

Signaling and Communication in Plants

Frantisek Baluska · Monica Gagliano
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Memory and Learning in Plants

 Springer

Signaling and Communication in Plants

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Preface

Plants are very complex organisms which use a suite of plant-specific sensory systems to monitor all relevant parameters, both abiotic and biotic, to optimise their metabolism, growth, development, morphogenesis and behaviour in their environment. Because plants are sessile organisms, cognitive processes such as learning, memory and decision-making are essential to enable them to cope with various environmental cues and certainly critical to their survival and reproductive success. Despite this, plants have been conventionally studied as stimulus–response mechanical systems devoid of cognition and behaviour. This volume is part of a series of recent books introducing an alternative perspective to this conventional approach on plants. From this perspective, plants are no longer marginalised into a position of lesser status and capacity but recognised for the complex behavioural repertoire they exhibit, which reveals remarkable cognitive competences. From this perspective, plants are indeed *cognitive* organisms because they are able to consolidate the wide range of sensory inputs collected by the perceptual system into a common signal that activates their body to generate plant-specific behavioural responses. By bringing together under one book cover various inputs from academic environments that span from ecophysiology, chemistry, genetics, behavioural ecology and evolutionary biology to psychology and philosophy, this volume attempts to consolidate this rapidly growing and renewed understanding of plants in order to generate a new engagement with the vegetal world as well as instigate fresh research approaches which are open to (re-)evaluate the significance and meaning of concepts such as memory, learning, intelligence and awareness across systems.

It must be said that the idea that plants exhibit complex and flexible behaviours that entail cognitive processes is not new. In fact, Charles Darwin himself had acknowledged the cognitive sensitivity of plants when he proposed that the tip of plant roots acts like the brain of some animals (i.e. the “root-brain” hypothesis). The latest research corroborates the earlier Darwinian insights and demonstrates that plants do behave and most of their behaviours are adaptive, thus ensuring their survival. For example, roots navigate through soil, spanning large distances and actively modifying their adjacent surroundings via biocommunication, i.e. active

exudation and modification of the rhizosphere in close cooperation with a large number of microorganisms and allied fungi. One single plant can have up to hundreds of these coordinated root apex-based Darwinian plant-specific brains, which are in a perfect position to perform parallel communication to provide sense of self and agency to the whole plant. This allows plants to store information about their past experiences and thus have an actively generated background of information about the state of the system at a given time, which can be accessed at a later time to compare and evaluate more recent experiences and respond better or faster in the future. Both memory and learning depend on a variety of successful communication processes within the whole organism. Various studies, including those mentioned in some of the chapters in this book, suggest that epigenetic-related mechanisms could play a key role in plant learning and memory. Epigenetic modifications are essential for the response to the environment at both somatic and transgenerational levels. The latter is especially important for the immediate plant survival and for the long-term adaptation to adverse conditions. As suggested in this volume, plants may also have different forms of memory such as sensory, short- and long-term memory. Besides chemical and molecular memory, electric memory in the form of memristors is also emerging as a possibility in plants.

Clearly, plants have neither an animal type of nervous system nor brain, and thus, the mechanisms for coordinating perception and behaviour must be quite different from the mechanisms present in animals. Nevertheless, plants are faced with the same basic challenges as animals and have evolved ways to interpret the information from their environment to solve them. As the editors, we hope the diverse contributions that constitute this volume will inspire readers to ask some of the long-standing questions as well as new ones and, most importantly, pursue their answers.

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Contents

Memory and Learning as Key Competences of Living Organisms	1
Guenther Witzany	
Deweyan Psychology in Plant Intelligence Research: Transforming Stimulus and Response	17
Ramsey Affifi	
General Issues in the Cognitive Analysis of Plant Learning and Intelligence	35
Charles I. Abramson and Paco Calvo	
Plant Cognition and Behavior: From Environmental Awareness to Synaptic Circuits Navigating Root Apices	51
František Baluška and Stefano Mancuso	
Role of Epigenetics in Transgenerational Changes: Genome Stability in Response to Plant Stress	79
Igor Kovalchuk	
Origin of Epigenetic Variation in Plants: Relationship with Genetic Variation and Potential Contribution to Plant Memory	111
Massimiliano Lauria and Vincenzo Rossi	
Plant Accommodation to Their Environment: The Role of Specific Forms of Memory	131
Michel Thellier, Ulrich Lüttge, Victor Norris, and Camille Ripoll	
Memristors and Electrical Memory in Plants	139
Alexander G. Volkov	
Towards Systemic View for Plant Learning: Ecophysiological Perspective	163
Gustavo M. Souza, Gabriel R. A. Toledo, and Gustavo F. R. Saraiva	

