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VIEWS AND COMMENTS

Plants learn and remember: lets get used to it

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> "*I think I've discovered the secret of life–you just hang around until you get used to it*"
>
> ~ Charles Schultz

In one of the most beloved comic strip of all times, the creator of Charlie Brown and Snoopy said it all. At the most basic level, this "getting used to it"—a decrease in response to a stimulus after repeated exposure—is what behavioural habituation is about. And, it is an extremely important (adaptive) aspect of life; thanks to it, organisms learn to pay attention to stimuli that are truly meaningful in their environment while ignoring those that have proven irrelevant and innocuous. Despite its simplicity, the concept of habituation seems to have always stirred great debate. For example, the earliest descriptions of what we would now call habituation came from studies conducted by Pfeffer using the sensitive plant *Mimosa pudica* in 1873 and the Peckhams using spiders in 1887; remarkably, no real agreement on the use of the word 'habituation' was to be found until (almost) a whole century later (see review by Christoffersen 1997).

As Christoffersen (1997) pointed out, the terminology debate regarding habituation could not be settled until the 1960s, because, only then, the number of studies that investigated the behavioural phenomenon had grown sufficiently large, so that Thompson and Spencer (1966) could establish an operational definition. Thompson and Spencer's definition of habituation was based on a list of nine behavioural characteristics, which have since been confirmed by most of the cases investigated and still constitutes a useful working framework today. While remaining largely unchallenged since its formulation, the list of characteristics was nonetheless expanded by Groves and Thompson in (1970), revised by Christoffersen in 1997 and updated again by Rankin et al. in 2009, for some examples. Hence, while providing a convenient primer for the study of habituation in a wide range of species and paradigms, this framework may not be taken as a set-in-stones rule manual but rather as an evolving guide. From an ecological perspective, such a framework would be most useful and its application most interesting when informing the study of habituation as the process enabling an organism to better respond and adapt to its constantly changing environment. This is how it was applied in the Gagliano et al. (2014) study, whose aim was to investigate the learning process of the *Mimosa* plant within the context of a trade-off between predation risk and foraging for light, a context that is ecologically relevant to this plant.

In considering these issues, Beigler (2017)'s commentary points out that Gagliano et al. (2014) correctly tested the most relevant behavioural characteristics of habituation. Beigler expresses concerns over the omission of characteristics Gagliano et al. (2014) did not test, and over the fact that other tests not mentioned in the list of criteria (as per Rankin et al. 2009) were included instead. As it is perhaps true of most ecological studies investigating habituation, Gagliano et al.'s paper never aimed nor claimed to be a test of all the criteria characterising the process of habituation as defined by Rankin et al. (2009). Besides, several of the characteristics not (expressly) examined by Gagliano et al. had been investigated in earlier studies of this plant (reviewed by Sanberg 1976 and more recently, Abramson and Chicas-Mosier 2016). What Gagliano et al.'s study did examine were the most relevant behavioural characteristics of habituation in the context of a broader ecological question—whether *Mimosa*'s ability to learn through the habituation of its defensive leaf-folding reflex was mediated by environmental circumstances such as low- and high-light

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levels. Hence, within this ecological context, Gagliano et al. established that (1) a repeated stimulus (i.e., a vertical drop) caused a progressive decrease in the amplitude of the defensive response (i.e., the leaf-folding behaviour), (2) habituation of the defensive response was stimulus specific, and (3) it could be distinguished from sensory adaptation (loss of sensitivity) and fatigue (loss of leaf-folding motion, because the response system becomes depleted). We take the opportunity to recap these findings here for the sake of clarity and to dispel any doubts regarding the validity of Gagliano et al.'s study.

First, the results confirmed that *Mimosa*'s defensive reflex habituates, and quite readily so. Gagliano et al. observed leaves starting to re-open after the first four-to-six vertical drops of a train of 60 drops; this is possibly for the very reason that, even in plants, defensive reflexes must be fast to be effective (as it has long been recognised in animals, Pinsker et al. 1970). The study also showed that with further repeated vertical drops over the course of the training, *Mimosa*'s leaves completely re-opened and the vertical drop no longer elicited leaf closure. At this point, it is important to test whether the observed behaviour is truly due to learning—had the plant learned, and was now 'choosing' to keep its leaves open or it was no longer capable of closing them?

