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# Evidence of Motor Intentions in Plants: A Kinematical Study

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“How” an action is performed is not solely determined by biomechanical constraints, but it depends on the agent’s intention, that is, “why” the action is performed. Recent findings suggest that intentions can be specified at a tangible and quantifiable level in the kinematics of movements; that is, different motor intentions translate into different kinematic patterns. In the present study, we used 3D kinematical analysis to investigate whether the organization of climbing plants’ approach-to-grasp action is sensitive to the kind of intention driving their movement toward potential support, namely individual or social. For the individual condition, a plant in isolation acted upon the support. For the social condition, two plants were located in the same pot opposite to each other with a support in the middle. Results indicate differences in kinematics depending on the context within which the plant is acting. In the presence of neighbors, climbing plants are able to modify their behaviors to maximize their long-term gains, including the grasping of a potential support. Overall, these data suggest that the organization of climbing plants’ kinematics is sensitive to the “intention” driving their movement toward a potential support. To discuss this phenomenon, we capitalize on the concept of motor intentionality in plants and on available theories concerned to motor cognition. We suggest how they could be revisited to explain the intentionality component inherent in plant life and other brainless organisms.

*Keywords:* social cognition, kinematics, competition, plant behavior

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The concepts of “intention” and “intentionality” of actions have been the focus of philosophical consideration for centuries (Wittgenstein, 1953). Nowadays, concepts such as “action” and “motor intention” are becoming to be well defined, and the relationship between an overt intentional behavior and its correspondent covert representations has begun to take form (Ansuini et al., 2014).

Nearly all theories concerned with motor intentions focus on the motor goal, which—although at different levels of complexity—constitutes the core of what intentions represent, that is, “goals and the means to those goals” (Pacherie, 2018). These issues are critical for any attempt to identify the mechanisms underlying the capacity to plan and perform intentional actions. In the time domain, “intentionality is the premotor detail of the desired result of movement: the

choice of what to do before the doing of it” (Llinás, 2002). “How” an action is performed is not solely determined by biomechanical constraints, but it depends on the agent’s intention, that is, “why” the action is performed. This raises the intriguing possibility that intentions, regarded as dispositions by standard theories of social understanding, may become “visible” in an agent’s overt motor behavior (Runeson & Frykholm, 1983).

In this respect, recent findings suggest that intentions can be specified at a tangible and quantifiable level in the kinematics of reach-to-grasp movements (Becchio et al., 2010); that is, different motor intentions translate into different kinematics patterns (Ansuini et al., 2006, 2008). Indeed, the way an object is grasped does not depend exclusively on the properties of the object, but is

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also influenced by the agent's intention. This was first demonstrated by Marteniuk et al. (1987) by asking participants to grasp a disk and either fit it into a container with great accuracy or throw it. The deceleration time was longer for fitting than for throwing. Since this seminal work, a plethora of studies have investigated how intentions influence the execution of reach-to-grasp movements (e.g., Ansuini et al., 2006, 2008; Armbrüster & Spijkers, 2006). The logic of these studies has been to "manipulate" the intention while keeping the object to be grasped (i.e., goal) as well as the situational requirements (i.e., context) constant. If within the same context, the same object is handled differently depending on the agent's intention, this would indicate that the intention influences the grasping kinematics. Ansuini et al. (2008), for example, asked participants to reach toward and grasp a bottle to accomplish one of four possible actions: pouring, displacing, throwing, or passing. Analysis of digit kinematics revealed that when the bottle was grasped with the intent to pour, both the middle and the ring fingers were more extended than in all the other considered intentions. Similarly, the choice of hand placement on the object has been shown to adapt to the upcoming intention. Participants place their thumb and index finger in a higher position when they grasp a bottle with the intention to pour than when they grasp it with the intention to lift (Crajé et al., 2011; Sartori et al., 2009).

Further studies have extended these effects to the domain of social intention. For instance, it has been shown that participants' maximal finger aperture is smaller and grip aperture velocity increases when an object is reached and grasped with the intent to move it compared to when it is grasped with the intent to pass it to another person (Becchio et al., 2008a; see also Quesque et al., 2013; Sartori et al., 2009). At a higher level of abstraction, Becchio et al. (2008b; see also Georgiou et al., 2007) showed that the kinematics of grasping movements differed depending on whether the object was grasped with the intent to cooperate with a partner, compete against an opponent, or perform an individual movement at slow or fast speed. Despite similar task requirements, movement duration was shorter and wrist velocity was higher for "competitive" than for "individual fast" movements. Conversely, movement duration was longer and wrist velocity was lower for "cooperative" than for "individual slow" movements.

