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REVIEW

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ABSTRACT

Motor intention/intentionality has been investigated from a wide variety of perspectives: some researchers have, for example, been focusing on the purely physical and mechanical aspects underlying the control of action, while others have been concentrating on subjective intentionality. Basically, all approaches ranging from the neuroscientific to phenomenological-inspired ones have been used to investigate motor intentions. The current study set out to examine motor intentions in connection to plant behavior utilizing the final goal of plant action as the definition of its motor intention. Taking a wide-angle approach, the first part of the review is dedicated to examining philosophical and psychological studies on motor intentions. Recent data demonstrating that plant behavior does indeed seem goal-directed will then be reviewed as we ponder the possibility of purposeful or intentional plant responses to stimuli and stress conditions in their environment. The article will draw to a close as we examine current theories attempting to explain plants' overt behavior and corresponding covert representations.

Introduction

The term "intention" embodies a multitude of concepts referring to a variety of domains.[1–7] An individual can harbor and even voice an intention, a desire, an active striving or disposition to do something, just as they can refer to something that is purposeful or value-laden. Intention can also refer to beliefs and/or ideas,[8] whereas intentionality, in the phenomenological sense, denotes a property of the mind of representing or standing for states of affairs and/or objects,[9] it has also been defined as a pervasive feature of many mental states, beliefs, and ideas.[10,11]

The current work focuses on the concept of "intention" and "intentionality" associated with actions (i.e., motor intentions), something that has long attracted the interest of philosophical and psychological theorists.[8,9,12–14] The majority of studies in the literature dealing with the role of motor intention suggest that the intention of carrying out a specific action is something that precedes its actual motor execution.[15–17] Precisely because they are sessile, plants were excluded when those studies were being designed and performed. Although plants are essentially sessile in nature, they are nevertheless very much in tune with their environment and are indeed capable of a variety of movements. While this may come as a surprise to many non-botanists, more than a century ago, Charles Darwin reported that plants produce movement. Darwin[18], for example, observed that the tendrils of climbing plants tend to assume the shape of whatever surface they come into contact with; that is, they progressively learn the shape of potential support characteristics.[19] The behavior described implies that the plants perceive the support and plan their movements appropriately. Climbing plants seem, in fact, to represent actions in terms of their perceivable consequences. To all appearances, the selecting, planning, and initiating of a movement is

mediated by action-effect anticipations. In accordance with this theory, plants may possess a type of intentionality that precedes their motoric behavior, that, as for animals, it becomes "visible" in the surface flow of an organism's motion.[15]

The current work set out to identify the places where some of the pieces of the puzzle (e.g., findings from recent studies and experimental evidence linking plant behavior and motor intention) of the wider picture can be positioned. The first part will explore the theoretical framework of motor intention in a comparative study of how intentions giving rise to action are represented in animal species. We will then go on to investigate some signs of motor intentionality found in plants and examine modular growth and phenotypic plasticity. We will conclude by endeavoring to match our pieces of evidence with hypotheses that have already been formulated as well as to offer some of our own ideas on how motor intentions in plants could be explored in the future.

Motor intentions in animals

According to Libet's criteria,[20] an act is regarded as intentional when (i) it arises endogenously, not in direct response to an external stimulus or cue; (ii) there are no externally imposed restrictions or compulsions that directly or immediately control subjects' initiation and performance of the act; and (iii) most important, subjects *feel* introspectively that they are performing the act on their own initiative and that they *are free* to start or not to start the act as they wish. The majority of studies dealing with the concept of motor intentions in animals espouse the view that motor intention is specified in advance of the actual movement execution.[15–17]

It was Merleau-Ponty[21] who first coined the term "motor intentionality," using it to refer to a pattern of intentionality exemplified by purposive, goal-directed, unreflective bodily activities. According to his definition, there are two ways to explain motor intentions: one involving an intentional relation to the object that is essentially cognitive or can serve as the input to cognitive processes. Another involves a bodily set or preparation to deal with the object.[13]

According to one authoritative view, intentions can be considered at two distinct levels: prior-intention, defined as an intention to act formed in advance of the action itself, and intention-in-action, which refers to the representation of the desire that causes the act.[9] The intentional content of an intention-in-action consists of self-referential causality.[22] While several theorists have embraced this dualistic approach,[2,14,23,24] nearly all theories focus on the motor goal, which – although at different levels of complexity – constitutes the core of what intentions represent, that is, "goals and the means to those goals".[14] That model, which is relevant for our own theory, will be discussed in the following section.