Mycorrhizal Networks Facilitate Tree Communication, Learning, and Memory 191
Suzanne W. Simard

Inside the Vegetal Mind: On the Cognitive Abilities of Plants 215
Monica Gagliano

Index 221

Memory and Learning as Key Competences of Living Organisms



Guenther Witzany

Abstract Organisms that share the capability of storing information about experiences in the past have an actively generated background resource on which they can compare and evaluate more recent experiences in order to quickly or even better react than in previous situations. This is an essential competence for all reaction and adaptation purposes of living organisms. Such memory/learning skills can be found from akaryotes up to unicellular eukaryotes, fungi, animals and plants, although until recently, it had been mentioned only as a capability of higher animals. With the rise of epigenetics, the context-dependent marking of experiences at both the phenotype and the genotype level is an essential perspective to understand memory and learning in all organisms. Both memory and learning depend on a variety of successful communication processes within the whole organism.

1 Introduction

Memory skills are an essential feature of living organisms in all aspects of life. It serves as a key competence to better react to environmental circumstances, to better adapt and therefore to represent a crucial identity motif in biological selection profiles. Whether such memorized experiences are genetically fixed and heritable or remain epigenetically variable, memory plays crucial roles for the organism. Until the detection of epigenetic markings, memory was investigated in humans and higher animal species as part of the cognitive processes. Now we know the epigenetic markings are present throughout all domains of life, whereas the cognitive capabilities remain as a core feature of higher animals. Otherwise, we would extend anthropomorphic motifs and central nervous system features into nonanimal domains. Similar to brain-specific capabilities that do not represent cognition, but sub-cognitive features such as sensing, monitoring, interpretation (comparison and

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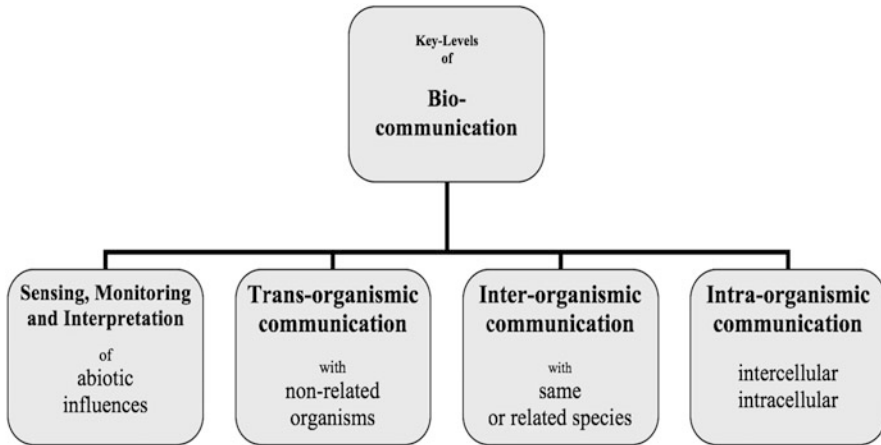


Fig. 1 Memory and learning and its basics, i.e. epigenetic markings, in all organisms of all domains of life depend on complex communicative interactions at several levels of biocommunication

evaluation against stored background information) which can be found in all organisms also communication can be found in all domains of life.

Currently known epigenetic modifications depend on histone modifications—such as acetylation and deacetylation, methylation and demethylation, deimination, phosphorylation and dephosphorylation, isomerization, O-palmitoylation, ubiquitination and ADP-ribosylation—that determine the gene-expression processes. This represents a rich source of tools to mark experienced events of the organism on the genomic level.

Epigenetic markings of certain chromosome sections to target memory relevant modes are essential for different identities of molecule groups, which represent the memorized identity as a kind of “frozen picture” of the total sum of biocommunication processes of an organism in an epigenetically relevant situational context. This means that the epigenetic marking of, for example, extraordinary stress situations—which activate all body parts and their dynamic interactional motifs represented in cells, tissues and organs—takes the “informational content” as the given relevant evaluation for imprinting processes (Fig. 1).