This peculiar organization of intentional actions seems to develop very early in life (Butterworth & Hopkins, 1988). Indeed, kinematic studies carried out on fetuses in the womb by means of ultrasonography revealed that by the 22nd week of gestation, fetuses' movements begin to assume the recognizable form of intentional actions, with kinematic patterns matching different goals—hand movements to-the-mouth or to-the-eyes (Zoja et al., 2007). Moreover, the social context of the action influences the movement—movement of a hand toward a twin differs to one performed individually (Castiello et al., 2010). These findings support the idea that an action, from very early in ontogeny, can be planned and organized as a whole chain of acts without the need for fully developed neural structures. Crucially, the biomechanical and temporal structure of motor acts embedded in the action depends on its goal, that is, the motor intention.

The idea that goal-directed actions not only do not require fully developed neural systems, but may not need neural structures at all has recently been demonstrated in plants, which are aneural (Castiello, 2021; Ceccarini et al., 2020, 2021; Guerra et al., 2019). This was achieved by studying circumnutation, a movement of the

growing portions of a plant to form spirals, irregular curves, or ellipses (Darwin & Darwin, 1880). Focusing on the kinematic signatures characterizing these movements, climbing plants can program their movement in advance, moving the tendrils according to the specific characteristics of the to-be-grasped support (Guerra et al., 2019). It was found that the plant perceives the support and during reaching modulates the kinematics of the tendrils' aperture depending on the thickness of the support (Ceccarini et al., 2020, 2021; Guerra et al., 2019). These results are particularly important as they indicate that the plants exhibit forms of motor intentions similar to those exhibited by a variety of animal species (Castiello & Dadda, 2019; Sustaita et al., 2013). For instance, through the perception of neighbors, plants are able to anticipate probable interactions and modify their behaviors to maximize their long-term gains (Novoplansky, 2009), including the grasping of a potential support (Gianoli, 2015). These results invert the general consensus that the movements of plants are only driven by cause-effect mechanisms and hard-wired reflexes and give rise to a question that only a few years ago could be considered absurd: to what extent can a plant intentionally plan a movement?

With this in mind, in the present study, we ask whether the organization of climbing plants' kinematics is sensitive to the "intention" driving their movement toward a potential support. We will capitalize on the concept of intentionality conceived in strikingly spatial terms, as "directedness toward..." (Marder, 2012). It is this directionality of growth, along with its deliberate regulation, that will hold the clue to the intentionality inherent in plant life. In light of this definition, the intentionality of plants may be understood as the movement of growth, directed toward the optimal patches of nutrient-rich soil and sources of light. When animals intend something, they enact their directedness toward by moving their muscles; when plants intend something, their intentionality is expressed in modular growth and phenotypic plasticity (Marder, 2012). In the phenomenological vernacular, each type of plant perception expresses a mode of its intentionality: directedness toward light in photosensitivity, directedness toward sources of heat in thermosensitivity, as well as toward (or away from) self and other in kin recognition. In each case, it is a matter not only of receiving but also of interpreting the signals and deciding among conflicting signals in a nonautomatic manner (Trewavas, 2009). Intentionality here assumes the more colloquial sense of a deliberate purposeful behavior. Piaget (1979) described behavior as follows: "By behavior, I refer to all the actions directed toward the outside world in order to change conditions therein or to change their own situation in relation to these surroundings." This definition is equally applicable to plant behavior but implies intention, usually defined as goal-directed behavior.

Here, we put plants in a condition to perform "intentional" actions in two different conditions offered by either an individual or a social context with the aims of conceptualizing motor intentions in the *green kingdom* and shedding light on the possibility to extend the framework of intentionality across taxa. For the individual condition, plants acted in isolation in order to reach toward and grasp a potential support. For the social condition, two plants were put in the same pot with a potential support in the middle. These are both intentional actions; both involve a movement of translation, from one spatial location to another spatial location. The critical difference is in the "intentional" component: whereas grasping a support realizes a purely individual intention, acting in the presence of another plant inevitably involves a social intention, i.e., the intention to affect a

conspicuous behavior as part of one's reason to act. This is what happened in the social condition in which one of the plants needed to put in place a social attitude to grasp the support. What we were interested in was the effect of social intention on kinematics. Are the characteristics of individual and social contexts played out in the kinematics of movement in plants?

