

Associative learning in plants: light quality history may matter

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Abstract: The possibility of associative learning in plants is a topic of ongoing controversy. In one published study, growing pea plants were reported to associate two stimuli (airflow and light) and thereafter use one (airflow) as an indicator for the other (light), similar to dogs in Pavlov's famous experiments. However, this observation could not be independently repeated. Here we examine a possible reason for the failure of a published reproduction attempt, which used substantially different light quality during plant cultivation prior to experimental treatments than in the original study. This could have resulted in dramatically different growth characteristics. While the relevance of the original report of plant associative learning remains questionable, greater attention should be paid to good documenting and standardizing the light conditions, in particular spectral quality, not only in studies of plant learning and memory, but also in other areas of experimental plant biology.

Introduction: Associative Learning Does Not Require a Brain

Five years ago, a study documenting classical conditioning in plants (Gagliano *et al.*, 2016) gained considerable attention (Rasmussen, 2018; Burgos, 2018; Calvo *et al.*, 2020; Mallatt *et al.*, 2021). However, a subsequent attempt to replicate the published experiments failed (Markel, 2020a). Thus, the possibility of associative learning in plants remains a subject of debate, despite efforts to find causes of the apparent lack of reproducibility of the originally reported results (Gagliano *et al.*, 2020; Markel, 2020b).

Obviously, the experimental studies that started the ongoing controversy need to be critically examined. Cognitive and behavioral scientists have readily embraced the notion that learning can take place in the absence of consciousness, and even of a nervous system of the kind known from metazoans (summarized, e.g., in Rasmussen, 2018; Burgos, 2018). Experimental observations suggest the possibility of some form of associative learning in bacterial and yeast populations (Mitchell *et al.*, 2009; for a critical re-assessment see Lyon, 2015) as well as in protozoans (de la Fuente *et al.*, 2019; Gershman *et al.*, 2021). Formal models predict the possibility of associative learning in unicellular organisms through reinforcement of regulatory pathways in biochemical and genetic networks, which may be modelled

as neural networks (Tagkopoulos *et al.*, 2008; Fernando *et al.*, 2009). In principle, any genetic regulatory network comprising bistable elements can form and store associations (Sorek *et al.*, 2013). Since such networks abound in any type of cells, the possibility of associative learning in plants is theoretically possible, although this does not mean that it has to exist.

Examples of Perception and Memory in Plants

Plants sense many environmental variables (e.g., the quantity, quality and photoperiod of light, temperature, humidity, CO₂ level, soil moisture, and nutritional status), and integrate their sensory outputs through complex signaling networks (Paik and Huq, 2019). It is thus not surprising that plants evolved mechanisms to remember past events and prime their responses in order to react faster or stronger to recurrent environmental change, i.e., learn from past experiences. Examples of both short-term and long-term memory formation, which is a prerequisite of (if not synonymous with) learning, have been documented in plants (for reviews see, e.g., Cvrčková *et al.*, 2009; Abramson and Chicas-Mosier, 2016; Crisp *et al.*, 2016). Some cases of plant memory, such as vernalization or abiotic stress priming (Bouché *et al.*, 2017; Oberkofler *et al.*, 2021; Bhadouriya *et al.*, 2021), involve known molecular mechanisms of epigenetic regulation of gene expression.

Light-related responses deserve special attention, because light plays a central part in plant life, providing not only energy for photosynthesis, but also information that triggers

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reactions to environmental changes. Examples such as developmental responses to sun and shade (Ballaré and Pierik, 2017) can be understood as relatively simple modifications of physiological processes by environmental inputs. However, in some cases, responses to light may involve memory formation or recall. For example, circumnutation—the periodic, typically circular movement of plant shoots, driven at least in part endogenously and often exhibiting an ultradian period (Stolarz, 2009)—may enable plants to perceive and record directional variation in light intensity by relating light exposure to specific phases of the circumnutation cycle. The growing apex can thereby generate an internal model of light distribution and grow towards the light source even in the absence of specialized organs for directional light sensing (Trewavas, 2017), analogous to a model recently proposed for orientation of roots in a heterogeneous environment (Loshchilov *et al.*, 2021).

