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Plant intelligence and attention

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This article applies the phenomenological model of attention to plant monitoring of environmental stimuli and signal perception. Three complementary definitions of attention as selectivity, modulation and perdurance are explained with reference to plant signaling and behaviors, including foraging, ramet placement and abiotic stress communication. Elements of animal and human attentive attitudes are compared with plant attention at the levels of cognitive focus, context and margin. It is argued that the concept of attention holds the potential of becoming a cornerstone of plant intelligence studies.

Introduction

Studies of plant intelligence have tended to concentrate on memory as a benchmark of intelligent behavior.^{1,2} Although memory has a bearing on all three modalities of time, including a remembered past event, the present of storage and the possibility of future retrieval, it is a marker of intelligence heavily biased toward the past. On the other hand, attention is a feature of intelligent conduct in the present, whereby an organism selectively responds to ever-shifting stimuli in a way that allows it to maintain adequate levels of adaptation to its environment. Before processing, evaluating and communicating information, plants must first attend to—or take note of—the bits that are relevant to their optimal growth and development. Attention's chronological precedence is matched in importance by its scope, insofar as attention accompanies all other components of intelligent conduct.

Attention as Selectivity

Attention in general is not reducible to the mental concentration that usually distinguishes this attitude in human beings. Rather, a cross-species and cross-kingdoms definition of attention I propose entails a disproportionate investment of physical or mental energy by an organism, tissue, or cell into a particular activity or into the reception of a singled-out stimulus or set of stimuli. Still falling short of a non-anthropocentric theory of attention, von Uexküll described how a relevant stimulus is noticed (*gemerkt*) by an animal subject, such that a portion of its environment is transformed into “perception signs” (*Merkzeichen*).³ In the course of this noticing, which stands for the most basic stratum of attention (*Aufmerksamkeit*: sharing, in German, the grammatical root with “noticing”), the world is imbued with significance for the particular life-form in question. Philosophically speaking, whatever is so noticed corresponds to the non-indifference of the cell or organism, whose survival often depends on registering the perception signs appropriate to it and vital for its survival.

For a vast majority of Western philosophers, plants are indifferent and insensate beings.^{4,5} Vegetative intake of nutrients and exposure to sunlight are taken to be symbolic of a passive mode of living that does not pursue any objectives whatsoever. Contrary to this bias, studies of plant foraging behavior have revealed highly selective adaptational responses to patchily distributed subsoil resources. Clonal plants selectively allocate offspring ramets to the preferential patches of soil in the presence of multi-patch environmental heterogeneity.⁶ In environments with

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homogeneous resource distribution, the presence of competition likewise solicited a stronger root proliferation response and “conferred a selective advantage to plants proliferating in the direction of the most recently acquired patch.”⁷ Morphological plasticity in foraging behavior explains the “different patterns of spacer production and hence different patterns in the placement of resource-acquiring structures.”⁸

As these examples demonstrate, foraging behaviors in plants are highly selective. They are accompanied by attention to numerous environmental factors, foremost among them resource availability and the presence or absence of competitors. Moreover, they help illustrate the general phenomenological theory of attention, usually restricted to human consciousness. According to this theory, the act of paying attention depends upon three interrelated and dynamically structured elements: (1) focus or thematization; (2) context; and (3) margins or horizons.^{9–11} The first element (focus) is a selective zeroing-in on a significant stimulus or set of stimuli. In the case of foraging, a stimulus plants focus on is the quality of the soil, which must be assessed as a precondition for selecting a resource-rich patch. But, in order to attend to an appropriate stimulus, the attentive subject must first single it out from a general field, or context, that surrounds it. If the stimulus is not significant for the subject, it will remain dissolved in the context, which ought to be understood as the background “white noise.” Growth in homogeneous environments in the absence of competition resulted in a random rooting of the ramets of *Leymus chinensis* and *Hierochloa glabra*.⁶ Under these conditions, neither of the species focused on any given patch of the soil. While information about resource density is still potentially useful, it is relegated to the context of attention and is not brought into the focus of the attending organism.

While a single-minded or unifocal attentive comportment is said to absorb the attentive subject, involuntary attention is dispersed throughout the sentient body.^{12–14} Multifocal attention is similarly characteristic of the green plants

that register blue and red/far-red light in the apical meristem’s cryptochromes and phototropins, as well as in leaf phytochromes, respectively.¹⁵ Plant signaling consequently involves communication from a focus of attention to other tissues not directly affected by the stimulus, or coordination among the multiple attentive foci, each of them singling out a vital piece of information about environmental conditions—often, by way of parallel processing, as in the case of leaf photosensitivity.

