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The mind of plants: Thinking the unthinkable

Monica Gagliano (ID)

Centre for Evolutionary Biology, School of Animal Biology, University of Western Australia, Crawley, Western Australia, Australia

ABSTRACT

Across all species, individuals thrive in complex ecological systems, which they rarely have complete knowledge of. To cope with this uncertainty and still make good choices while avoiding costly errors, organisms have developed the ability to exploit key features associated with their environment. That through experience, humans and other animals are quick at learning to associate specific cues with particular places, events and circumstances has long been known; the idea that plants are also capable of learning by association had never been proven until now. Here I comment on the recent paper that experimentally demonstrated associative learning in plants, thus qualifying them as proper subjects of cognitive research. Additionally, I make the point that the current fundamental premise in cognitive science—that we must understanding the precise neural underpinning of a given cognitive feature in order to understand the evolution of cognition and behavior—needs to be reimagined.

Big and small, myriads of choices are made every day about everything. Based on past experiences and shaped by one's preferences, motivations and the expectation of where they may lead, choices are made through the process of decision-making, a way of pruning out presumably bad options in order to select the best ones possible. Of course, not all choices are always 'the best' possible and suboptimal (maladaptive) decision-making behaviors have been observed in both humans and non-human animals (e.g. gambling behavior[1]). Nevertheless because poor choices are likely to affect performance and survival in many biological systems (including human societies), individuals have evolved a remarkable capacity for making overall good decisions to successfully achieve their ends. This capacity to make sound decisions is not simply hard-wired in a behavioral blueprint, but is a *learned skill* that can be developed and honed through experience. This implies that the complex computational processing that enables the faculty of decision-making is closely reliant on internal representations of one's historical experience (i.e. memory), developed and stored over the course of the learning process. By remembering what happened when (i.e., recollecting the past) as well as what to do when (i.e., anticipating the future), these representations inform on what is *not* in the immediate environment, thereby "extending" the amount of information available to the perceptual system in the present. In humans, such

"extension of perception" that allows an individual to infer possible causal relationships and evaluate what opportunities are "afforded" by a given environment (i.e., 'affordances' à la Gibson[2]), is defined as *thinking*.[3] This core capacity of simulating or representing information of absent objects, and use the information in flexible ways in order to predict or anticipate an external event and align behavior to the current state of the world has also become increasingly evident in several non-human animal species.[4-7] Many of the examples come from experiments conducted in the context of associative learning, where even 'simple' conditioning tasks can result in complex representations and the behavioral flexibility generally attributed to "higher" learning.[4,8]

While the range of complexity of these representations may remain an ongoing point of discussion, the fact is that classical conditioning in both human and non-human animals has provided a powerful framework for exploring processes like learning, memory, anticipation, awareness, decision-making and more, which are, broadly speaking, attributes of what we call, the mind. Recently, this classical conditioning approach has been successfully applied to the vegetal world.[9] Using a Y-maze task, our latest study demonstrated that seedlings of the garden pea (*Pisum sativum*) are able to acquire learned associations to guide their foraging behavior and ensure survival (Fig. 1). The ability of seedlings to

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Figure 1. As the model organism that inspired Mendel's idea of hereditary units and ushered in the modern science of genetics well over a century ago, the common garden pea (*Pisum sativum*) continues to play a key role in expanding scientific thinking and specifically, the way we understand behavior, cognition and the mind. © M. Gagliano. Reproduced by permission of M. Gagliano. Permission to reuse must be obtained from the rightsholder.

anticipate both the imminent arrival of light ("when") and its direction ("where") based on the presence and position of a neutral conditioning stimulus (CS) demonstrates that plants are able to encode both temporal and spatial information and modify their behavior flexibly. By revealing that plants, too, are capable of associative learning and consequently, qualify as proper subjects of cognitive research (as discussed previously[10]), these findings invite us to earnestly think about the question of the vegetal mind.