The concept of goal in animals

The concept of goal is central to the literature dealing with the correlates of intentional actions. Generally speaking, an action is associated with a single goal. Movements can be considered goal-directed if they are tuned to the task, and their execution is under voluntary control. According to this definition, the desired result of the movement, that is, the final goal of the action persists in the agent's phenomenological experience throughout the time the action is unfolding and until it has been completed. Research on goal-directed reach-to-grasp movements has produced insightful findings revealing how specific kinematic landmarks are modulated depending on the object's attributes, such as how far away it is, its size, shape, texture, fragility, and weight.[25] To attain a goal, an agent must organize a reaching-grasping action sequence taking into account the structural features of the object and planning and executing the movement accordingly. A number of human behavioral studies have indicated that the first part of a complex action sequence (e.g., the arm reaching and the hand shaping to grasp an object) is influenced by the final action goal and, more specifically, by the motor acts that follow the first part (e.g., lifting, placing). [26–31]

Humans seem to be able to perform coordinated intentional actions very early on in life.[32–34] Indeed, kinematic studies carried out via ultrasonography have revealed that the movements of fetuses appear coordinated already by the 14th week of gestation, and from the 22nd week, they begin to assume the recognizable form of intentional actions, with kinematic patterns reflecting the goal of the action (i.e., hand movements to the mouth or the eyes).[35] Comparative studies have revealed similar types of kinematic patterns of reach-to-grasp movement in human and non-human primates as well as in other animal species such as tetrapods.[36–39] These findings support the idea that actions in human ontogeny and across species are planned and organized *before* they are actually performed, while the biomechanical and temporal structure of motor acts depends on their *final* goal, that is, the motor intention of the acting organism.

In the next section, we will endeavor to apply the notion of "motor intention," defined as the final goal, to plants via "consciousness of . . . " or, in spatial terms, of "directedness toward . . . " Their directionality of growth and interpretation of and interaction with their environment may hold the key to the intentionality inherent in plant life. To be conscious is to intend something, that is to say, to be directed toward an intended object. In that light, the intentionality of plants could be thought of as movements directed toward nutrient-rich soil, water, sources of light, and/or potential supports.

Motor intentions in plants

As pointed out by Marder[40]: "*when animals 'intend' to do something, they enact their directedness-toward by moving their muscles; their intentionality is expressed in modular growth and phenotypic plasticity.*" Plants, instead, generate action potentials and synthesize the protein RHD3, which is responsible for the correct arrangement of root cell files underlying the direction of root growth.[41] This directionality, along with its deliberate regulation, is relevant to our quest for plant intentionality. Plant and animal behaviors are the outcomes of the goals underlying intentional comportments. In phenomenological terms, each type of plant perception expresses a mode of its intentionality: directedness toward the light in photosensitivity, directedness toward sources of heat in thermosensitivity, as well as toward (or away from) self and/or other in kin recognition. In each of these cases, it is not just a question of perceiving, but also of interpreting signals and making decisions in a non-automatic manner in the face of at times conflicting conditions. Intentionality here assumes the more colloquial sense of deliberate purposeful behavior, raising the questions: Do plants intend to defend themselves against herbivores? Do they intend to resist the force of gravity and the common stresses they experience?

Studies reporting on individual root systems that are growing in such a way as to limit the resources of their competitors seem to imply that there is some form of intention.[42,43] The communication network of the cells and tissues making up an individual plant may be the mechanistic basis of intention in plant behavior. Just as human beings, plants seem to gather information about their surroundings, to check it out with their internal and external network systems, and to make decisions that reconcile their own well-being with that of the environment. Spacers, defined as the plant's underground root systems and aboveground stems or shoots which explore the environment in the quest for optimal patches of nutrient-rich soil,[44,40] are relevant to our argument about plant intelligence and intentionality. As Marder[40] suggested, spacers are another sign of plant intentionality and goal-directed behavior and confirm that plants should not be considered organisms that are passive to their own needs and to what is going on in their environment.