But to evaluate or interpret memory, certain molecular identity groups must play relevant roles within the organism. This means they must trigger a different communication to the interconnected cellular tissues than the previous state where certain memory markings did not exist. If we look at the currently known facts on how organisms store experiences as a memory tool to learn how to better react and quickly adapt within the best energy-saving strategies, we can investigate an abundance of chemicals that serve as signalling molecules for coordination and organization of behavioural patterns. This means that not only memory and learning but all coordination and organization processes in organisms are the result of communicative interactions between cells, tissues and organs (Witzany 2010, 2011, 2012, 2014, 2017; Witzany and Baluška 2012; Witzany and Nowacki 2016). In this respect, the

cellular coordination and organization of memory and learning processes are part of a broader realm of the whole communicative interactions in and between cells, tissues and organs of an organism.

If communication processes fail, then coordination and organization such as in memory storing processes by epigenetic imprinting, evaluation by comparison between more recent experiences and the stored background information and changing reaction patterns according to environmental influences within the organism will not occur appropriately. Additionally, this will have consequences for the communication of the individual organism with organisms of the same or related kind or between organisms and non-related organisms.

2 Memory and Learning in All Domains of Life

Why is memory and learning so essential for living organisms in general? And how did these capabilities and techniques of memory and learning—as a result of appropriate interpretation, i.e. comparison of experiences with memorized information and evaluation—emerge?

If we look at evolutionary history, we can identify common patterns that remained the same since the beginning of life, even since the beginning of the RNA world and, later on, cellular life forms. The Darwinian principles of variation and selection are embedded into an unforeseeable environmental dynamics. Such abrupt or long-lasting changes due to climatic, geophysical and gravitational reasons and their interconnections with the environmental life world ecospheres are a characteristic of animated planets. With the advent of RNA world/living organisms, the constant and continued competition for resources needed for survival started as a predominant factor of evolution and adaptation (Atkins et al. 2011).

In addition to abiotic factors that determine evolutionary history in all domains of life, also biotic factors, i.e. behavioural motifs, play essential roles such as competition, cooperation, mating, attack and defence. Besides, we must not forget that each organism is sometimes focused on individual problems within its body such as damage or disease, which may strongly determine its behaviour.

Since the rise of RNA world concepts and the basic knowledge about the roles of viruses and subviral RNAs as genetic parasites and mobile genetic elements (in formatting the gene word order and the roles of non-coding RNAs in the genetic regulation at all stages of cellular processes), we know the importance of group behaviour, group identity and the capability to differentiate between self and non-self to cooperate or to ward off competing biotic agents (Villarreal 2009a, b).

Although memory of experiences seems to be a natural capability of organisms, they usually belong to a complex life world where they communicate with members of the same kind or related organisms. Additionally, the variety of symbiotic and even symbiogenetic interactions demonstrates communicative interactions with non-related organisms. These life-world specific and highly context-dependent

interactional patterns are the main resources of memory aspects within the interacting organism.

Flexible genome markings are the precondition of fixing content identity on the genetic level and their regulatory tools, respectively (Slotkin and Martienssen 2007). Certain environmental circumstances, caused by abiotic influences or by biotic agents, may influence the epigenetic storage of such events (Talbert and Henikoff 2014). One best known event is stress situations that cause a different methylation pattern or histone modification, respectively (Santos et al. 2017). But prior to cellular life in the ancient RNA world too, cooperation of RNA stem loops provided the first capability to store information as the starting point of biological memory, by replicating RNA species as recently demonstrated (Urtel et al. 2017).

2.1 Memory: Context-Dependent Information Storage

Besides the flexible epigenetic markings that are not part of heritable information transfer, transgenerational immune memory (siRNA, RNAinterference, CRIPRs/Cas) indicates that genetic parasite invasions that are warded off by the immune system will modify and mark those invasive genetic identities to be transferred as memory content via heredity to the offspring.