The ecology of associative learning: A case for plants

In the real world (outside the laboratories), individuals continuously encounter circumstances and events the consequences of which are, more often than not, uncertain. The presence of uncertainty is an indication that the individual is yet to acquire the specific internal representation that reliably predicts its current environment. In other words, it needs to learn about the stimuli that are associated to and predict the occurrence of important outcomes, so that they can be anticipated with the least amount of uncertainty and consequently, risk. This is best illustrated in the context of predator-prey interactions, where a close match between perception and actual reality is advantageous as it allows individuals to avoid mistakes that could have fatal consequences. In a wide range of animal species, for example, naïve prey individuals can learn to recognize a predator by being simultaneously exposed to the cue of an injured conspecific paired with predator odor;[11] through repetition, a

prey increases its certainty associated with correctly labeling a newly learned species as a predator.[12] Beyond the realm of predation, a plethora of animal studies across functional domains has shown that associative learning enables animals to forage efficiently while avoiding potentially poisonous food,[13] to navigate their environment,[14] securing territories[15] and reproductive success,[16-18] highlighting the importance of associative learning in shaping adaptive behavior in a wide range of contexts and species, including humans.[19] Then, what about plants?

Plants have been omitted from the conversation because no experimental evidence for their ability to learn by association was available, until now.[9] It is logical then, that the adaptive value of associative learning in vegetal species has never been considered. However in light of the new evidence, it is equally logical to expect that, in plants too, associative learning has a range of ecological purposes from foraging to danger avoidance to social interactions above and below ground. For example, a 2014 study demonstrated that plants are able to detect and distinguish between the sound of feeding caterpillars and those caused by wind or singing insects.[20] Like in the animal example provided above, naïve plants could learn to recognize the presence of a predator by being exposed to the cue of an injured conspecific (i.e., volatile emission) paired with predator sound (i.e., feeding caterpillar). This herbivore-generated acoustic cue alone could then be used by the plant to mount up their chemical defenses in response to subsequent threats of herbivory.[20] A testable hypothesis could be formulated that acoustic cues by virtue of their rapid transmission in the environment reinforce the effectiveness of other known warning signaling systems relying, for instance, on airborne volatiles.[21] If true, learning to associate sounds produced by feeding insects with the release of volatile emissions by plants under attack could reduce a plant's perceptual uncertainty and enable a rapid pre-emptive response to looming attacks as and when required. As we all know well, it is more effective to anticipate rather than wait for events to present themselves, especially when involving dangerous interactions. Accordingly, selection should favor associative learning mechanisms that enable plants to distinguish whether and when cues are indicative of impending harmful or attractive conditions and thus, allow them to take advantage of new resources and avoid novel threats.

Not *what*, but *who* is learning inside the maze?

The ability to learn through the formation of associations involves the ability to detect, discriminate and categorize cues according to a dynamic *internal value system*.[22,23] This is a subjective system of *feelings* and *experiences*,

motivated by the overall sensory state of the individual in the present and its extension via internal representations of the world experienced in the past; representations that, as mentioned earlier, play a fundamental role in the decision-making process by providing a reference for the kind of expectations that the individual projects in the future. By demonstrating that plants are able to learn by forming associations, our recent findings make some important insinuations in regards to vegetal subjectivity and awareness.

Firstly and for the simple reason that feelings account for the integration of behavior and have long been recognized as critical agents of selection,[24] plants too must evaluate their world *subjectively* and use their own experiences and feelings as functional states that motivate their choices. Through careful experimental design, the seedlings in our study were *allowed* to display a number of behavioral responses to inform us—the human observers—of their cognitive states. In our second experiment, for example, in which some seedlings were asked to make a decision on their growth direction during the evening hours when light would not normally be available, the young plants informed us of their lack of confidence in the neutral conditioning stimulus (CS) as a reliable predictor for the light—a decision they, otherwise, rendered most readily during daylight hours. The expression of the conditioned response (CR) in our study is certainly a good indicator of learning, but the absence of the CR in some experimental groups does not necessarily indicate that learning did not occur. Keeping in mind that in a conditioning experiment, what an individual does is not the same of what it knows,[25] is it possible that those seedlings asked to perform outside the daylight hours, *chose* to opt out of performing the conditioned light-foraging behavior? Because the consequences of performing the CR at a time that is misaligned with the internal circadian signals are uncertain (but likely to be energetically costly), is it possible that the plants opted for what they perceived as (but in actuality, was not) a "sure bet"—namely, their innate positive tropism to light—as a solution to the uncertainty problem? As a matter of fact, we do not know whether this is possible or else, but we now have an experimental framework to find out.