## Material and Method

### Transparency and Openness

How we determined our sample size, all data exclusions, all manipulations, and all measures in the study are reported below.

### Subjects

Twenty-four snow peas (*Pisum sativum* var. *saccharatum* cv. Carouby de Maussane) were chosen as the study plants (see Table 1). Pea seeds were selected, potted, and kept at the conditions outlined below. The plants were randomly assigned to the experimental conditions. We did not perform a power analysis to determine the sample size, because kinematics for social contexts have never been investigated in plants. Thus, running a power analysis is not recommended because it may lead to arbitrary decisions concerning sample size.

### Stimulus

The stimulus (i.e., support) was a wooden pole (60 cm in height and 1.2 cm in diameter; Figure 1). The in-ground part of the stimulus was 7 cm, while the above-ground part of the stimulus was 53 cm. The pole was positioned at 12 cm from the plant's first unifoliate leaf.

### Experimental Conditions

Two experimental conditions were considered (Figure 1): (a) individual condition, in which the plant grew in isolation; and (b) social condition in which two plants grew within the same pot. Treatments were replicated eight times by randomly assigning treatments to the eight growing chambers. Please note that for technical problems, the data for one couple of plants could not be considered in the analysis for the social condition.

### Germination and Growth Conditions

The seeds were made to germinate in absorbent paper for 6 days, and then the healthy and same-height plants were potted. Depending on the experimental condition, two types of cylindrical pots were used. For the individual condition, the pot was 20 cm in diameter and 20 cm in height. For the social condition involving two plants,

the pot was 30 cm in diameter and 14 cm in height to duplicate soil volume. The pots were filled with silica sand (type 16SS, dimension 0.8/1.2 mm, weight 1.4). At the beginning of each treatment, the pots for the individual condition were watered and fertilized using a half-strength solution culture (Murashige and Skoog Basal Salt Micronutrient Solution; 10 $\times$ , liquid, plant cell culture tested; SIGMA Life Science). For the social condition, both the volume of the soil and the solution culture were doubled to maintain the same fertilizing conditions for the two plants. The plants were watered three times a week. Each pot was enclosed in a growth chamber (Cultibox SG combi 80  $\times$  80  $\times$  160 cm) so that the plants could grow in controlled environmental conditions. The chamber air temperature was set at 26  $^{\circ}$ C; the extractor fan was equipped with a thermo-regulator (TT125; 125 mm diameter; max 280 MC/H vents) and there was an input-ventilation fan (Blauberg Tubo 100–102 m<sup>3</sup>/hr). The two-fan combination allowed for a steady air flow rate into the growth chamber with a mean air residence time of 60 s. The fan was placed so that air movement did not affect the plants' movements. Plants were grown with an 11.25-hr photoperiod (5.45 a.m. to 5 p.m.) under a cool white led lamp (V-TAC innovative LED lighting, VT-911-100 W, Des Moines, IA, USA or 100 W Samsung UFO 145Lm/W—LIFUD) that was positioned 50 cm above each seedling. Photosynthetic Photon Flux Density at 50 cm under the lamp in correspondence of the seedling was 350  $\mu$ mol<sub>ph</sub> m<sup>2</sup> s (quantum sensor LI-190R, Lincoln, Nebraska USA). Reflective Mylar<sup>®</sup> film of chamber walls allowed for better uniformity in light distribution (Figure 1).