From the beginning of nucleic acid sequence-based entities on this planet, the behavioural motif of genetic parasites is the driver of constant interactions—whether it be RNA viruses or similar RNA stem loop groups that are in constant interactions with other invading genetic parasites that must be identified, integrated as cooperative parts or warded off (Vaidya et al. 2012). Additionally, this interaction profile means identity problems to the RNA group, because it changes the genetic identity of the RNA group as well as that of the invaded agent (Villarreal and Witzany 2015). This may be disastrous if the former identity was successfully fixed and now may become irrelevant for the host organism, because the function cannot be continued. The new sequence order has to be identified as invasive species and as the relevant target to be warded off (Lambowitz and Zimmerly 2011). On the other side, this flexibility in identity features may cause the rise of a new and unexpected invasive agent identity, being a successful invader of formerly immune hosts (Villarreal 2012). This feature hints at a core feature of life and biotic planets: the constant and continued capability of RNA groups to resist or integrate novel genetic parasites, which drives (i) immune systems, (ii) genetic identities of host organisms and additionally (iii) genetic parasite identities in parallel.

2.2 Learning and Interpretation

If an organism in real-life world context with its unique evolutionary and developmental history and identity is able to mark certain genetic setups that represent an

environmentally determined specific replication pattern or transcription process, then memory is the result. Memory marks a certain experienced event or multiple similar events to enable this organism to faster and/or more appropriate reaction, if similar situations occur. This capability for better reaction may be termed successful “learning” of the organism based on this stored background information. The organism must differentiate between situations of the same structure without memory and with memory and then be able to evaluate the memory against stored background information. This evaluation process may be termed “interpretation”, as stored information leads to “learning”, i.e. changing behavioural motifs such as faster/more appropriate reaction to similar real-life experiences. Evaluation of past experiences and comparison with present ones may lead to variable sensing, monitoring, evaluating and making decisions with far-reaching and differentiated consequences. In the long run, biological selection processes will lead to populations who represent an optimized memory/learning/interpretation competence.

3 Memory and Learning in Viruses and Subviral RNA Networks

For a long time, viruses have been considered as molecular invaders unable to replicate themselves. Meanwhile, it is more and more accepted that viruses have an abundance of genes not found in any cellular organism and are therefore older than cellular life. Several researchers have found that viruses, subviral networks and virus-derived parts (such as non-coding RNAs and mobile genetic elements) that are co-opted for host cellular needs play major roles in evolution and development of host organisms (Hayden and Lehman 2006; Smit et al. 2006). Interestingly, short (miRNAs and siRNAs) and long non-coding RNAs and their derivatives, which can function as epigenetic marks of transcriptional gene silencing, also serve as defence tools against transposable elements and viruses (McKeown and Spillane 2014).

Some researchers are of the opinion that the whole genetic content order of cellular organisms is determined by and regulated through such viral and subviral (defective) competencies (Villarreal 2005, 2015). This is because all viruses mark their genomes for self/non-self differentiation, e.g. the virus-first hypothesis suggests that epigenetic markings are transferred to cell-based organisms as infection-derived key competence of viruses that lead to innate and adaptive immune systems in all domains of life, which have been exapted for host purposes (Villarreal 2009a, 2011).

More recently, it was found that even viruses communicate via small peptides and are therefore able to commonly coordinate interactions. More concrete, some phages make decisions whether they should develop into a lytic pathway or choose a temperate (persistent) lifestyle. This communication system strongly influences the decisions of their descendants and may become relevant for epigenetic markings within the phage as well as within the invasion target (Davidson 2017; Erez et al.

2017). All of these features indicate an amplification/suppression system, which is regulated via epigenetic methylation patterns (Villarreal 2009b).

4 Memory and Learning in Akaryotes

Bacteria as well as Archaea, with their different evolutionary histories, are “small but not stupid” (Shapiro 2007). Akaryotes communicate and are therefore able to organize and coordinate their behaviour similar to a multicellular organism (Losick and Kaiser 1997; Schauder and Bassler 2001; Ben Jacob et al. 2004). They continuously monitor and sense their environment and their internal processes such as metabolism, protein regulation, immunity and DNA repair status (Shapiro 2007). Additionally, they are highly competent in cell-cell communication within akaryotic swarm behaviour such as quorum sensing (and quorum quenching) for colonizing biotic or abiotic surface structures and are highly coordinated in complex attack and defence strategies. Also, they have to interact on a transorganismic level with a variety of symbiotic partnerships, being essential for both, such as documented for rhizobacteria within the root zone of plants.

