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On-line control of movement in plants

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ABSTRACT

At first glance, plants seem relatively immobile and, unlike animals, unable to interact with the surroundings or escape stressful environments. But, although markedly different from those of animals, movement pervades all aspects of plant behaviour. Here, we focused our investigation on the approaching movement of climbing plants, that is the movement they perform to reach-to-climb a support. In particular, we examined whether climbing plants evolved a motor accuracy mechanism as to improve the precision of their movement and how this eventually differs from animal species. For this purpose, by means of three-dimensional kinematical analysis, we investigated whether climbing plants have the ability to correct online their movement by means of secondary submovements, and if their frequency production is influenced by the difficulty of the task. Results showed, not only that plants correct their movement in flight, but also that they strategically increase the production of secondary submovements when the task requires more precision, exactly as humans do. These findings support the hypothesis that the movement of plants is far cry from being a simple cause-effect mechanism, but rather is appropriately planned, controlled and eventually corrected.

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1. Introduction

Plants exhibit a wide range of movements, from the opening of tiny stomata to the tropism of trunks in response to gravity, sunlight, and other numerous ecological niches [1]. Most of these movements are imperceptible by layman's eyes, but not by Charles Darwin's ones, who in the late '800 described in great details the movement of plants with specific reference to the trajectories of climbing plants during their approach to a support [2]. Darwin observed that the tendrils of climbing plants perform an elliptical movement around their axes of elongation. This movement, known as *circumnutation*, allows plants to explore the environment in search of resources and climbable supports [3].

Interestingly, Francis Darwin [4] speculated that climbing plants were able to "see" the support and adjust tendrils' movement in flight according to its features. Implicitly, this may signify that climbing plants program their actions in terms of their perceivable

consequences: selecting, planning, and initiating an action is thus mediated by action-effect anticipations [5]. Recent studies support this contention pointing out that plants are cognitive agents controlling their movement by means of anticipatory processes [5]. Guerra and colleagues [5] investigated the movement of a climbing plant (*Pisum sativum* L.) by equating its tendrils to an hypothetical hand reaching and grasping a support. Results demonstrated that the movement of climbing plants looks remarkably similar to the human's one [6]. Indeed, they are able to distinguish whether the support is graspable or not, and most importantly, they program different kinematics depending on support's thickness. This aspect is particularly important because it signifies that they extract the 'graspable' properties of the stimulus to determine how to engage motor modules to produce suitable behavioural outputs.

Plants also benefit of complex tradeoff mechanisms until recently considered a preserve of brained organisms. For instance, aspects concerned with speed-accuracy tradeoff mechanisms have been investigated by Ceccarini and colleagues [7] by applying the Fitts' law [8] to plants' movement. According to Fitts [8,9] the human sensory-motor "channel" is a limited-capacity system, so that the time to perform an action is proportional to the amount of

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information required for controlling the movement. This quantity, also known as index of difficulty (ID), depends on the ratio between the size and the distance of the target [9]. Aside from humans, Fitts' law has been shown to hold across a wide range of animal species [10–13]. Moreover, Ceccarini and colleagues [7] demonstrated that these principles also apply to plants. Indeed, plants are able to process the properties of the support before contact and, similarly to animal species, strategically modulate movement velocity according to task difficulty [7].

Given that the accuracy of movement has a crucial adaptive importance for climbing plants and influences their long-term chances for survival [14], here we take a step forward. We ask whether climbing plants, as animals, have evolved a motor accuracy mechanism which allows for adjusting their movement online and reducing the probability of errors. In human beings, one of the major mechanisms for movement accuracy regulation is the production of corrective adjustments [15], also known as *secondary submovements*. Movements that people perform in everyday life, such as eating, walking, picking up a bottle of juice, showing something to others, dancing and even pointing to some targets consist of complex and subtle submovements, with lots of imperceptible corrections. In this perspective, movements can be divided into two stages: an initial impulse and current control [16]. The initial impulse aims to move to the target quickly, whereas the current control is aimed at improving the accuracy of the movement [17,18]. The main movement (the first submovement) is generated by intention, then it is adjusted by the subsequent submovements so to apply a natural control of smooth and continuous trajectories.