### Video Recording and Data Analysis

For each growth chamber, a pair of RGB-infrared cameras (i.e., IP 2.1 Mpx outdoor varifocal IR 1080P) were placed 110 cm above the ground, spaced at 45 cm to record stereo images of the plant. The cameras were connected via Ethernet cables to a 10-port wireless router (i.e., D-link Dsr-250n) connected via Wi-Fi to a PC, and the frame acquisition and saving process were controlled by CamRecorder software (Ab.Acus s.r.l., Milan, Italy). To maximize the contrast between the peas' anatomical landmark (e.g., the tendril) and the background, black felt velvet was fixed on some sectors of the walls of the boxes and the wooden stimuli were darkened with charcoal. The intrinsic, extrinsic, and the lens distortion parameters of each camera were estimated using a Matlab Camera Calibrator App. Depth extraction from the single images was carried out by taking 20 pictures of a chessboard (squares' side 18 mm, 10 columns, seven rows) from multiple angles and distances in natural nondirect light conditions. For stereo calibration, the same chessboard used for the single-camera calibration process was placed in the middle of the growth chamber. The photos were then taken by the two cameras to extract the stereo calibration parameters. In accordance with the experimental protocol, a frame was synchronously acquired every 3 min (frequency 0.0056 Hz) by the cameras. The tendrils developing from the considered node were studied. In those cases in which the plant grasped the stimulus, the coiled leaf was analyzed. When no grasping occurred, the last terminal node was examined. The initial frame was defined as the frame in which the tendrils of the considered leaf were visible from the apex. The end of the plant movement was defined as the frame in which the tendrils of the leaf started to coil around the stimulus or a frame in which the tendrils remained apart. An ad hoc software

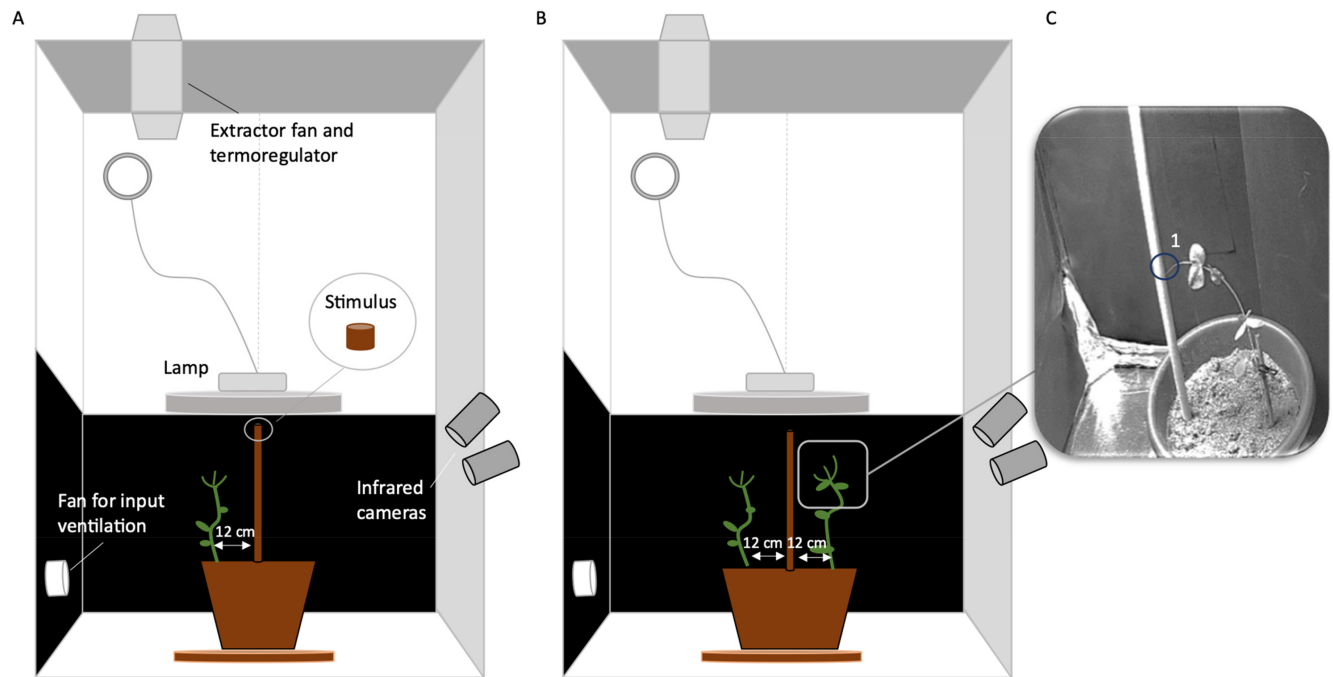
**Table 1**  
Sample Description

	Experimental conditions	
	Social	Individual
Subjects		
No.	16	8
Germination period	6 d	6 d

Note. The germination period is expressed in days.