All this coordinated behaviour, as well as biofilm organization that is possible based on signalling within and between akaryotic cells to coordinate and organize, needs some memory system to which actual circumstances can be compared and evaluated as being more relevant to react or represent less priority (Mathis and Ackermann 2016). This leads us to epigenetic imprintings within the akaryotic cell which stores environmental experiences, which are then part of an internal evaluation and also the interpretation system in a simple sense (Casadesús and Low 2006; Oliverio and Katz 2014).

At the origin of such epigenetic imprintings in akaryotes, it is known that these are restriction modification systems, successfully investigated by Kobayashi and his team (Kobayashi 2001; Mruk and Kobayashi 2014). Later on, it was detected that the restriction modification system is a system of counterbalanced, persistent viral infection-derived capabilities, defending the host organism from related genetic parasites. A similar defence system has been found more recently—the CRIPRs/Cas system—which indicates another counterbalanced immune system that is inherently more adaptive and therefore represents an immune function that stores information of viral attacks in a more context-dependent way to ward off genetic parasites that are now memorized more specifically.

5 Memory and Learning in Unicellular Eukaryotes

Unlike the akaryotes, which have highly sophisticated capabilities to communicate, i.e. to generate sign-mediated interactions for various goals and are therefore able to coordinate their single lives within populations like that of a multicellular organism,

we can find a more complex behaviour in unicellular eukaryotes also throughout all species. Very good examples can be found in ciliates, where the knowledge about signalling within the ciliate body has been investigated by many research groups (Witzany and Nowacki 2016).

In contrast to akaryotes, in ciliates, the division of labour between the soma and germ line functions is strictly divided, which indicates a different evolutionary ancestor of the two nuclei of ciliates. In unicellular eukaryotes, we are confronted with the evolution of the eukaryotic nucleus and the genetically fixed symbiogenetic integration of various formerly free living akaryotes. The Serial Endosymbiotic Theory (SET) of Lynn Margulis explains the origin of nucleated eukaryotic cells by a merging of archaeobacterial and eubacterial cells in anaerobic symbiosis, historically followed by acquisition of mitochondria or plastids (Margulis 1996). In contrast to former evolutionary theories which consider ramification as a driving force of evolution, Margulis initiated a paradigmatic change, bringing merging into the focus of the discussion. But the use of terms like “merging”, “fusion”, “incorporation” and “amalgamation” is less helpful if we look at the genetic level in symbiogenetic processes (Witzany 2006). If symbiosis leads to symbiogenetic processes, to the development of a new species and thus to the disappearance of the formerly independent individuals, then the result is generative DNA processing, in which genetically different gene pools are combined into one genome. This requires a recombination that assimilates the non-self data set into a “self”, converting the external into the internal. This also means the epigenetic markings must be adapted.

Which genome editing competences are able to integrate an endosymbiotic genome in a host genome? Manfred Eigen would ask how we should think about the correct rearrangement of the “molecular syntax” (Witzany 1995). Successful DNA/RNA processing requires numerous, specifically tailored enzyme proteins. In all cases, the DNA/RNA-processing enzyme proteins and also the interacting RNAs together with the epigenetic markings are involved in very precisely conducting these varied DNA-processing steps.

The ciliate epigenetic imprinting is a main source of memory storage and learning to quickly and more appropriately react to changing environmental circumstances (Nowacki and Landweber 2009). In limited nutrition environments, the better reaction modus may lead to the more successful survival strategy. Also, in other unicellular eukaryotes, non-coding RNAs play essential roles in gene regulation and its epigenetic marking. Remnants of former infection events by genetic parasites, such as transposable elements, are exapted, i.e. used and integrated in another function than when previously active. In this respect, we may look at exaptation of the small nuclear and nucleolar RNAs (snRNAs and snoRNAs) to regulate cellular genes and in parallel to mediate transgenerational epigenetic inheritance of essential phenotypic polymorphisms (Singh et al. 2014).

6 Memory and Learning in Fungi

Epigenetics of fungal organisms may be investigated as reversible heritable changes in gene expression without changes in DNA sequence. This refers to gene regulation such as changes in the chromatin structure, although such changes are not necessarily heritable.

