



On plants and principles

Invited commentary on Birch, Ginsburg and Jablonka's target article *Unlimited Associative Learning and the Origins of Consciousness: A Primer and Some Predictions*

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A critical oversight in the authors' (Birch et al.) UAL framework arises in its stated basis in an “unlimited heredity” (UH) argument. Specifically, the foundational UH claim is that there is a possibility space constrained by the known properties of DNA, and that, within that space, a subset of specific “real” lineages arise. These lineages are actualisations of possibilities, under the assumption that no amount of time would be sufficient to actualise all possibilities. The oversight—already present in UH, but ‘inherited’ by UAL—regards what pressures produce the actual subset of lineages from the *in principle* possible lineages.

Significantly, the subset is neither due solely to the “constraints” granted by Birch et al., nor is it arbitrary. Rather, the subset of actual lineages is the result of a reciprocal process with the environment that has been highlighted in research on the Extended Evolutionary Synthesis (EES) (e.g. Laland et al. 2017). In this commentary, we will underscore how this critical oversight concerning reciprocal pressures poses a core problem for the target article's characterisation of UAL.

To begin with, we note that plants are indisputably lifeforms, according the criteria set forth in Birch et al., and plants of course share the Earth with animals. To the authors' credit, their argument does *not* reflexively locate the transition marker for UAL and consciousness between plants and animals. Instead, they take a principled approach, by first claiming that a certain kind of learning—UAL—should be transition marker for consciousness, and then attempting to explore where we might find such learning by organisms.

On the other hand, even with a “UAL appears no later than” escape clause, their rhetoric suggests an impoverished view of plants: e.g., “Can we find a property that requires [the] hallmarks of consciousness, yet is possessed by a wide range of

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non-human animals?"; "UAL [...] can tell us which animals are conscious, but it does not aspire to tell us which are not"; "which animals are capable of UAL?". This zoocentric attitude readily obscures the ways in which plants meet many criteria that are typically assumed to be unique to animals (Linson and Calvo 2020). The authors' self-imposed selection bias is not only problematic in theory, but also substantially limits the proposed empirical tests of their predictions, based on "neural signatures", psychophysics, etc.

To describe UAL, Birch et al. offer a list of "enhanced forms of associative learning"—hypothesised to comprise a "natural cluster"—while granting that these forms have fuzzy boundaries and do not logically imply each other. Instead, they may be observed to be working together in organism behaviour within "realistic ecological settings". Crucially, however, "realistic ecological settings" are not a mere backdrop against which organism action unfolds. The authors maintain that lineages were evolving to occupy newly discovered niches—a viewpoint entrenched in the Modern Synthesis that has not taken on board the insights about niche construction developed in EES. Specifically, there is a constant two-way interaction and mutual reshaping of organism and niche, which affects not only lifespan, but also lineage (Laland et al. 2017). This brings us back to the relevance of the fact that animal and plant lifeforms share the same planet.

Birch et al. hypothesize that associative learning must have been a major driving force behind the rapid animal diversification during the 'Cambrian explosion', prior to the emergence of life on dry land. But the subsequent terrestrialization that took place throughout the Early Paleozoic Era was not exclusively animal; plants and fungi were key actors. In fact, animal diversification in the Cambrian has a parallel in the evolution of a solar-energy-harvesting lineage that includes aquatic charophycean green algae, and that gave rise to land plants (the algae may have become terrestrial before the advent of plant roots; see Harholt et al. 2016). Land plants flourished in the early Devonian period when the main body of some land plants started to lignify, becoming woody, and the root-shoot/leaf polar morphologies found in higher plants became settled. In short, there is no reason to exclude the possibility that forms of learning similar to those of animals were among the driving forces behind the rapid plant diversification during that period.