Plants' motor intentions: Lessons from Charles Darwin

In *The Power of Movement in Plants*, Charles Darwin described how he monitored the slow growth/movement of plants that was visible to the human eye or carefully measured it at regular intervals.[18] On the basis of his records, he was able to conclude that the leaves, stems, and roots of plants move in circles over long periods of time; at a later date, he coined the term "circumnutation" to describe the elliptical/spiral growth movement around the plant's central axis that could be modified for the good of the plant.[18] He was of the opinion that the driving/regulating apparatus responsible for circumnutation was internal (i.e., Darwinian internal oscillatory model).[18,45] This would explain climbing plants that are able to modify their circumnutation movement to reach and grasp a potential external support (e.g., a pole, a host plant) in the surrounding environment in the effort to grow vertically.[45–50]

Darwin also advanced the hypothesis that climbing plants are able to sense the properties of support structures and to "make decisions" on the basis of that information. Indeed, he was able to illustrate plants' purposeful behavior when he showed that climbing plants perceived a support that was objectively unsuitable because of its smoothness or thickness [45,46]. Commenting on his experiment with the *Bignonia capreolata* plant, he pointed out that the plant initially exhibited an oscillatory movement when an unclimbable smooth glass rod support was presented, but then began to show an irregular unwinding movement as if it were seeking to find a suitable support elsewhere. In another experiment, he provided the plant with a blackened zinc plate and noted that the tendrils initially bent themselves around the edges of the plate but soon recoiled and straightened themselves out, as if they were correcting an erroneous decision. In addition, he described experiments with the *Solanum dulcamara* L., a plant that he found could twine around supports with a 3 mm diameter but not around one with a 5 or 6 mm diameter, which was perceived, evidently, as inappropriate.[45]

A growing body of evidence has confirmed Darwin's observations, and there are numerous reports that plants are able to modify their circumnutation movement in order to reach, hang on to, and climb up a support.[46,47,49–53] Some botanists and vegetation ecologists have investigated the *Cuscuta pentagona* plant, which needs to find and attach itself to a host plant such as the cultivated tomato (*Lycopersicon esculentum* L.) in order to gain nutrient from it and to survive. It has been demonstrated that the *Cuscuta pentagona* is able to locate a host plant via volatile compound cues and to direct its growing movement toward it.[48] Moreover, it is able to distinguish between different types of host plants such as the tomato and Impatiens plants (*Impatiens wallerana*) and to choose the one that is most appropriate for its needs.[48] These examples unquestionably demonstrate that at least some climbing plants intentionally seek out a support or host that will guarantee their survival.

Evidence of intentional actions in plants

Recent findings have demonstrated that plants program their movements purposefully and in ways that are flexible and anticipatory.[47,52–54] The tendrils of *Passiflora* exhibit an incredible flexible control of circumnutation while they are searching for supports.[54] In one experiment, circumnutating *Passiflora* tendrils modified their direction in conformity with a plant-made support that kept moving from one place to another. The support was switched to a different position whenever the tendril approached it, and the tendril continued to change its circumnutating movement in pursuit of the support.

Researchers focusing on the kinematic signatures characterizing the movement of climbing plants have reported that pea plants (*Pisum sativum* L.) can program their movement in advance and can move their tendrils (i.e., specialized stems, leaves, or petioles used by climbing plant to seek, find and attach to a support) depending on the specific characteristics of the to-be-grasped support. When researchers studied the kinematic features of a pea plant's movements while it approached and grasped a thick or a thin support, they found that the plant perceived the support and modulated the kinematics of its tendrils' aperture depending on the support's thickness. The peak of the average and the maximum velocity of the tendrils were higher for the thin supports than for the thicker ones. Moreover, the times at which the tendrils reached peak velocity and the tendrils reached the maximum aperture, both calculated as a percentage of the movement duration, were later for the thinner than for the thicker supports. Likewise, the maximum distance between the tendrils was significantly greater for the thinner support than for the thicker one.

Another study demonstrated that the movement of pea plants (*Pisum sativum* L.) complies with the speed-accuracy trade-off principle (SAT),[55] which is the inclination or decision to choose speed over accuracy.[52] While it has long been known that SATs are a key feature of animal movement, the idea that plants use SATs is coming into its own.[56] By studying the trajectories of the tips of the shoots of climbing pea plants leaning to reach a support, Cerccarini et al.[51] uncovered that the plants perceived the properties of the support even before they made contact with it. Additionally, similar to some animal species, the plants were able to modulate movement velocity strategically depending on the difficulty of the task. The average and the maximum velocities of the tendrils were, in fact, faster when the plants had to reach and grasp a thinner with respect to a thicker support.[51] In a subsequent study, Ceccarini and colleagues[52] set out to investigate if climbing plants are able to improve the accuracy of their movement plan by correcting their secondary submovements. Their findings showed that the plants were, in fact, able to correct their movement plan and, just as humans,[57] they can strategically increase the production of secondary submovements when the task requires more precision. These findings support the hypothesis that the movement of plants is not a cause-effect mechanism but an appropriately planned, controlled, and, if necessary, corrected operation.