Attention individuates whatever falls within its focus or foci by bringing the stimulus into sharper relief against the blurry background of the relatively undifferentiated context, experienced as “white noise.” For humans, this individuation (or phenomenologically speaking, thematization) yields the objects of experience, along with the conscious directedness (intentionality) toward these objects. Consciousness and its acts do not preexist the attentive attitude but are co-originary with this attitude. Attentionality and intentionality share the same functional and structural scope.^{9,20}

While it plays the role of putting into focus and thereby singularizing crucial environmental inputs, the attention of plants is objectless. Their unique sight does not translate visual stimuli into pictures but into instructions for growth or reproduction.¹⁵ Plant attention is likewise active, rather than contemplative, as it feeds directly into the plants’ phenotypic plasticity and capacity for adaptation. To individuate the foci of attention, it is not necessary to transform them into objects, that is to say, forms that are cruder still than the discernments and discriminations of which plants are capable. Not only do plants distinguish between mechanical and herbivore-induced damage but they also respond by releasing appropriate airborne volatiles or communicate through belowground stress cues, indexed to the specific stress factor.^{16–19} The more dire a threat, the more does the need arise for an attentive singling out of its source with the view to its mitigation or to altering a relevant facet of plant morphology and physiology so as to reduce the impact of the stressor.²⁰ Plant behavior is a cumulative outcome of its

attentive focusing on varied events in its environment.

Attention as Modulation

Given the variability of environmental circumstances, it is unreasonable to maintain a constant focus on a single stimulus or group of stimuli. Attention implies as much fixity as movement or change^{9,11–13} keeping the attentive organism attuned to the variations in its surroundings. In other words, attention motivates a chain of focusing-defocusing-refocusing, in keeping with the needs of the attentive subject at any given time, or, as in the case of non-sessile organisms, place. In the tripartite scheme of attention, these modulations are expressed in the interchangeability of the present focus and other, previously insignificant, points in the context wherein it is situated.

Before the onset of abiotically-induced stress, such as in drought conditions, plants perceive cues emitted by their already-damaged neighbors.^{2,17,21,22} In plant-plant communication, the foci of attention can therefore overlap, even if the contexts from which they stand out are different, namely actual drought conditions in the one case and proximity to a stressed plant in the other. Due to an identical focus, the response to a communicated cue will also be the same as to the onset of drought. Since plant attention is active, rather than merely contemplative, its stress-related modulation results in behavioral changes that often entail the activation of stress-inducible genes—*rd* (responsive to dehydration), *erd* (early responsive to dehydration), *cor* (cold regulated) and *kin* (cold-inducible) in *Arabidopsis*—and subsequently, an extensive transcriptional reprogramming.²³

In accordance with their evolutionary rationale, acts of attention put the attentive organism on its guard, emphasizing with greater intensity some stimuli over others. External dangers and threats vary for different species and kingdoms, and so does the attentive comportment that responds, at times preemptively, to these. Although in Husserl’s phenomenology attentional changes are taken to be signs of freedom—“the free turning of the regard”⁹—they in fact are determined by changes in the

environmental conditions of an attentive organism. To be sure, phenomenological freedom does not entail arbitrariness: the attentive attitude is “wandering in a determinate manner,”⁹ determined, that is, by the temporal and spatial fluctuations in the subject’s life-world. In plants, these modulations are predominantly temporal, though the frontiers of growth do not preclude a spatial “wandering,” which we will explore in a subsequent section of the present study.

The open-ended morphology of a plant objectively expresses its acts of attention over time, as its body plan is adjusted to environmental conditions, for instance through the hormonal control of shoot branching.²⁴ The decision on activating a particular axillary meristem is taken at the intersection of local information processing and a global network of hormonal signaling, attuned at the same time to the external environmental factors and the plant’s internal physiological and developmental needs.²⁴ The interplay between these various levels of attention in plants is thus no less complex than in animals and humans, who permanently shift between attention to an external object and to their internal (mental and physical) states.

The rudimentary freedom of attention is palpable in the reversibility of behaviors attributed to attentional modulations. Along these lines, “foraging responses are reversible over the long run” and, in some species such as *H. glabara*, can be reversed very quickly, in tune with the fluctuations in environmental heterogeneity.⁶ The modular architecture of roots and branches, seeking optimal growth, spatially reflects the modulations in the plants’ attention.⁷ The interactions among at least 15 environmental factors, to which this attention can turn, and the enormous range of responses their combinations are responsible for²⁵ further contribute to the freedom of attention-laden behavior in plants. In phenomenological terms, these factors and their interactions delineate the context of attention, within which foci may shift (or wander) in a determinate manner.

In animals and humans, the turning of attention signifies, in the first instance, the mobility of relevant body parts and sense organs, directed toward the newly salient

stimulus. In plants, mobility belongs in the domain of signaling and cell-to-cell communication—the mobile hormonal signals that play an important role in the control of shoot branching²⁴ and plant action potentials, resulting, for instance, in a rapid transmission of oxidative and nitrosative stress signals between root and shoot apices of *Arabidopsis*.^{26,28} As reaction times (and hence quick shifts from one focus within the context of attention to another) make a difference for the survival of an organism, the relative speed of intercellular communication in plants is crucial for their inclusion among attentive subjects. If plants are “fast biosensors for molecular recognition of the direction of light, monitoring the environment and detecting insect attacks,”^{27,30} then their attentional modulations are on the par with sudden changes in environmental conditions that make up the concrete context of their growth and development.