Development and growth of fungal organisms depend upon successful communication processes within, and between, cells of fungal organisms. However, on the other side, sign-mediated interactions are necessary to coordinate behaviour with the same, or related, fungal species and with non-related organisms such as bacteria, plants and animals. In order to generate appropriate response behaviour, fungal organisms must be able to sense, memorize, and interpret indices from the abiotic environment as well as from the ecosphere inhabitants and react to them appropriately. However, these communication and interpretation processes can also fail. In such cases, the overall consequences could be disease-causing or even lethal for the fungal organism. Interestingly, certain rules of fungal communication are very similar to those of animals, while others more closely resemble those of plants.

Fungi are heterotrophs. This means they feed by absorbing dissolved molecules. Prior to that, they must, therefore, secrete digestive enzymes into their environment. In contrast to plants, fungi do not photosynthesize. Their mobility occurs by growth, or in the case of spores, they dissipate through air or water. Fungi serve as the main decomposers in ecosphere habitats. As with animals and plants, seasonality is found in fungi as a part of the circadian rhythm (Dunlap and Loros 2004), e.g. light-regulated physiological processes that coordinate the internal fungal clock, which relies on epigenetic markings as the memory system (Aramayo and Selker 2013; Kronholm et al. 2016).

Because fungi seem to represent less complex multicellular eukaryotes (they also have single-celled species), they have to coordinate a rich signalling repertoire within the fungal body, between fungi and related organisms and between fungi and non-fungal organisms. For all of these coordinations, it is essential to produce signalling molecules. The most powerful tool to have access to the rich chemical vocabulary of fungi is epigenetic silencing for regulating the production of semiochemicals. Because fungi can reach tremendous size and life span, it can be expected that the epigenetic memory storage in fungi is rather specialized and will promote life-saving interactions and suppress dangerous or life-damaging causes (Cichewicz 2012).

Especially, symbiotic interactions in the root zone of plants are multilevel communication processes between various plant root cells, mycorrhizal fungi and rhizobacteria in a highly complicated and dynamic process in which memory, learning, interpretation and the organization and coordination of variable reaction motifs are essential tools for optimal symbiotic interactions. In this respect, memory and learning of participant organisms are involved and co-dependent on each other. This means if one or more communicating patterns or epigenetic disturbances are indicated, this will have far-reaching consequences for all participants of the whole symbiotic interaction.

7 Memory and Learning in Animals

With the evolutionary invention of the animal central nervous system and the brain organ with its neuronal interaction complexity, a new kingdom arose with a really complex intraorganismic communication competence. The linear information processing in animals strengthens the central nervous system's decision making. In contrast to communicative interaction patterns of viruses, akaryotes, protozoa, fungi and plants, animals use vocal and visible signs to communicate.

Accordingly, the epigenetic marking of experiences in memory formation increases in neuronal patterns (Mercer et al. 2008; Sacktor and Hell 2017). Epigenetic imprintings such as DNA methylation, histone modifications and micro-RNA processing with changes in gene expression according to concrete and context-dependent activities are the main source of memory formation patterns (Barlow 2011). The learning process results out of comparison of concrete interactional situations with the background of memorized informations, which may lead to sustained behavioural change. A second point is passing epigenetically memorized information across generations, which means the acquired information that is memorized will be object to inheritable transport (Blaze and Roth 2013).

In contrast to other kingdoms, animals, in most cases, share a mobility which is not found in any other kingdom (Witzany 2014). This makes them vulnerable to a geometric increase of experiences, even for their symbionts or attack enemies. Another interesting aspect is that simple animals, such as *C. elegans* and *Homo sapiens*, share a similar number of protein coding genes, whereas the non-coding regulatory RNA makes the complete difference. Interestingly, the basic memory storing processes in animals (from insects to humans) are comparable within the general concept of cognition (Menzel 2012; Biergans et al. 2016).

8 Memory and Learning in Plants

Plants have often been viewed and studied as machine-like growth automatons. Today, we know that the coordination of development and growth in plants is made possible only by the use of sign(al)s, rather than by pure mechanics. Plants are sessile, highly sensitive organisms that actively compete for environmental resources, both above and below the ground. As do all living organisms, they must assess their surroundings, estimate how much energy they need for goals and then realize the optimum variant. Similarly, they must take measures to control certain environmental resources; as it has been shown that they perceive themselves and can distinguish between self and non-self (Trewavas 2003, 2005), this capability allows them to protect their territory and ward off parasites.