All told, these findings are important because they demonstrate that plants exhibit forms of motor intentions that are

similar to those of a variety of animal species.[25,36–39] They also contradict the scientific consensus that plants' movement is driven exclusively by cause-effect mechanisms and hard-wired inflexible reflexes. Ultimately, they have heralded a change in the way that plant behavior is usually considered.

Integrating plant intentionality with available theories

Recent findings[47,52,53,58] suggest that plants interact with objects in the environment in an intentional manner. It has been demonstrated, for example, that they perceive a support and modulate their kinematics depending on its thickness. It has also been reported that the biological and behavioral dynamic nutation patterns of bean plants are influenced by the presence of a support in their vicinity.[53] These findings are in line with some theories regarding motor intentionality. Merleau-Ponty's[21] definition of motor intention as purposive, unreflective goal-directed activities is a pretty accurate description of a climbing plant leaning toward a support. Further, as we said above, according to Libet[20], an act is intentional when (i) it arises endogenously, not in direct response to an external stimulus or cue; (ii) there are no externally imposed restrictions or compulsions that directly or immediately control subjects' initiation and performance of the act; and (iii) subjects *feel* introspectively that they are performing the act on their own initiative and that they *are free* to start or not to start the act as they wish. The behavioral manifestations of climbing plants reported here seem to agree with Libet's definition of intentional actions. In fact: (i) climbing plants move and choose a support on the basis of their endogenous need to seek the sun. An unsuitable or no support fails to satisfy their intention; (ii) climbing plants control their circumnutation movement and interact with their surroundings without any externally imposed compulsions; it is a behavior that arises from their very nature; (iii) climbing plants act freely and are able to terminate the process when the support is not suitable or when there is no support.

Some may say that this conceptual framework does not work for plants because, in order to act in a goal-directed manner, they need to be able to construct a representation of the environment, including potential supports. And it goes without saying that many argue *a priori* that cognition is impossible in plants.[59] According to classical views, mental representations are created by a number of neurophysiological mechanisms in the brain that are activated after perceptual processing occurs. The events activating mental representations take place, according to this view, in the following order: physical signals are received through the perceptual systems and transmitted to the brain, then the physical signals are translated into mental representations (e.g., concepts, intentions) with the mind in charge of processing them, finally the motor system operationalizes the mind's will.

This explanation of mental representations does not take plants as cognitive agents into consideration since they lack a brain and a centralized nervous system (CNS) where mental states and representations can be localized. Scholars favoring the embodied cognition theory are able to challenge the notion of representational content by taking into consideration extra-

neural bodily structures and the environment.[60–66] According to Gibson[67], for example, cognitive activities do not necessarily depend on mental representations but on *affordances*, defined as structural supports or resources the environment offers. What an organism perceives of an object is not only its physical properties but also its *affordances*, in other words, what it can do with them.[68] The key to understanding *affordance* is that it is relational and characterizes the suitability of the environment to the organism, which means that it depends on their current intentions and capabilities. The notion of intention is crucial here because the same environment can provide various *affordances* to different organisms or to the same organism at different times. The defensive leaf-folding behavior of the *Mimosa pudica* plant in response to repeated physical disturbances exemplifies how *affordances* can be adjusted by the same organism.[69]

For those subscribing to the extended cognition theory, the environment plays an active role in cognitive processes which are not confined to the CNS or to the body.[61] According to this theory, cognition extends beyond the physical boundaries of the organism into its environment and is inclusive of objects that are not part of the body. Then there is the case of the extended spider cognition, which involves the outsourcing of information processing to the body or the environment.[70] It has been documented that web builder spiders adjust the tension of their thread by extending their cognition and adjusting the tension of the web threads. Tighter web threads lead to a lower threshold of disturbance needed to catch the spider's attention. Thread tension thus calibrates the threshold level for attention. When tight, tinier objects such as prey items are registered, the causal chain is satisfied in one direction. The spider, in turn, adjusts its web tension based on its hunger state. In practice, a hungrier spider will tend to tighten the web as even smaller prey is worth its attention. This demonstrates that the cognitive capacities of the spider also affect its environment.[70]

According to Parise et al.[71], plants too can extend their cognitive processing into their environment by actively modifying the rhizosphere and the soil directly influenced by root secretions, as well as shaping the root microbiome to the microbial community of the roots. It has been seen, for example, that the accumulation of exudates between obstacles and the roots is related to the plant's perception of obstacles in the soil, causing inhibited root growth in the direction of the accumulated exudates.[72] It has also been experimentally proven that the plant is prevented from perceiving obstacles and even grows toward an obstacle as if they were not there if exudates have been removed from the substrate.[72] The relationship between plants and their exudates is similar to that of the spider with the web; together with its exudates, the plant forms a single cognitive system.