Submovements emerge during the homing-in phase and contribute to the reduction of any spatial discrepancy between hand and target positions. In other words, when the task requires more precision, more secondary submovements are needed. So, for example, when the need for accuracy increases movement velocity decreases, whereas the production of the secondary submovements increases in order to reduce the end-point variability of an effector (e.g., arm for humans), and thus, the probability that the effector falls outside of the target bound [16,19].

With this in mind, our research was driven by two main questions: are plants equipped with a form of movement accuracy mechanism, which adjusts the movement by means of secondary submovements? Is this mechanism influenced by the difficulty of the task?

To test this, we used kinematic analysis to describe the trajectory of climbing plants (*Pisum sativum* L.) during their approach-to-grasp a thin or a thicker support, and measured the number of submovements performed in proximity of the stimulus. Further, to assess the precision of the movement, we measured the endpoint variability, that is the variability of tendrils position at the end of the movement.

2. Method

2.1. Subjects

A total of 10 snow peas (*Pisum sativum* var. *saccharatum* cv Carouby de Maussane) were used in the present experiment. Pea is an annual plant from the Fabaceae family growing filamentous organs, called tendrils, which serve the plants to anchor themselves upright to supporting structures. Plants were randomly assigned to each experimental condition.

2.2. Stimulus

The stimulus was a wooden support of 60 cm height of either

3 cm (thick stimulus) or 1.2 cm (thin stimulus) in diameter positioned at a distance of 12 cm in front of the first unifoliate leaf for each plant (see Fig. 1A).

2.3. Apparatus

The experimental apparatus is described in Fig. 1A. Pea seeds were sowed in cylindrical pots (diameter = 20 cm, height = 20 cm) containing agricultural soil. We sowed 1 seed per pot, at a depth of 2.5 cm, by placing the seed at a distance of 6 cm from the pot center. Pots were then enclosed in growth chambers (Cultibox SG combi 80 × 80 × 10 cm) for germination and growth in controlled environment conditions. Chamber air temperature was set at 26°C by an extractor fan equipped with a thermo-regulator (TT125; 125 mm-diameter; max 280 MC/H vents) and an input-ventilation fan (Blauberg Tubo 100–102m³/h). The combination of the two fans allowed for a steady air circulation into the growth chamber with an air mean residence time of 60 s. The disposition of the fan was such that air circulation did not affect the natural plants' movements. Plants were grown with a 11.25-hour photoperiod (5.45 a.m.–5 p.m.) under a cool white led lamp (V-TAC innovative LED lighting, VT-911-100W, Des Moines, IA, USA) that was exactly centered at 50 cm above each seedling. Photosynthetic Photon Flux Density at 50 cm under the lamp in correspondence of the seedling was 350 $\mu\text{molPh m}^{-2} \text{s}^{-1}$ (quantum sensor LI-190R, Lincoln, Nebraska USA). Reflective Mylar® film of chamber walls allowed for better uniformity in light distribution. Pots were watered with tap water as needed three times a week. Experimental treatments were applied to single plants while individually growing in one growing chamber. Treatments were replicated five times by randomly assigning treatments to the four growing chambers.

2.4. Video recording and data analysis

The recording of plants movement was performed using a pair of RGB-infrared cameras (i.e., IP 2.1 Mpx outdoor varifocal IR 1080P) placed inside each growth chamber, 110 cm off the ground and spaced at a distance of 45 cm to record stereo images of the plant. The cameras were connected through Ethernet cables to a 10-port wireless router (i.e., D-link Dsr-250n) used to send images via Wi-Fi to a PC on which the frames acquisition and saving process was controlled by means of CamRecorder software (Ab.Acus s.r.l., Milan, Italy). A black felt velvet was fixed on some sectors of the growth boxes walls and the wooden stimuli were darkened with charcoal in order to maximize contrast between the pea anatomical landmark (i.e., the node below the tendrils) and the background. The intrinsic, extrinsic and the lens distortion parameters of each camera were estimated using Matlab Camera Calibrator app. Twenty pictures of a chessboard (10 columns and 7 rows of squares 18 × 18 mm) taken from multiple angles and distances, in natural non-direct light conditions were used for the single-camera parameters extraction process. The same chessboard was placed in the middle of the growth chamber and used for the calibration of each pair of cameras. In particular, a picture was taken by the two cameras, to extract the stereo calibration parameters. In the experimental protocol, each frame was acquired every 3 min (frequency 0.0056 Hz) synchronously from each camera of the growth chamber. To track the position of markers and reconstruct their 3D trajectory, we used an ad hoc software (Ab.Acus s.r.l., Milan, Italy) developed in Matlab. The initial frame was defined as the frame at which the tendrils of the coiled leaf were visible from the apex. The end of the plant movement was defined as the time at which the tendrils started to coil the support. The anatomical landmark of interest, namely the node below the tendrils, was considered as marker and tracked offline. For characterizing plants approaching