Thus, the ability of plants to store and use information about past events, i.e., to memorize and recall, is a well-documented phenomenon.

Plant Associative Learning: A Problem of Replicability

Historical attempts to detect associative learning in plants have focused mainly on short-term responses, such as mechanically induced folding of *Mimosa pudica* leaflets, and produced inconclusive results (reviewed in Adelman (2018)). Experimental evidence for associative learning in plants was, however, reported in a recent study (Gagliano *et al.*, 2016) exploring longer term growth phenomena. In the experiments of Gagliano *et al.* (2016), young pea (*Pisum sativum*) plants, pre-grown in an illuminated controlled environment chamber and subsequently kept in the dark with brief repeated “training” exposures to blue light coming from changing directions, were found to orient their growth with respect to airflow from a fan, administered from either the same or opposite direction as light during the training. Control plants, exposed only to directional light but no airflow, oriented their growing apices toward the last light position. Thus, brief directional illumination could be considered as an unconditioned stimulus, while airflow served as a conditioned stimulus, utilized by the plants to anticipate the position of next light pulse.

However, in a repetition of these experiments (Markel, 2020a), the plants’ ability to remember the direction of last light exposure and grow consistently towards it in the absence of airflow, as reported by Gagliano *et al.* (2016), was not reproduced. Some of the growing apices oriented in a random direction instead, possibly related to their vigorous circumnutation (Markel, 2020b)—i.e., the unconditioned stimulus did not work in the reproduction attempt as reliably as it did in the original study.

There are several obvious possible causes of the reported non-reproducibility of the Gagliano *et al.* (2016) results, reflected in the subsequent published discussion (Gagliano *et al.*, 2020; Markel, 2020a, 2020b). The plant’s ability to remember past light direction appears to be rather sensitive to environmental variations. For example, in the original study, training had to take place at specific phases of the circadian cycle to achieve the “learned” outcome (Gagliano *et al.*, 2016; Gagliano *et al.*, 2020). The original study

(Gagliano *et al.*, 2016) and the subsequent failed repetition (Markel, 2020a) also differed in other aspects as discussed below; thus, the Markel (2020a) report should be considered an attempt at reproduction (with substantial variation to the experimental material and procedures) rather than replication in an identical setup (Plesser, 2018).

First, different pea cultivars have been used because of unavailability of the original Australian variety in the USA, and the soil composition may not have been identical. While there are reasons to believe that this is unlikely to be the cause of observed discrepancies, this possibility cannot be entirely dismissed especially concerning the genotype difference between the cultivars (Markel, 2020a). For example, even subtle differences in diurnal starch and sucrose turnover (Stitt and Zeeman, 2012) could have translated into noticeable changes in growth and/or in light responses of the two pea varieties under near-continuous light starvation. Notably, the two studies used plants of different chronological ages (about 3-4 days in Gagliano *et al.* (2016) vs. 5-8 days in Markel (2020a)), suggesting different seedling growth characteristics. In other cultured plants, quite dramatic responses to light signals could be traced to a single mutational event, as documented, e.g., for continuous light sensitivity in the tomato (Velez-Ramirez *et al.*, 2014); single mutations thus could be responsible for major differences in the responses of two otherwise similar plant varieties.

Furthermore, there could also have been some differences in the light conditions during the experiments, with the Markel study having a higher level of background light, as thoroughly examined in the subsequent discussion (Gagliano *et al.*, 2020; Markel, 2020b).

Are Light Conditions Prior to Experimental Treatment to Blame?