As correctly pointed out by Beigler's commentary, it is necessary to distinguish habituation from mere fatigue, which would result in the inability to detect or respond to any stimulus due to exhaustion of energy or other physiological resources. In other words, if *Mimosa*'s closing/reopening response mechanism had being depleted, the leaves would have lost their actual ability to move in order to close in response to a novel stimulus (i.e., the shaking) presented after the repeated stimulation (i.e., the vertical drop). In an ecological context, the inability to respond appropriately to unfamiliar stimuli would be extremely dangerous, as it would leave the plant unguarded in the face of potentially harmful circumstances. However, this is not what happens. When presented with the shaking stimulus after several consecutive trains of vertical drops, all leaves responded to the new stimulus by folding completely closed, a most likely adaptive defensive response to what may be a threat (and plants would not have been able to perform the leaf closure if the response system was depleted). This indicated that *Mimosa* was indeed able to detect the new stimulus (no sensory adaptation) and respond to it (no fatigue). Next, when the familiar vertical drop stimulus was re-presented soon after this brief, one-off experience of the shaking stimulus, the original habituated response could be fully elicited again. The fact that habituated *Mimosa* plants responded again to the vertical drop stimulus after the shaking stimulus indicated that those plants were still able to perceive the original drop stimulus (thus excluding sensory adaptation). It also showed that *Mimosa* could, as Holmes and Yost had already observed back in 1966, "tell the difference" between stimuli and responded accordingly. In other words, it is precisely through its own previous experience that *Mimosa* learned to adjust its actions in a presumably adaptive manner. Thanks to the process of habituation/dishabituation, *Mimosa* was able to avoid unjustified energy expenditure when confronted by a learned harmless stimulus (i.e., the habituated response was specific to the repeated stimulus, the vertical drop), while keeping its energy reserves to be able to respond to stimuli that could truly pose a threat (i.e., the plant remained responsive to sporadic stimuli, which are typically of greater significance). Like much defensive behaviour in nature, *Mimosa*'s leaf closure is costly and thus displayed selectively only in response to an actual or perceived threat. It is by investigating how environmental circumstances influence such behavioural trade-off thus shaping how plants learn and remember that Gagliano et al.' s study made a significant contribution to this field.

In conclusion and contrary to Beigler's suggestions, the status of *Mimosa*'s habituation is not uncertain at all; the various facets of it have been examined for decades (see review by Abramson and Chicas-Mosier 2016) and in keeping with the proper process of science, Gagliano et al. (2014) have built on this knowledge by greatly expanding the experimental method and looking at a wider range of questions than previously reported. Much of the evaluation (and reservations) offered by Beigler seems to stem from a conviction that the *Mimosa* plants in Gagliano et al.'s study were energetically exhausted (i.e., motor fatigued). Not only is this probably incorrect, but it is also a major assumption, an assumption that Beiger himself acknowledges might explain some data but does not easily explain other results. Perhaps, this is because the plants were *not* fatigued at all; if anything, their behaviour reveals quite the contrary, as outlined above. Clearly, the best challenge for these findings is further empirical work. In addition, while we feel that Beigler offers some good suggestions on how to further improve investigations of *Mimosa*'s habituation, it is a little disappointing to see no experimental data accompanying his arguments—especially given that Gagliano et al.'s study was published some time ago. Accordingly, we hope to see Beigler or others following up on those suggestions with new experimental data. We believe that this would make a most constructive contribution to a growing body of literature on behaviour and habituation of *Mimosa*'s leaf closure (e.g., Jensen et al. 2011, Cahill et al. 2013, Amador-Vargas et al. 2014, Simon et al. 2016, Reed-Guy et al. 2017) as well as the wider area of plant behavioural research (e.g., Trewavas 2014, Karban 2015). We have no doubts that the research community would welcome it.

On this note, we would like to thank Beigler for taking our study seriously and opening up the opportunity to further explore questions of plant learning. Combined with

the more recent research demonstrating the occurrence of even 'higher' forms of learning in plants (e.g., Pavlovian conditioning; Gagliano et al. 2016), we take this as an overall positive sign that the study of plant learning is ready to receive proper consideration by the wider research community. Finally, after some initial defensive reactions to the perceived danger of considering plants much more capable of performing cognitive feats (e.g., learning, memory, decision making, problem solving, and more) than we would like to acknowledge (Pollan 2003), perhaps, the time has come to finally get used to it.

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