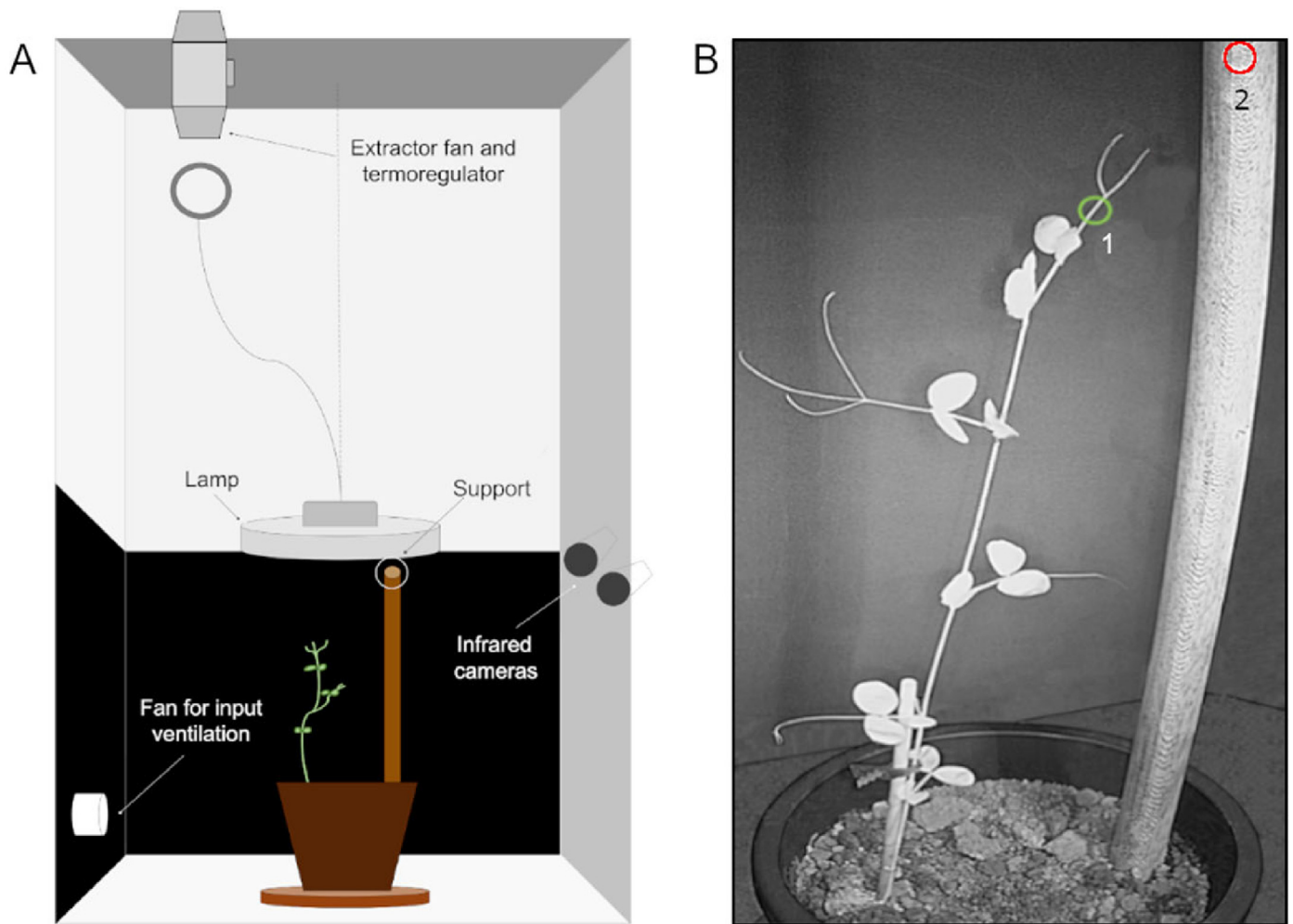


Fig. 1. (A) Graphical representation of the experimental set-up. (B) The node below the tendrils (1) was tracked in time through video digitalization procedures. Marker 2 was positioned upon the stimulus and served as reference point.