**Figure 1**

Graphical Representation of the Experimental Setup for the Individual Condition (A) and for the Social Condition (B). The Callout Represents the Anatomical Landmark (i.e., the Tendril) That Will Be Tracked for Kinematical Analysis (C)



Note. See the online article for the color version of this figure.

(Ab.Acus s.r.l., Milan, Italy) developed in Matlab was used to identify anatomical points to be investigated by means of markers and to track their position frame-by-frame on the images acquired by the two cameras to reconstruct the 3D trajectory of each marker. The markers on the anatomical landmark of interest, namely the tip of the tendril, were inserted post hoc (Figure 1C). The tracking procedures were at first performed automatically throughout the time course of the movement sequence using the 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 3D trajectory of each tracked marker was computed by triangulating the 2D trajectories obtained from the two cameras (Figure 3). At the end of the experiment, the plants were removed from the pot to measure the roots' surface area (RSA), an important indicator for the uptake of water and nutrients (Himmelbauer, 2004). The analysis was performed by using scanned images of the roots (CamScanner INTSIG Information CO., Ltd, Shanghai, China; Version 5.51.0). The images were captured by means of a smartphone (iPhone X) providing an image of high quality, sharply contrasted, high resolution as well as with minimal deformation (Mohamed et al., 2017; see Figure 2). Then the obtained 8-bit grey scale images were uploaded on ImageJ. A scale was set to obtain the correct measurements of the roots, and the same threshold was chosen for every image.

### Dependent Measures

The dependent variables specifically tailored to test our experimental hypothesis on the basis of previous kinematical studies on

approach-to-grasp in pea plants (e.g., Simonetti et al., 2021) and motor intentions in humans (Georgiou et al., 2007; Becchio et al., 2008a) were: (a) the spatial trajectories designed by the tip of the tendril (Figure 1C); (b) the duration of the total number of circumnutations by the tendril. This time was calculated from the time the *plantula* was planted and the time the tendril grasped the support; (c) the maximum velocity of the tendril; (d) the percentage of time at which the maximum tendril velocity was reached during *circumnutation*; (e) the mean duration of the *circumnutations*, (f) the distance of the center of the *circumnutation* from the stimulus. In addition, for the social condition, (g) the roots area of the radical mass was examined.

### Statistical Analysis

Statistical analyses were performed using the Bayesian approach. In Bayesian estimation, the aim is to allocate credibility to a distribution of possible parameter values (posterior distribution) consistent with the observed data, by generating a large number of samples using a Markov chain Monte Carlo method (MCMC). Next, 95% high-density intervals (95% HDI) are calculated to define which points of the distribution are most credible, and which cover most of the distribution (for a review, see Kruschke, 2013). In the present study, we performed Bayesian *t* tests to compare the means of the “social” ( $\mu_{\text{social}}$ ) and the “individual” ( $\mu_{\text{individual}}$ ) conditions regarding different variables. Moreover, within the social condition, we compared the means of the “winner” ( $\mu_{\text{winner}}$ ) and the “loser” ( $\mu_{\text{loser}}$ ) groups. For this purpose, using the BEST (Bayesian ESTimation supersedes the *t* test) model implemented by Kruschke (2013), we calculated the difference ( $\beta$ ) between the

**Figure 2**  
*Images of the Roots' Surface. Graphical Representation of Roots' Images*



*Note.* The plant was positioned on a black velvet panel with a meter aside as a reference scale. See the online article for the color version of this figure.

mean of the social ( $\mu_{\text{social}}$ ) and the individual ( $\mu_{\text{individual}}$ ) stimulus conditions and compared the credibility of  $\beta > 0$  with  $\beta < 0$ .

To detect the strength of the correlation between the kinematical components of the winner and the loser plants, we performed Bayesian correlational analyses. All statistical analyses were performed using the computing environment R (R Core Team, 2014) and the packages BEST (Meredith & Kruschke, 2018) and BayesianFirstAid under the default settings, specifying our own priors by providing a list on the basis of our previous studies (Meredith & Kruschke, 2018).

## Results

### Qualitative Results

The tendril for all plants showed a growing pattern characterized by *circumnutation* (Figure 3A–C). Once a plant detected the support, it strategically modified the tendrils so that they bent toward the stimulus as to approach and clasp it (Figure 3A–C; see “Individual condition” in the online supplemental material). When considering the social condition, the “loser” plants showed a pattern of circumnutation along the vertical axis, without manifesting any orientation toward the stimulus (Figure 3C; see “Social Condition”

in the online supplemental material), whereas the “winner” plant exhibited deviated pattern of circumnutation toward the stimulus (Figure 3B; “Social Condition” in the online supplemental material).