More than 20 different groups of molecules having communicatory functions have currently been identified, and up to 100,000 different substances—known as secondary metabolites—are actively used in the root zone. Such diversity, as it has

been proposed, is necessary due to the high abundance of microbes, insects and related or non-related plant roots in this zone and all the interactions made necessary thereby (Bais et al. 2004; Badri et al. 2009). Integration of signalling molecules into coordinated sensing, production and release is highly complex and must be regulated in a precise, timely manner. This is epigenetically imprinted and regulated (Pikaard and Mittelsten Scheid 2014; Matzke et al. 2009, 2015; Birnbaum and Roudier 2017).

More recently, the youngest of all kingdoms is also in focus in research about capabilities which were formerly restricted to higher animals. Although several features of plants such as plant epigenetics, attack and defence mechanisms as well as mating have been observed to change in certain timescales with the change of environmental circumstances such as abiotic stress or new enemies, memory and learning of plants were not the predominant investigation focus (Boyko and Kovalchuk 2011; Baulcombe and Dean 2014; Haak et al. 2017; Rajewski et al. 2017). Especially the epigenetic marking of stress experiences is well documented (Grativol et al. 2012; Gutzat and Mittelsten-Scheid 2012; Lämke and Bäurle 2017).

Some features in heredity demonstrated that plants have the skills to store genetic information on different levels with different evaluation patterns, which indicate some behaviour motifs of interpretation of incoming information and some sort of choice between variable options.

Plants can, for instance, overwrite the genetic code they inherited from their parents and revert to that of their grand- or great-grandparents (Lolle et al. 2005; Pearson 2005; Weigl and Jürgens 2005). This contradicts traditional DNA-textbook conviction that children simply receive combinations of the genes carried by their parents. Now we know that plants are able to replace less appropriate parental code sequences with the regular code possessed by earlier generations—not the inherited parental sequences are translated and transcribed but the backup copy of grand- or great-grandparents. Under normal conditions, the operative genetic make-up stems from the parents. This means, not only a combination of parental genes is inherited but also ancestral genome regulating features in non-coding DNA.

More recent advances in studying memory skills of plants on the genetic level demonstrated that memory is initiated by binding of a transcription factor, leading to essential changes in the chromatin structure and allowing binding of a poised form of RNA polymerase II to promote the rate of future reactivation (D’Urso and Brickner 2017). Communication of plants is not only triggered by chemical compounds for signalling. Most interestingly, more recent experiments demonstrated that plant roots react to sound input also (Gagliano et al. 2017).

8.1 “Communicative Identity” in Plant Behaviour

The capabilities of plants to store information representing experiences and learn by comparing and evaluating the stored experiences with more recent events raise the question of “cognition”-like capabilities of plants, with possible connotations such as “mind” or even “consciousness” of plants. Besides, in humans, the cognition

debate is struggling, because scientific descriptions, in many cases, confuse scientific sentences (to describe observations in the realm of theoretical assumptions to reach a common agreement in highly specialized scientific communities) with an imaginary tool that could depict reality.

There is a clear reason why philosophy of consciousness was abandoned and was replaced by the philosophy of language: It was not possible to reach a satisfactory definition of consciousness for many centuries until today, because of inescapable problems of definition. The various consciousness concepts of the last centuries met the pre-assumptions of humans as they defined themselves. But with the success story of neurobiology, it became clear that the term consciousness is an anthropocentric construction to integrate the signalling interactions between several brain tissues in a unifying narrative. If some of the communication brain parts are deformed or damaged, consciousness looks rather strange, and the deficits in the different concepts of consciousness become obvious (Parvizi and Damasio 2001, 2003). For example, the generalizing term consciousness is like how we speak about the national character of, for example, Austria. But, Austria does not exist, except the 8 million people who coordinate and organize the Austrian lifeworld every day by communication processes that even may fail with unexpected consequences.

Because all quantitative models of communication—which are basically founded on hidden metaphysical assumptions (all-is-one holism or all-is-many atomism, physicalism, mechanism, e.g. “cellular machinery”)—did not function to coherently explain how two interacting biotic agents can reach a common agreement on how to commonly coordinate, the philosophy of consciousness was replaced by the philosophy of language in a long-lasting discourse between 1920 and 1980 (Witzany 1995, 2000). The quantitative methods ignored the results of this discourse, because they could not reflect their own hidden metaphysical assumptions and got stuck in the narratives of subject-object split or similar narratives (body-mind duality), such as sender-receiver (coding-decoding) models.