movement, the human reaching model was used as reference [6]. In particular, we equated the node below the tendrils (Fig. 1B; marker 1) to a hypothetical wrist that accompanies the tendrils (hypothetical fingers) towards the support. One marker was also positioned on the top of the support and served as reference point. Tracking procedures were performed at first automatically throughout the time course of the movement sequence using Kanade-Lucas-Tomasi (KLT) algorithm on the frames acquired by each camera, after distortion removal. The tracking was manually verified by the experimenter, who checked the position of the markers frame-by-frame.

The dependent measures considered in this experiment were the total number of submovements and the endpoint variability. We considered the three submovements traditionally reported in reaching literature [16; see Fig. 2]: reversals in the trajectory (Type 1 submovement), defined as a zero crossing from positive to negative value occurred in the velocity profile; re-accelerations toward the target (Type 2 submovement), defined as a zero-crossing from negative to positive value occurred in the acceleration profile; decreases in the rate of deceleration (Type 3 submovement), defined as a zero-crossing from positive to negative value appeared in the jerk profile.

Only secondary movements emerging in the final 5% of the movement time were considered, because corrective adjustments

usually emerge in close proximity to the target [15]. The endpoint variability of the approaching movement was defined as the standard deviation of the Euclidean distance between the final position of the node below the tendrils and the reference marker located upon the stimulus (marker 2).

2.5. Statistical analysis

Statistical analyses were performed using the Bayesian approach, which provides an accurate parameter estimation. On the contrary, the frequentist approach runs a strong risk of false negatives for small samples [20].

In the present study, we compared the 'Thin' and the 'Thick' stimulus condition, in terms of total number of submovements and endpoint variability. For this purpose, we used the BEST (Bayesian ESTimation supersedes the *t*-test) model, implemented by Kruschke [21]. All statistical analyses were performed using the computing environment R (www.r-project.org/), and the packages BEST under default setting. We also examined the correlation between the total number of submovements and the endpoint variability using *bayes.cor.test* of the package *BayesianFirstAid*.

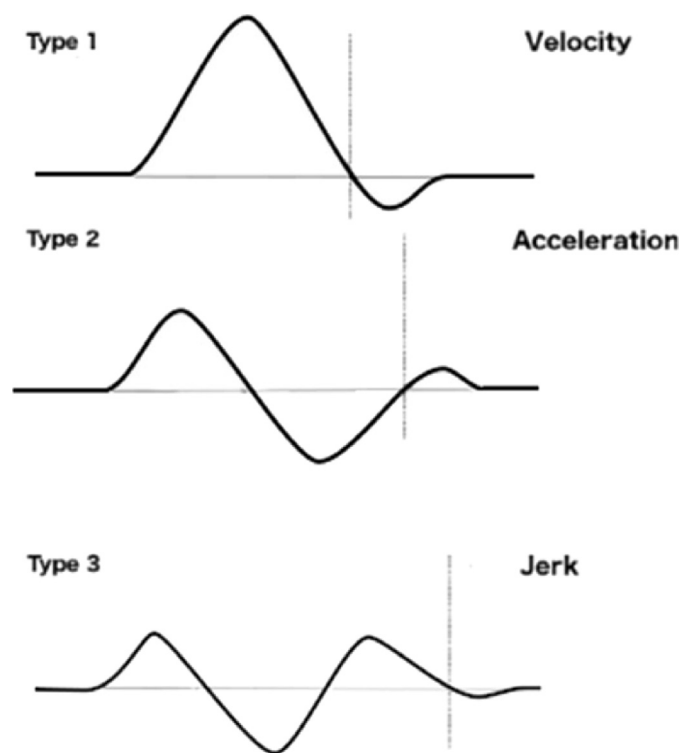


Fig. 2. Examples of a discrete movements with secondary submovements of types 1, 2, and 3. The vertical line represents the hypothetical beginning of the secondary submovement.