Surprisingly, none of the participants in the ongoing discussion mentions a possibly much more important discrepancy in the light conditions during the early cultivation of seedlings between germination and the experimental treatments. While both groups used comparable irradiance (light flux per area) and photoperiod, Gagliano *et al.* (2016) employed cold white fluorescent light, while Markel (2020a) used illumination by blue and red LEDs “balanced for an approximation of white light” (whatever this means, possibly a blue-to-red ratio comparable with daylight). Neither of the groups provided a full description of the light sources they used, but it is clear that the spectral compositions of their lights could not have been alike.

For illustration, we are providing spectral characteristics of several light sources used in our plant culture chambers, compared to natural daylight (Fig. 1).

While none of our light sources directly corresponds to the lights used in either of the studies, we can nevertheless document that a combination of red and blue LEDs (Markel, 2020a) obviously lacked multiple spectral bands present in white fluorescent light, including wavelengths known to be perceived by plants, such as green light (Zhang *et al.*, 2011). It is equally clear that neither of the experimental light conditions can be considered a faithful emulation of natural daylight. Additionally, as the lights

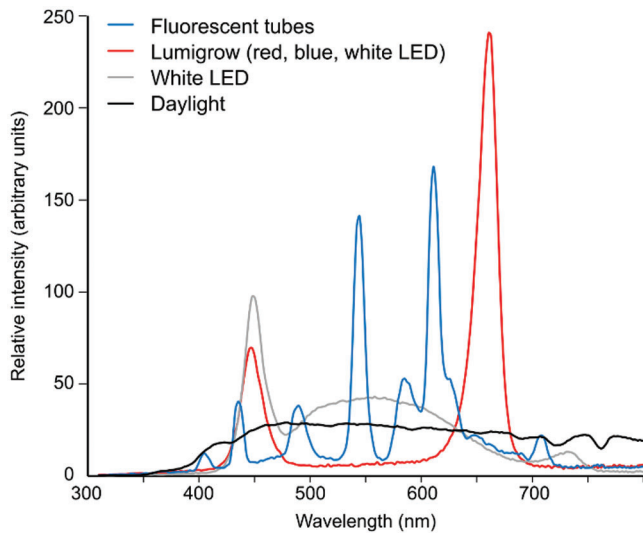


FIGURE 1. Examples of spectral profiles of several light sources commonly used for experimental plant cultivation. Light sources were: fluorescent tubes (Osram Lumilux deluxe warm white, similar to the lights used in [Gagliano et al. \(2016\)](#), which, however, were “cold white” and therefore apparently had a stronger blue component); a Lumigrow 325 LED panel consisting of an array of red, blue and white LEDs, with most of the light provided by the red and blue elements (similar to the lights used by [Markel \(2020a\)](#), except for a different blue-to-red ratio and presence of low level intermediate wavelengths); white LEDs as in the FytoScope FS-WI walk-in culture chamber (Photon Systems Instruments, Drásov, Czech Republic). The Daylight plot represents early afternoon, overcast sky daylight. Light composition was measured using the SpectraPen mini spectroradiometer (Photon Systems Instruments, Drásov, Czech Republic) and normalized to equal areas under the curves in the range of 300–800 nm.

used by the two studies differed substantially in their spectral composition, the energy available to the plants likely differed in total, as well as in particular biologically active wavelength ranges.

Light History Affects Morphological and Physiological Traits

Plants have developed complex adaptive responses to cope with variable light conditions, involving multiple organs and tissues and dependent on many genes (reviewed in [Ruban \(2009\)](#)). A difference in the history of light quality during early growth may result in physiologically and/or morphologically different plant individuals. Indeed, spinach plants exhibit subtle but consistent developmental differences when grown under two types of white LED lights with slightly different spectral compositions ([Buratini et al., 2017](#)). In a well-characterized example, the ratio of far-red/red light, which is increased in light reflected from or filtered through leaves, initiates the “shade avoidance response”—A very complex set of structural, developmental and physiological reactions to ongoing or imminent shading. This response often includes elongation, altered flowering time, increased apical dominance and altered partitioning of resources ([Ballaré and Pierik, 2017](#)). Changes in blue-to-red light ratio also profoundly affect a plant’s structure and physiological responses, and are frequently used by horticulturalists to avoid the use of growth

retardants ([Lykas et al., 2008](#)) and to modulate shoot elongation *in vitro* ([Bello-Bello et al., 2016](#)).