### Kinematical Results: Individual Versus Social Condition

In these analyses, for the “social” condition, the data for “winners” (i.e., the plants that grasped the support) are represented. By doing so, the reach-to-grasp movement for the two conditions (individual vs. social) could be compared.

### Movement Time

The mean difference of movement time between the individual ( $\mu_{\text{individual}} = 2,106 \text{ min} \pm 390$ ) and the social ( $\mu_{\text{social}} = 2,402 \text{ min} \pm 305$ ) conditions was  $\beta = 296 \text{ min}$ , with a 95% uncertainty interval ranging from  $-6,710$  to  $1,270 \text{ min}$ . The probability of  $\beta < 0$  (i.e., the probability that the movement time was shorter for the social than for the individual condition) was 27.1%, whereas the probability of  $\beta > 0$  (i.e., the probability that the movement time was shorter for the individual condition) was 72.9%.

### Amplitude of Mean Velocity Peak

The amplitude of mean velocity peak reached by the tendrils during circumnutations between the individual ( $\mu_{\text{individual}} = 4.974 \text{ mm/min} \pm 0.82$ ) and the social ( $\mu_{\text{social}} = 4.265 \text{ mm/min} \pm 0.71$ ) condition was  $\beta = -0.707 \text{ mm/min}$ , with a 95% uncertainty interval ranging from  $-2.830$  to  $1.510 \text{ mm/min}$ . The probability of  $\beta < 0$  (i.e., the probability that the amplitude of mean velocity peak was higher for the individual than for the social condition) was 75.9%, whereas the probability of  $\beta > 0$  (i.e., the probability that the amplitude of the mean velocity peak was lower for the Individual condition) was 24.1%.

### Percentage of Movement Time at Which the Peak of Mean Velocity Occurred

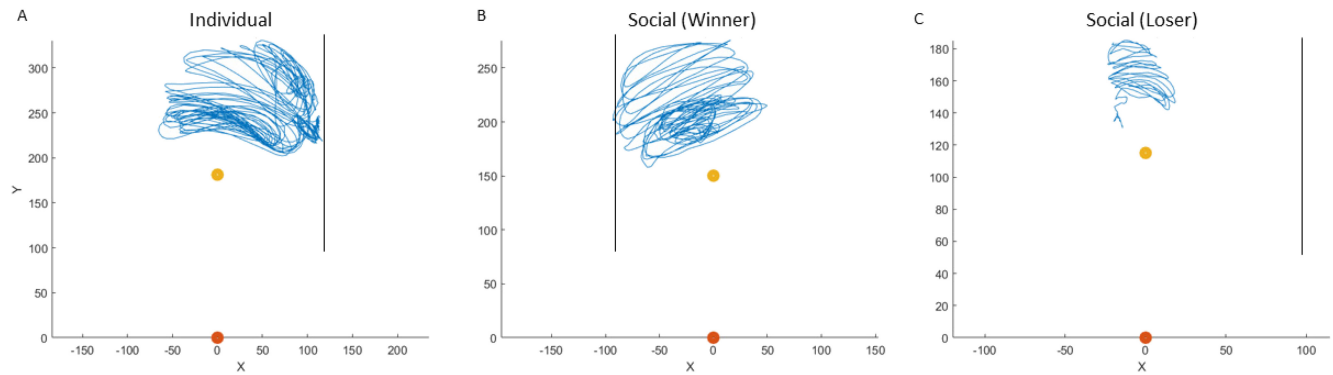
The percentage of movement time at which the peak of mean velocity was reached by the tendrils during circumnutation between the individual ( $\mu_{\text{individual}} = 63.77\% \pm 8.950$ ) and the social ( $\mu_{\text{social}} = 66.04\% \pm 9.320$ ) condition was  $\beta = 2.21\%$  with a 95% uncertainty interval ranging from  $-23.30\%$  to  $28.00\%$ . The probability of  $\beta < 0$  (i.e., the probability that the % time for the peak of the mean velocity reached by tendrils was earlier for the social than for the individual condition) was 42.2%, whereas the probability of  $\beta > 0$  (i.e., the probability that the % time for the peak of the mean velocity reached by tendrils was later for the social condition) was 57.8% (Figure 4A).