3. Results

3.1. Qualitative description of movement

As shown in Fig. 3, the analysis of the spatial trajectory revealed that the considered landmark showed a growing pattern characterized by circumnutation [2] that is an elliptical movement performed by plants during growth.

3.2. Submovement analysis

The mean difference of the total number of submovements between the Thick ($M = 34.56 \pm 17.35$) and the Thin ($M = 22.46 \pm 5.19$) stimulus condition was 12.10, with a 95% uncertainty interval ranging from -20.60 to 46.10 (see Fig. 4A). The probability that the total number of submovements is larger for the Thick stimulus condition was 82%.

3.3. Endpoint variability

The mode differences of the endpoint variability (tendrils position at the end of the movement) between the Thick ($Mo = 17.72$) and the Thin ($Mo = 23.32$) stimulus condition was -5.60 , with a 95% uncertainty interval ranging from -71.30 to 48.70 (see Fig. 4B). The probability that the endpoint variability is smaller for the Thick Stimulus condition is 66.70%.

3.4. Correlation analysis

The correlation between secondary submovements and the endpoint variability is -0.26 , with a 95% uncertainty interval ranging from -0.75 to 0.42 . The probability that the endpoint variability is negatively correlated with the total number of

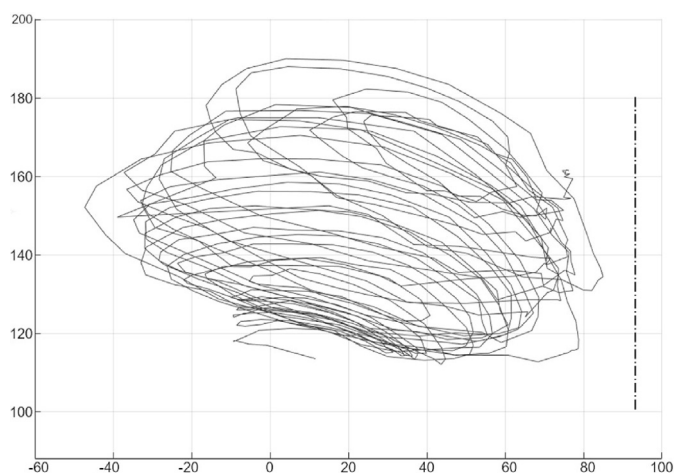


Fig. 3. Representative spatial trajectory of the node below the tendrils (Subject 1). The vertical line represents the support.

submovements is 73.2%.

4. Discussion

The aim of the present study was twofold. Firstly we investigated whether the movement of pea plants is adjusted online by means of secondary submovements. Secondly, we examined if the production of secondary submovements is influenced by task difficulty. The results showed that peas are able to recognize the support [4,6,22], and adjust online the position of the node accompanying the tendrils as they approach it. More interestingly, peas modulate the production of submovements as a function of the support's thickness. The frequency of submovements tends to increase when the support is thick. This evidence suggests that plants can process the properties of the support and benefit of a motor accuracy mechanism for improving the precision of their movements. The analysis of the endpoint variability confirms this evidence: the standard deviation of the final position of the node below the tendrils is smaller for the thicker than for the thinner stimulus. Moreover, the total number of submovements is negatively correlated with the endpoint variability, which suggests that an increase of submovements production is associated with an improvement of performance accuracy.

However, plants exhibit an opposite pattern than humans. Indeed, human beings experience more difficulty to interact with a thinner than a thicker target [8]. Consequently, the frequency of submovements is larger when the task requires to interact with thinner stimuli [15]. On the contrary, plants produce more secondary submovements when they reach-to-coil a thick support. In other words, our results seem to suggest that plants exhibit more difficulty to grasp a thicker than a thinner support.