In the last decade, there arose a discussion about plant “cognition” or plant “consciousness”, because of their yet unknown capability for sensing, monitoring, learning, decision making, etc. (Baluška et al. 2006, 2010; Baluška and Mancuso 2009). Because all these capabilities critically depend on successful communication processes within the plant body, I would like to suggest some kind of “communicative identity”. This clearly differs from previous assumptions such as mathematical theories of language and communication, e.g. the game theory, but can be investigated as any behavioural coherence of communicative agents that have a historical identity and try to be successful in the main survival strategies, such as commonly reached coordination and organization (intraorganismic, interorganismic and transorganismic).

With “communicative identity”, someone can differentiate signal-mediated interactions on every level of every organism of every kingdom. Additionally, it looks at the primacy of context dependence and—most importantly—of group identity (to belong or not to belong, i.e. self/non-self identification competence), and it investigates all semiochemicals in detail and in general. Clearly, “communicative identity” is absent in abiotic matter. No living agents, no sign-mediated interaction

(communication) and no rules of sign use are present if water freezes to ice. A clear cut between living and non-living can be drawn here, from RNA groups up to humans.

In contrast to the game-theoretical definition as strictly selfish-orientated behaviour, meanwhile, we can assume that “communicative identity” means any behavioural coherence within the context of an ecosphere-specific real-life world. Because living organisms are no *solus ipse* entities, but, in most cases, interwoven in a social interacting network with same, related or non-related organisms, the communicative behaviour serves not only for selfish but essentially for common goals of participants of an ecosphere habitat with all its symbiotic repercussions.

9 The Emergence of Self/Non-self Differentiation Competence

In symbiotic processes, species-specific communication competence has to be adapted to trans-species communication processes, which means that symbiotic processes depend on adaptation to signalling codes that transgress species borders in most cases. Natural codes function if three levels of rules are followed: syntactic rules determine coherent combination of signals, pragmatic rules determine how code-using agents interact according to changing contexts, and semantic rules determine which meaning/information can be transported with signals.

As all more complex eukaryotes are colonized by symbiotic akaryote settlers that play vital roles for the benefit of their host, they must have adapted to the host ecology. This means they must be able to communicate within their population to coordinate, e.g. population growth, apoptosis, virulence, measurement, decision making, movement and election (quorum sensing), according to group signalling, which does not confuse similar molecules of other (non-self) communities. This seems rather difficult if we imagine, for example, 500 different bacterial species in the human oral cavity (Kohlenbrander et al. 2005). Besides, bacteria are overruled by viral settlers by a magnitude of 10 (Rohwer et al. 2014).

Obligate persistent viral settlers of bacteria (phages) that integrate into host genomes must be competent to integrate without damage of the genetic content order and benefit for host capabilities to adapt to fast changing environmental contexts. As viral settlers are obligate in all living organisms on earth, symbiotic interactions represent multiple code compatibility between viruses, akaryotes and eukaryotic hosts (Diaz-Munos et al. 2017). To guarantee a highly sufficient population-based communication to coordinate appropriate group behaviour, a competence to differentiate self from non-self is necessary.

In our context, this means that besides the epigenetic context, which is an essential tool for memory and learning capabilities, such contextual markings are also relevant for the reaction patterns on non-self organisms, even if they represent another species or even an organismic kingdom. The epigenetic marking of certain

reactions or general behavioural patterns may affect the epigenetic markings of the symbiotic cooperation partner also. We may look here at the complexity of globally interwoven interactions between organisms of the same, related or non-related ecosphere habitats.

10 Conclusions

Memory and learning are common features of all organisms throughout all domains of life. Additionally, the organization and coordination of memory and learning within the cells need basic motifs of communication—signal-mediated interactions—that coordinate a limited number of steps of epigenetic imprinting at various ways to fix memory relevant experiences of the organism either on the genetic/genomic level or even at the phenotypic level that does not remain as a heritable feature, such as most memorized contents in higher animals. Within the realm of the biocommunication perspective, memory and learning complete a broader realm of communication capabilities as basic characteristics of living organisms.

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