the question of what modifications occur in plant mnemonic tissue as a result of experience in interacting with the environment.

4 MEMORY MEMRISTORS

Memory memristors are electronic devices that store information through variations in electrical resistance. In plant physiology, plant memristors are based on the ability of plants to store information in their cellular structure. Plants can store information through physical and chemical changes in their cells, which alter their electrical resistance (BALUŠKA et al., 2006; MASI et al., 2009). Plant cells consist of a cell wall, a plasma membrane, and a nucleus. The cell wall is the outermost layer, which gives shape and rigidity to the cells. The plasma membrane is the layer that separates the cell's interior from the external environment. The nucleus is the control center of the cell, containing the plant's genetic material.

Plant memristors are located in plant cells and function by altering the cells' electrical resistance in response to environmental stimuli. According to studies conducted by Baluška et al. (2006) and Masi et al. (2009), plant cells can store information through physical and chemical changes in their cells that alter their electrical resistance.

These changes in electrical resistance can be caused by environmental stimuli such as light, temperature, humidity, and nutrients. For example, studies show that plant cells can store information about nutrient availability in the soil, adjusting their electrical resistance in response to these stimuli (BALUŠKA et al., 2006; MASI et al., 2009).

Moreover, for plants to conserve memory through plant memristors, there must be continuity in the environmental stimulus that caused the change in the cell's electrical resistance. If the stimulus is interrupted, the cell may return to its original state of electrical resistance (BALUŠKA et al., 2006; MASI et al., 2009). Plant memristors play an important role in plant learning, allowing them to store information in their cells through changes in electrical resistance. This ability to store information is crucial for plants to adapt to their environment and survive under variable conditions (BALUŠKA et al., 2006; MASI et al., 2009).

5 EPIGENETIC MEMORY

Epigenetics is a branch of biology that studies the interaction between genes and their products that lead to the formation of the phenotype. It focuses on mitotic and/or meiotic heritable changes in gene expression patterns that occur without alterations in the DNA sequence. These changes can be influenced by external factors such as environmental conditions and can lead to modifications of chromatin, affecting both DNA and histone proteins. Understanding epigenetics has significant implications for developmental biology, medical genetics, and evolutionary biology (BERGER et al., 2009). Epigenetic studies often focus on chromatin chemical modifications, such as DNA methylation and post-translational modifications of histone proteins, which can lead to activation or repression of gene expression. In plants, epigenetics has been associated with various processes such as development, response to environmental stresses, and regulation of gene expression (Chinnusamy and Zhu, 2009). Additionally, epigenetics may also be related to learning and memory processes in plants (WU et al., 2010).

The ability of learning and memory in plants was initially demonstrated through experiments with the movement of Mimosa pudica leaves in response to repeated stimuli.

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This adaptive response was suggested as a mechanism of learning and memory in plants, which may be mediated by epigenetic alterations (GAGLIANO et al., 2014). Recent research has identified various epigenetic mechanisms involved in gene expression regulation in plants during learning and memory. For example, DNA methylation and histone modification have been associated with gene expression regulation in plants subjected to repeated environmental stimuli. Additionally, the role of small RNAs in gene expression regulation in response to environmental stimuli has been widely studied in plants (Ma and Chen, 2012).

Therefore, epigenetics may be directly related to learning and memory processes in plants, and understanding these mechanisms may have important implications for agriculture and plant adaptation to climate change. It is important to continue investigating the interaction between epigenetics and learning and memory in plants to better understand the biology of these organisms and develop strategies to improve their productivity and resistance to environmental stresses.

6 INTELLIGENCE IN PLANTS

According to Trewavas (2005, p. 414), plant intelligence can be characterized by adaptively variable growth and development during the individual's lifetime, resulting in intelligent behavior as an aspect of the complex adaptive behavior that enables problem-solving. In turn, Brenner et al. (2006, p. 413) define plant intelligence as the intrinsic ability to process information from biotic and abiotic stimuli, allowing decision-making about future activities in a given environment.

Plant Neurobiology has raised debates about the existence of cognition in plants, an issue of great importance. The assertion that plants have cognitive abilities is not new, as Charles Darwin, in 1880, in his work "The Power of Movement in Plants," declared that the root apex functioned as a diffuse brain, similar to the brain of lower animals, suggesting the existence of a system for processing and storing information in plants (GAGLIANO, 2014).

In this context, memory memristors have been pointed out as important components in the learning and memory capacity of plants, being able to store information through physical and chemical changes in their cells (Volkov, 2021). Located in various parts of the plant, such as roots, leaves, and flowers, these electronic devices alter their electrical resistance based on the amount of electrical current passing through them, allowing for the variation of stored information (Volkov, 2021).

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In order for plants to be able to retain memory, changes in their cells need to occur, which can be triggered by environmental stimuli such as light, temperature, humidity, and nutrients (Foa & Mondino, 2021). These changes can lead to alterations in the electrical resistance of memristors, enabling the creation of a kind of "electrical memory" that can be used in solving future problems (Volkov, 2021). Therefore, the understanding of cognitive processes in plants and their relationship with memory memristors is a rapidly evolving field and has significant importance in comprehending the adaptive behavior of these organisms in different environments.

7 ON THE COMMUNICATION AND BEHAVIOR OF PLANTS

The findings of plant neurobiology demonstrate that plants are capable of communicating and interacting with their surroundings in complex ways, through chemical and electrical signals. This helps to explain how plants adapt and respond to changes in their environment and may lead to new techniques for optimizing plant growth.

Improvements in agricultural production: Understanding how plants respond to their environment can help improve agricultural production, for example, through the development of more precise and sustainable cultivation techniques with lower use of water and fertilizers.

Impacts on environmental conservation: Plant neurobiology can also inform environmental conservation by showing how plants respond to changes in their environment and how habitat degradation can affect these responses. This can help guide conservation and restoration efforts, especially in threatened ecosystems.

Benefits for human health: Some compounds produced by plants have medicinal properties, and by better understanding how plants produce these compounds, we can better explore these benefits for human health.

8 CONCLUSION

In summary, associative learning is fundamental for the development of adaptive behavior in organisms, allowing the acquisition of new ways of behaving and adjusting to variable environmental conditions. Although initially associated with animals, associative learning can also be found in other life forms, such as plants. The work of physiologist Ivan Pavlov, with classical conditioning, was crucial for the study of associative learning in animals. Plant intelligence is a demonstration that natural life is characterized by continuous interaction of organisms with multiple events that bring uncertain consequences, and the

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intrinsic ability of plants to process information from biotic and abiotic stimuli allows for decision-making about future activities in a given environment. Associative learning appears as an essential component of plant behavior, representing an adaptive mechanism shared by animals and plants. Studies in neurobiology have been describing the neural and molecular bases of memory formation in animals. However, less prominent advances are observed regarding the mechanisms underlying memory in plants. In this context, plant neurobiology emerges as a field of study that aims to investigate the biochemical basis of learning and behavior in plants. In summary, the discussion about the existence of plant intelligence and the occurrence of associative learning in plants and animals raise questions about the limits of intelligence. The implications of these findings could help to better understand the evolution of life on Earth. Future research can explore these important questions.

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DECLARATIONS

Conflict of interest The authors declare that they have no conflict of interest.
Informed consent Informed consent was obtained from all individual participants included in the study.
Ethics approval The authors declare that the present research did not involve any experimentation on humans or animals.
Author's contribution
Authors also contributed to the manuscript.

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