This contention is supported by previous studies showing that support thickness affects the twining force and stability of climbing plants [23]. Tendrils might be unable to express the energy necessary to maintain tensional forces with thicker supports. As the grasping success depends on the number of coils around the trellis, larger supports will eventually require the development of longer and thicker tendrils. Therefore, this adaptation can be interpreted as a tradeoff between developing longer and thicker tendrils and a more efficient grasping movement control. In fact, there is evidence of loose attachment to the trellis when the support diameter increases beyond some point [14,24]. The support-size biomechanical constraints are particularly evident for tendril climbers, whose

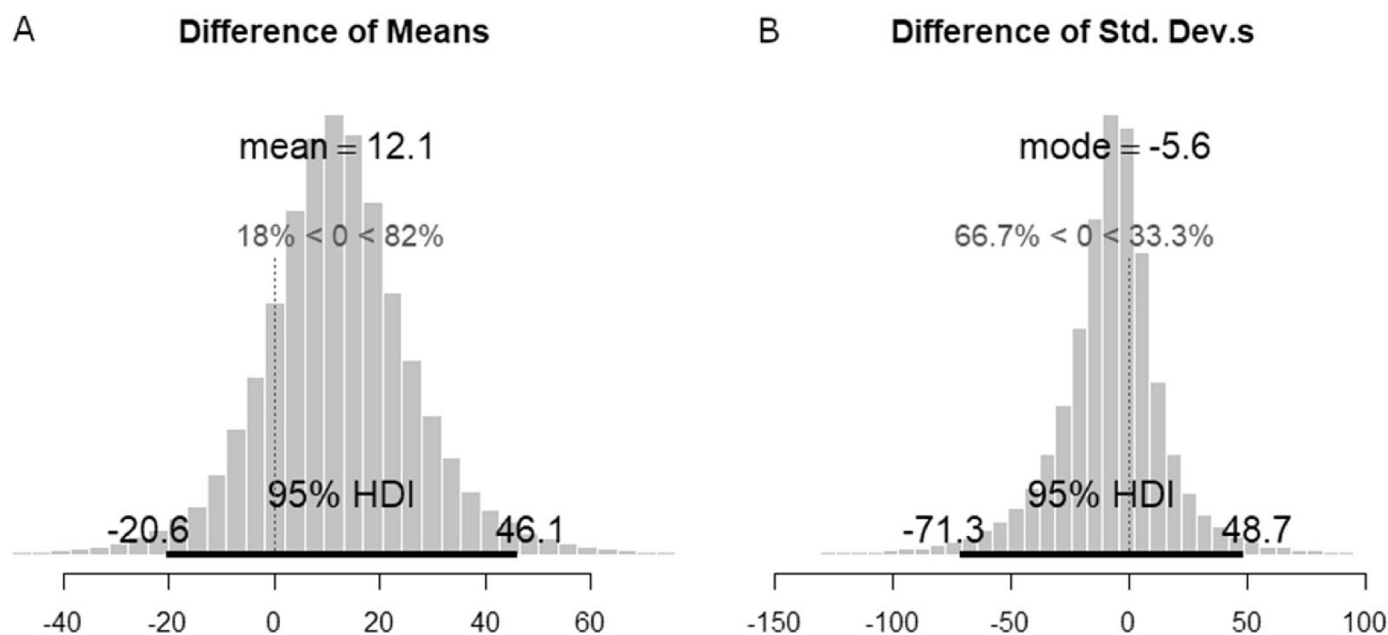


Fig. 4. Posterior distributions for total number of submovements (A), and the endpoint variability (B).

upper limit of usable support diameter is rather low [14,24,25]. In line with this hypothesis, Carrasco-Urra and Gianoli [14] pointed out that the presence of climbing plants in rainforests tends to decrease in areas in which there is a prevalence of thicker supports. These findings can be ascribed to a lower success rate of attachment for thick supports [26], and a preference for plants to climb supports with a smaller diameter [2,24]. Along these lines, Guerra and colleagues [5] found that when plants interact with thicker supports, they implement a more cautionary strategy aimed at coiling the support more efficiently. In particular, tendrils tend to reach their maximum aperture earlier in time when the surface of the stimulus is thicker with respect to when the surface of the stimulus is thinner. This strategy allows plants to lengthen the time window (i.e., the time between the point of tendrils' maximum grip aperture and the beginning of the coiling) within which contact points can be established leading to a more precise and firmer grip [5].