There is certainly a basis in the empirical literature on plants to entertain the idea that not only are the key features of UAL found in plants, but also the *requirements* for UAL (Birch et al., Fig. 3). An increasing body of research suggests that there are plant counterparts of UAL features and requirements characterizable in cognitive and behavioural terms. Plant-level and inter-plant communication takes place customarily; the capacity to discriminate kin from non-kin is present in plants too. Plants can weigh different stimuli and prioritise their responses according to different needs. Plants are able to choose between alternative courses of action, engaging in complex decision-making that calls for the integration of multiple informational sources, allowing them to implement different strategies for nutrient foraging. Plants exhibit behaviours that are anticipatory and goal-directed (Raja et al. 2020). (For a thorough review see Calvo et al. 2020a; Segundo and Calvo 2019; 2021).

We have space to consider a few more specific points here. For instance, while Birch et al. recognise that "a food source can suddenly acquire a nearby predator",

they somehow overlook that the adaptive behavioural response may point to fixed survival priorities, rather than flexibility. They implicitly concede (in their section on false alarms) that there is no sense in getting nourishment from food if only to perish by predation moments later—better to survive hungry for a bit and get food later. In this regard, it hardly seems that formed value associations are being “rewritten” in such cases, in line with their elaboration of UAL features. Following the authors’ examples, the flexibility they seek is found in plants: a plant might have roots growing upward in the soil, to reach a nutrient-rich patch, until it breaks through the soil to the surface, where bare roots are harmed by sunlight. It then ‘learns’ to grow its roots downward instead. For other plants nearby, the nutrient-rich soil may extend in parallel to the surface, so they ‘learn’ to grow their roots outwards.

Perhaps such plant responses are adequately flexible but not quick enough (see feature #5). Yet, given the central role of lifespan in UAL, shouldn’t quickness be treated as a relative measure? Or, are we to use the same standard of quickness for insects that live just one day and trees that live hundreds of years? With respect to ‘false alarms’ in plants, over-reacting due to over-learning may explain the evolution of ameliorating mechanisms specific to plants, analogous to those Birch et al. consider in the case of animals (e.g., plant stress responses in terms of an increase in levels of overall phenotypic integration) (Calvo, Gagliano, Souza & Trewavas 2020b; Calvo and Trewavas 2020).

But one needn’t slow down for plants across the board. Another UAL feature (#4) concerns the “escape from immediacy”, learning “how stimuli that are no longer present relate to current stimuli”. In rain forests, under-canopy trees steadily orient their foliage towards future sunfleck patterns, in ways that show extrapolation from past patterns.

Returning to our opening point, the “unlimited” attribute, whether of heredity or associative learning, as Birch et al. acknowledge, is constrained. But what they do not acknowledge is that these possibility spaces are not merely constrained, they are actively shaped by pressures that appear to undermine the very promise of being unlimited. Organisms are in constant interaction with their local environment, and their complexity as alleged “experiencing systems” must be tailored to their concrete needs (Mediano et al. 2021).

Despite the zoocentric framing of their proposed experimental tests, Birch et al. concede that the distribution of UAL might be larger, and are thus open to the possibility that future experiments confirm the existence of UAL in some other taxa/ phyla. Can experiments be devised to empirically measure plant forms of learning (Baluška et al. 2018) that would meet UAL expectations? Existing experimental studies exploring associative learning in plants report mixed results (see Adelman 2018 for the review). Most of these studies have been carried out in 1960–70s and lack sufficient experimental rigor. Gagliano et al. (2016) provide the most recent evidence of associative learning in pea plants. However, the one and only recent attempt to replicate it has not succeeded and remains contested as of today (Markel 2020a, 2020b; Gagliano et al. 2020). Replication studies of Gagliano et al.’s results are needed (Abramson and Chicas-Mosier 2016). More recently, the model plant

Arabidopsis thaliana has been reported to exhibit aversive conditioning (Bhandawat et al. 2020), but this, too, awaits independent replication.

Overall, there is not enough conclusive empirical evidence to either accept or rule out what would amount to UAL in plants. Current experimental research at MINT-Lab aims to find out whether plants are responsive enough to coaching to meet or surpass basic associative learning. At least we are in agreement with the authors about one key point, in line with their recognition that molluscs and annelids have been insufficiently studied. Namely, as to the matter of which organisms exhibit UAL and consciousness: the jury is still out.

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