Attention as Perdurance

Attention cannot be entirely isolated from other characteristics of intelligent and deliberate behavior, and especially from memory and anticipation. Following the insights of the phenomenology of time consciousness, experience is a continuum of retention, attention and protention, irradiating from the present back into the organism’s past and future.²⁹ The inclusion of attention in this uninterrupted chain testifies to its dialectical nature, combining the opposites of fixity and movement, freedom and determinateness, rapid reaction and lingering with whatever one attends to.

The starkest illustration of the idea that there are no acts of attention without memory and anticipation is the Venus flytrap, or *Dionaea muscipula*. If attention betokens a disproportionate and fluctuating investment of energy into vital areas of activity, then the Venus flytrap is the case-in-point of attention to its prey, in that “closing its trap requires a huge expense of energy.”^{2,15,31} Described in phenomenological terms, the context of *Dionaea*’s attention includes everything around the sensory hairs that detect the presence or absence of an insect on the plant’s lobes. The insect itself would be situated at the

focus of attention, except that a single focal point, with its limited action potential, is insufficient as an investment of energy into the act of trap closure. A twenty-second delay between the respective stimulations of two sensory hairs allows for the accumulation of an action potential strong enough to shut the trap.^{3,15,32} In the present moment of the second stimulation, attention builds upon the short-term electrical memory of the first stimulation to complete the investment of energy with a Ca^{2+} influx at a threshold where it can attain its intended foraging goal.^{15,33} The continuum of intelligence thus extends from the retention of short-term electrical memory, through the monitoring of further developments within the focus of attention, to the anticipation of prey—the intended target of this deliberate behavior. Only as a temporally coherent ensemble do the three behavioral modalities add up to purpose-driven, intelligent conduct.

What the example of *Dionaea* so clearly conveys is that the practical success or failure of attention does not depend on attention alone. The duration of attention is due to the memory, on which it draws in the temporal continuum extending toward the future attainment of a goal. This is so not only in the “sensitive” plants, *Dionaea muscipula* or *Mimosa pudica*, but also in every plant species that relies on monitoring circadian rhythms to make decisions on the most appropriate flowering time.^{34–36} The decreasing red to far-red (R:FR) light ratios that are responsible for the bud burst in *Betula pendula*^{37,38} evidence a complex interaction of plant memory and attention, where the calculation of the ratios, as well as their storage and retrieval, are mediated by attention to the last far-red and the first red lights of each photoperiod. Attention as perdurance refers to this interaction, oriented toward a future goal (germination, flowering, etc.).

Attention at the Margin

The last element in the tripartite phenomenological model of attention, the margin outlines the limits of the context and determines the horizons of the field, within which acts of attention unfold. The margins of animal and human attention shift along with the mobile attentive subject

itself, whose dislocation to different parts of its environment defines the horizons of its experience. The margins of attention of a sessile organism—whether a sessile animal or a plant—vary predominantly along the temporal axis, and this variation is a behavioral feature that responds to the changing needs of the organism, from foraging to reproduction and defense. Indeed, the definition of plant behavior as “a response to an event or environmental change during the course of the lifetime of an individual”^{38–40} largely overlaps both with the temporal variations in the margins of attention and with phenotypic plasticity.

Besides temporal shifts, the margins of plant attention also change in space. Leaf expansion and contraction, spacer lengthening and shortening, branching and ramet production (among other aspects of plant growth) translate into variations in the spatial horizons of attention. Leaf expansion that increases the surface of these “iterated green antennae specialized for trapping light energy, absorbing carbon dioxide, transpiring water and monitoring the environment;”⁴¹ spacer lengthening in resource-poor soils;⁴² and the plasticity of shoot branching, regulated by networks of hormonal signals⁴³ extend the context of plant attention within its growing margins. In turn, the maximization of surface exposure facilitating a greater capture of energy⁴⁴ introduces more possible focal points into the expanding sphere of attention. Thus, while the margins of animal and human attention follow the shifting horizons of these self-dislocating subjects, the margins of plant attention irradiate outward, both vertically and laterally, encompassing new areas adjacent to their immediate environment.

Conclusions

Phenomenology of attention enriches the theoretical understanding of ways in which plants perceive signals and monitor light, temperature and gravity gradients in their physical environments.⁴⁵ The challenge specific to the study of plant attention is that frequently what plants attend to does not coincide with the targets of human attention.

While animal communication displays “eye-catching” movements, plant communication transpires mostly “out of sight,”⁴⁶ in the release of volatile airborne substances, in the transition zone of the root apex,⁴⁷ and so forth. Despite these fundamental differences, plant attention elucidates the general functioning of attentive comportment in a dialectical combination of fixity and modulation. It sheds light on the intimate relation between intentionality and the sphere of attention, as well as between attention and memory put in the service of goal-oriented behavior. Finally, it substantiates the tripartite model developed by phenomenologists and confirms its applicability to non-human, as well as non-animal, life forms.

Disclosure of Potential Conflicts of Interest

No potential conflicts of interest were disclosed.

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