Enactivism, which is the capacity of organisms to adaptively, flexibly, and sophisticatedly interact with an environment to maintain their systematic autonomy is another theory in cognitive science.[64,73,74] Enactivism posits that the dynamic interaction between organisms and their environment is a kind of action-oriented cognition.[67,75–77] More radical versions of enactivism eschew representationalism[63] and argue that cognition is not a matter of representing the environment, but rather the active

exploration of an environment by an organism, known as "sense-making".[78] The enactivist approach to cognition is an alternative one that would allow us to consider plants as cognitive agents and circumvent some of the challenges linked to the mental representation theory.[58,79–81] De Carvalho and Rolla[78] proposed an enactivist-ecological approach according to which complex cognitive capacities such as ones involving representations are deeply rooted in the basic processes that enable biological organisms to survive and maintain their integrity in a dynamic environment. The approach offers a base upon which the theory of cognition in single-cell organisms, plants, animals, and humans can be constructed.

Both enactivist and extended cognition theorists maintain that cognition is not-just-in-the-head and goes beyond the constraints of the body. But how would an extended or enactivist process function in a plant? What is the physiological mechanism underlying a plant's reactions to its environment? Frankly, right now we cannot answer that question; however, we can say that just as animals, plants possess cells that are capable of generating electrical signals, including action potentials,[82] variation potentials, hydraulic (e.g., turgor pressure), and chemical potentials (e.g., auxin).[83,84] These are cellular components that have been implicated in plant movement and might be modulated on the basis of the motor intention driving the action.

Once we have put aside a representational approach, plant behavior can be interpreted in a different light. Guerra et al.[47], for example, who carried out experiments on pea tendrils, reported that they acted in an 'intentional' goal-directed manner in an embodied form of cognition in which the plant and the stimulus (i.e., the support) interacted as a single unit. The environment, in this case, could be considered part of the plants' intention as it approached the support it intended to grasp.

Future directions

This review has, alas, uncovered more questions than it has answered. Foremost on the list of issues requiring clarification are plants' social intentions and behavior. Like animals, plants interact with their kin and non-kin and the environment, and their response to their surroundings is sophisticated and plastic depending on a variety of cues and signals. Just as animals, plants use phenotypic plasticity to forage, compete, acquire resources, cope with stress, and defend themselves against predators.[85] In the midst of all these activities, plants seem to be able to recognize their kin from strangers, this ability affects their social attitude and translates into behaviors that may be driven by either cooperative or competitive motor intentions.[86] Dudley and File[87] reported that when kin offshoots (i.e., from the same mother) were planted together in a pot, the total root mass produced was less than when non-kin individuals [i.e., from different mothers) were planted together. Biedrzycki and colleagues[88] demonstrated identity recognition in the seedlings of *Arabidopsis thaliana*, a finding that supports the theory that the kin recognition response in plants may have major implications with regard to their competitive/collaborative interactions with other plants.

It also needs to be pointed out that interactions with other plants do not take place exclusively underground. Crepy and Casal[89] reported that plants recognized their kin neighbors by showing more horizontal leaf growth reorientation with respect to that noted for the non-kin neighbors. All of these findings support the idea that plants are capable of distinct social intentions, both cooperative and competitive in nature, and take action accordingly, exactly as humans do. We can truthfully say that based on the findings outlined here, plants do seem to possess the ability to perceive other plant's actions and to process them in a way that enables them to react optimally.

Future research projects could investigate if the interactive behavior exhibited by plants is driven by social intentions. Can plants, like humans, interpret other organisms' motor intentions[90]? Should this be the case, in what way could intention reading facilitate their behavior? Needless to say, we are expecting fascinating results from research investigating the mechanisms underlying motor intentions in plants.

Conclusions

The review set out to find a common platform for an integrated conceptual-methodological approach to plant behavior and motor intentionality. We posited that the fundamental elements underlying motor intentions in humans and animals are also present in plants. Many studies examining plant movements have provided evidence that some form of intentionality in plants does indeed exist; that possibility has led to more questions that only a few years ago might have been considered absurd. Some of these are: to what extent can plants intentionally plan their movements? Is plant movement affected in any way by the behavior of their plant neighbors? Does the intention to interact socially involve basic processes that are shared with animals, or are they plant-specific? A fascinating frontier awaits, in short, physiologists, botanists, biologists, and bioengineers, attempting to break the code of plant behavior and intentionality.

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