Secondly, the ability to have experiences and feelings, rather than mere sensations, can be explored as a facet of the ability to learn through the formation of associations. If we agree that associative learning and internal value systems based on feelings are evolutionarily linked and constitute what we may refer to as (basic) consciousness,[23] then plants could open a new interface into exploring the processes that have led to the emergence of consciousness (assuming it to be a process that actually emerged or a trait that was acquired through an evolutionary event). By uprooting it from the idea that it is a process or trait that occurs as the intrinsic operation of neural circuitry[26-29] and thus, it is *generated* by neurological substrates (as mentioned in the 2012 Cambridge Declaration on Animal Consciousness), plants help us to unnerve our premise that consciousness entails attributes derived from specific physical structures such as brains and neurons. Moreover, they encourage us to put forward a quantitative theory of consciousness that accounts, more adequately, for its *expression* through the incredible diversity of living species. Just what kind of theory this may be is an open question (but see Integrated information theory[30]), but at the very least it should include analyses of behavior and ecophysiology in a wider range of species that transcends the animal kingdom (including the human).

And lastly, questions about the cognitive capacities of animals and specifically, animal consciousness often play a role in discussions about animal welfare and moral status. This debate has been recently extended to include plants[31,32] and as experimental evidence for the cognitive capacities of plants accrues, the controversial (or even taboo) topic regarding their welfare and moral standing and our ethical responsibility toward them can no longer be ignored.

Disclosure of potential conflicts of interest

ORCID

Monica Gagliano http://orcid.org/0000-0002-2414-6990

References

[1] Zentall TR, Stagner J. Maladaptive choice behaviour by pigeons: An animal analogue and possible mechanism for gambling (sub-optimal human decision-making behaviour). Proc R Soc Lond B 2011; 278(1709):1203-08; PMID:20943686; http://dx.doi.org/10.1098/rspb.2010.1607

[2] Gibson JJ. The theory of affordances. In: Shaw R, Bransford J, editors. Perceiving, acting, and knowing: Toward an ecological psychology. Hillsdale, NJ: Erlbaum; 1977. p. 67-82.

[3] Hastie R, Dawes RM. Rational choice in an uncertain world: The psychology of judgment and decision making. London, UK: Sage Publications; 2010.

[4] Shettleworth SJ. Animal cognition and animal behaviour. Anim Behav 2001; 61:277-86; http://dx.doi.org/10.1006/anbe.2000.1606

[5] Pickens CL, Holland PC. Conditioning and cognition. Neurosci Biobehav Rev 2004; 28:651-61; PMID:15555675; http://dx.doi.org/10.1016/j.neubiorev.2004.09.003

[6] Cheke LG, Clayton N. Mental time travel in animals. WIREs Cogn Sci 2010; 1:915-30; PMID:26271786; http://dx.doi.org/10.1002/wcs.59

[7] Crystal JD. Remembering the past and planning for the future in rats. Behav Process 2013; 93:39-49;

PMID:23219951; http://dx.doi.org/10.1016/j.beproc.2012.11.014

[8] Andrews K. The animal mind: An introduction to the philosophy of animal cognition. Abingdon, UK: Routledge; 2015.

[9] Gagliano M, Vyazovskiy VV, Borbely AA, Grimonprez M, Depczynski M. Learning by association in plants. Sci Rep 2016; 6:38427; PMID:27910933; http://dx.doi.org/10.1038/srep38427

[10] Gagliano M. In a green frame of mind: Perspectives on the behavioural ecology and cognitive nature of plants. AoB PLANTS 2015; 7:plu075; PMID:25416727; http://dx.doi.org/10.1093/aobpla/plu075

[11] Ferrari MCO, Wisenden BD, Chivers DP. Chemical ecology of predator–prey interactions in aquatic ecosystems: A review and prospectus. Can J Zool 2010; 88:698-724; http://dx.doi.org/10.1139/Z10-029

[12] Ferrari MCO, Vrtelová J, Brown GE, Chivers DP. Understanding the role of uncertainty on learning and retention of predator information. Anim Cogn 2012; 15:807-13; PMID:22547399; http://dx.doi.org/10.1007/s10071-012-0505-y

[13] Shettleworth SJ. Cognition, evolution and behavior. Oxford, UK: Oxford University Press; 2010.