Impact of a plant’s light history may be long-lasting, even going beyond the individual life span. Epigenetic changes propagated by clonal as well as generative reproduction may allow offspring to pre-adapt to environments similar to those experienced by parent plants ([Galloway and Etterson, 2007](#); [Baker et al., 2019](#)).

Light Signals Contribute to Plant Memory Formation

Light conditions play an important role in stress priming and similar plant memory phenomena ([Hilker and Schmölling, 2019](#)). Plants can modulate the activity of their photosynthetic apparatus by photoelectro-physiological signaling, processing information on past light status ([Karpiński and Szechyńska-Hebda, 2010](#); [Szechyńska-Hebda et al., 2010](#)). In another example, a previous history of growth under monochromatic (red or blue) light decreased the photosynthetic performance of rose plants under subsequent high light conditions ([Bayat et al., 2018](#)).

Light also modulates plant responses to non-light stimuli. In *Arabidopsis*, salt stress induces the expression of the key proline biosynthetic enzyme (encoded by *P5CS1*) and the accumulation of proline. Both of these responses return to baseline upon recovery from the stress but are enhanced by recurring salt stresses, depending upon light exposure during the recovery stage. This phenomenon, which could be understood as salt-induced transcriptional memory, involves the light-dependent transcriptional regulator HY5 and light signaling-dependent maintenance of histone methylations ([Feng et al., 2016](#)). A similar mechanism may also operate during other stresses.

Other defense responses of plants, especially induction of acquired resistance and detoxification mechanisms to eliminate reactive oxygen species, are also regulated by light, including by its spectral quality prior to stress exposure ([Lee et al., 2015](#); [Han et al., 2019](#); [Gallé et al., 2019](#)). Several lines of evidence (reviewed in [Müller-Xing et al. \(2014\)](#)) suggest that plants developed an epigenetic memory of UV and visible light stress. Low, ecologically relevant doses of UV-B radiation induce alterations in antioxidant status, likely protecting plants from distress when conditions worsen.

Based on such findings, we expect that prior light history affects plants’ responses to adverse conditions, such as the near-total light deprivation encountered by the pea plants in the associative learning experiments ([Gagliano et al., 2016](#); [Markel, 2020a](#)). It is quite possible that different light conditions employed in the early stages of these two studies may have contributed to their discordant outcomes. If, however, the outcome of associative learning is not robust towards growth conditions, its biological relevance may be questioned. Nevertheless, there are other phenomena that “come and go” (or teeter on the edge of statistical significance) depending on light conditions. Application of fluctuating light was, for example, recently found to elicit unexpected phenotypic variability, not observed under constant light, among *Arabidopsis* accessions ([Kaiser et al., 2020](#)).

Conclusions

Given the central role of light in the life of plants, it is not surprising that the light history of an individual plant can profoundly affect not only its ontogeny and structure, but also its responses to various environmental stimuli.

Regarding the current controversy over Markel (2020a) inability to reproduce Gagliano *et al.* (2016)'s findings of associative learning in pea seedlings, we hypothesize that different light conditions during plant cultivation prior to the experiments may have accounted, at least in part, for the discrepancy between their results, perhaps in combination with other factors, such as the use of different plant cultivars. It thus remains to be seen whether the plant associative learning observations can be replicated under conditions identical to those employed in the original report. In the absence of additional experimental data (possibly also involving other species and different experimental setups), the question whether plants are capable of associative learning remains open.

On a more general note, the controversial case of plant associative learning should remind us of the importance of using consistent and well-documented light conditions, especially with respect to spectral quality of light, during all steps of experimental material cultivation—not only in plant memory studies but in all areas of experimental plant biology.

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