Other studies have pointed out that climbing plants scale movement velocity during circumnutation with respect to the thickness of the support [7]. The average and the maximum tendrils velocity tend to be faster when plants had to reach and grasp a thinner than a thicker support. Again, these findings can be imputed to a greater difficulty for plants to interact with a thicker support, and to the necessity to control more precisely the movement in order to ascend accurately the support [7].

As a consequence, we hypothesize that climbing plants increase the incidence of submovements when they have no other choice but climbing a thick support. These submovements reduce the scatter of tendrils end-position and coil the support with a geometrical configuration that develops some extra forces for resisting gravity.

In human beings, submovements' production depends on visual and proprioceptive feedbacks of limb position, which are used to make necessary trajectory corrections [7,15,16]. But, what sensory modality provides the necessary information to control and adjust online the movement of plants is unknown. It should be noted that plants are physically self-aware so that they can perceive the configuration of their own body [27,28]. Recent reports demonstrate that the proprioception of plants is mediated by the long actin filaments in elongating fibre cells, which, acting as a bending

tensile sensor, perceive the plant's posture [28]. These findings are corroborated by studies on *Arabidopsis* mutants defective in actins (specifically ACTIN-8), which exhibit an abnormal reaction in response to gravity, tilting or other external perturbations [27]. Proprioception may allow climbing plants to know the position of their tendrils and contribute in generating the necessary feedback information required for adjusting movement execution working in tandem with other sensory modalities. Indeed, in addition to proprioception, plants have at their disposal a great variety of sensory modalities [29], including vision [30], acoustic perception [31], chemosensory perception [32]. In light of this, we can hypothesize three possible scenarios which might be responsible for the perception of sensory cues. All scenarios might be correlated with ecologically-important functions. Firstly, climbing plants may have evolved a *plant-specific vision system* processing the intrinsic and extrinsic properties of the support. As early as 1905, Gottlieb Haberlandt suggested that the leaf upper and sub-epidermis comprise cells acting as *ocelli*, eye-like structures allowing plants to gather visual information about their environment [33]. Support to this contention comes from studies on *Boquilla trifoliolata*, a climbing wood vine, which modifies its leaves with perfect mimicking of the host plant leaves, even without a direct contact with it [34]. Coherently, plants may correct the trajectory of their tendril using visual information.

Secondly, plants may use *echolocation* to acquire information about the support. In this perspective, recent reports showed that plants emit sonic clicks and capture the returning echoes as to get information regarding the surroundings [35]. This *bio sonar* may provide information about the correct position of the support, and direct the tendrils towards the object to be grasped.

Finally, plants may acquire information about the support using *chemoreception of volatiles*. In this respect, it is well known that some plants localize host plants via airborne chemicals [36]. For instance, the parasitic plant *Dodder* (*Cuscuta pentagona*) uses volatile cues to direct its growth toward nearby plants [36]. Interestingly, *Dodder* vines are able to discriminate among potential hosts. In particular, they tend to coil host of high nutritional quality (stems with high nitrogen levels) and grow away from lower quality host (with less or no nitrogen) [37].

With our pioneer study, we cannot single out the specific sensory modality involved in the online control of plants' movement. Therefore, further research is needed to clarify this aspect. However, our results speak against the idea that the movement of plants is simply driven by cause-effect mechanisms and hard-wired reflexes. On the contrary, they can accurately control their movement, and correct it in a very flexible way, implementing a more conservative motor pattern when the task requires more precision. In this sense, plants can be considered as intelligent organisms that modify strategically their behaviour to improve their chances of survival [38–42].

In a broader perspective, the present findings suggest that plants meet the precondition for cognitively guided behaviour and provide empirical support to the construction of a theory of cognition that includes organisms outside the Animal Kingdom such as plants.

Historically, plants have been excluded from the wider cognitive domain as they do not have freedom of movement within their environment. But it may not be necessary to link cognition to free-movement within an environment. As we demonstrate, while plants are stuck in the ground, their movements are programmed and controlled through the perception of the features of their surrounding environment.

Open practices statement

All relevant data and R scripts are available at <https://osf.io/s7hna>. The experiment was not preregistered.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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