[14] Menzel R, Greggers U, Smith A, Berger S, Brandt R, Brunke S, Bundrock G, Hülse S, Plümpe T, Schaupp F, et al. Honey bees navigate according to a map-like spatial memory. PNAS 2005; 102(8):3040-45; PMID:15710880; http://dx.doi.org/10.1073/pnas.0408550102

[15] Hollis KL, Dumas MJ, Singh P, Fackelman P. Pavlovian conditioning of aggressive behavior in blue gourami fish (*Trichogaster trichopterus*): Winners become winners and losers stay losers. J Comp Psychol 1995; 109:123-33; PMID:17296997; http://dx.doi.org/10.1037/0735-7036.109.2.123

[16] Adkins-Regan E, MacKillop EA. Japanese quail (*Coturnix japonica*) inseminations are more likely to fertilize eggs in a context predicting mating opportunities. Proc R Soc Lond B 2003; 270:1685-89.

[17] Dukas R, Duan JJ. Potential fitness consequences of associative learning in a parasitoid wasp. Behav Ecol 2000; 11:536-43; PMID:25576445; http://dx.doi.org/10.1093/beheco/11.5.536

[18] Ejima A, Smith BP, Lucas C, Levine JD, Griffith LC. Sequential learning of pheromonal cues modulates memory consolidation in trainer-specific associative courtship conditioning.

Curr Biol 2005; 15:194-206; PMID:15694302; http://dx.doi.org/10.1016/j.cub.2005.01.035

[19] Heyes C. Simple minds: A qualified defence of associative learning. Phil Trans R Soc B 2012; 367:2695-2703; PMID:22927568; http://dx.doi.org/10.1098/rstb.2012.0217

[20] Appel HM, Cocroft RB. Plants respond to leaf vibrations caused by insect herbivore chewing. Oecologia 2014; 175(4):1257-66; PMID:24985883; http://dx.doi.org/10.1007/s00442-014-2995-6

[21] Gagliano M, Renton M. Love thy neighbour: Facilitation through an alternative signalling modality in plants. BMC Ecol 2013; 13:19; PMID:23647722; http://dx.doi.org/10.1186/1472-6785-13-19

[22] Ginsburg S, Jablonka E. The transition to experiencing: I. Limited learning and limited experiencing. Biol Theory 2007; 2:218-30.

[23] Ginsburg S, Jablonka E. The transition to experiencing: II. The evolution of associative learning based on feelings. Biol Theory 2007; 2:231-43.

[24] Packard A, Delafield-Butt JT. Feelings as agents of selection: Putting Charles Darwin back into (extended neo-) Darwinism. Biol J Linnean Soc 2014; 112:332-53; PMID:24843434; http://dx.doi.org/10.1111/bij.12225

[25] Bouton ME, Moody EW. Memory processes in classical conditioning. Neurosci Biobehav Rev 2004; 28:663-74; PMID:15555676; http://dx.doi.org/10.1016/j.neubiorev.2004.09.001

[26] Edelman GM, Tononi G. The universe of consciousness: How matter becomes imagination. New York: Basic Books; 2000.

[27] Koch C. The quest for consciousness: A neurobiological approach. Englewood, CO: Roberts; 2004.

[28] Seth AK, Izhikevich E, Reeke GN, Edelman GM. Theories and measures of consciousness: An extended framework. PNAS 2006; 103(28):10799-804; PMID:16818879; http://dx.doi.org/10.1073/pnas.0604347103

[29] Edelman GM, Gally JA, Baars BJ. Biology of consciousness. Front Psychol 2011; 2:4. PMID:21713129; http://dx.doi.org/10.3389/fpsyg.2011.00004. eCollection 2011.

[30] Tononi G, Koch C. Consciousness: Here, there and everywhere? Phil Trans R Soc B 2015; 370:20140167.

[31] Marder M. Plant-thinking: A philosophy of vegetal life. New York: Columbia University Press; 2013.

[32] Pelizzon A., & Gagliano M. (2015). The sentience of plants: Animal rights and rights of nature intersecting? AAPLJ 2015; 1:15-14.