### Mean Duration of the Circumnutations

The mean duration of circumnutation between the individual ( $\mu_{\text{individual}} = 72.36 \text{ min} \pm 3.04$ ) and the social ( $\mu_{\text{social}} = 88.10 \text{ min} \pm 6.10$ ) condition was  $\beta = 15.7 \text{ min}$  with a 95% uncertainty interval ranging from  $-2.52$  to  $29.0 \text{ min}$ . The probability of  $\beta < 0$  (i.e., mean duration of the circumnutations was larger for the individual than for the social condition) was 1.3%, whereas the probability of  $\beta > 0$  (i.e., the probability that the mean duration of the circumnutations was larger for the social condition) was 98.7%.

**Figure 3**

Graphical Representation of a Representative Exemplar for a Plant Acting Individually and for a Winner and a Loser Plant Acting Socially



*Note.* The spatial trajectory of the tendril for the individual condition (A), for the winner plant within the social condition (B) and for the loser plant within the social condition (C). The black vertical line represents the stimulus, while the dots represent the origin (lower dot) and the last internode of the plant (upper dot), respectively, in order to have a reference of the stem from which the tendril moves. See the online article for the color version of this figure.

### Center of the Circumnutation and Its Distance From the Stimulus

The center of the circumnutation and its distance from the stimulus between the individual ( $\mu_{\text{individual}} = 93.64 \text{ mm} \pm 10.81$ ) and the social ( $\mu_{\text{social}} = 87.04 \text{ mm} \pm 5.65$ ) condition was  $\beta = -6.61 \text{ mm}$  with a 95% uncertainty interval ranging from  $-30.9$  to  $17.3 \text{ mm}$ . The probability of  $\beta < 0$  (i.e., center of the circumnutation was more distant from the stimulus for the individual than for the social condition) was 72.1%, whereas the probability of  $\beta > 0$  (i.e., the probability that the center of the circumnutations was more distant from the stimulus for the social condition) was 27.9%.

### Kinematical Results for the Social Condition: “Winner” Versus “Loser” Plants

#### Amplitude of Mean Velocity Peak

The amplitude of the mean velocity peak reached by the tendrils during circumnutation between the winner ( $\mu_{\text{winner}} = 4.431 \text{ mm/min} \pm 0.83$ ) and the loser ( $\mu_{\text{loser}} = 2.918 \text{ mm/min} \pm 0.95$ ) condition was  $\beta = 1.52 \text{ mm/min}$ , with a 95% uncertainty interval ranging from  $-0.908$  to  $4.09 \text{ mm/min}$ . The probability of  $\beta < 0$  (i.e., the probability that the mean velocity peak was larger for the loser than for the winner condition) was 9.9%, whereas the probability of  $\beta > 0$  (i.e., the probability that the mean velocity peak was highly for the winner condition) was 90.1%.

### Percentage of Movement Time at Which the Peak of Mean Velocity Occurred

The percentage of movement time at which the peak of mean velocity reached by the tendrils during circumnutation between the winner ( $\mu_{\text{winner}} = 71.37\% \pm 7.133$ ) and the loser ( $\mu_{\text{loser}} = 57.41\% \pm 11.158$ ) condition was  $\beta = 13.9\%$  with a 95% uncertainty interval ranging from  $-12.2\%$  to  $39.9\%$ . The probability of  $\beta < 0$  (i.e., the probability that the mean velocity peak reached by tendrils was earlier for the loser than for the winner condition) was 12.5%, whereas the probability of  $\beta > 0$  (i.e., the probability

that the mean velocity peak of the tendrils was larger for the winner condition) was 87.5% (Figure 4B).

### Mean Duration of the Circumnutations

The mean duration of the circumnutations between the winner ( $\mu_{\text{winner}} = 89.53 \text{ min} \pm 7.098$ ) and the loser ( $\mu_{\text{loser}} = 99.78 \text{ min} \pm 11.778$ ) condition was  $\beta = -10.3 \text{ min}$  with a 95% uncertainty interval ranging from  $-37.5$  to  $17.5 \text{ min}$ . The probability of  $\beta < 0$  (i.e., mean duration of the circumnutations was larger for the loser than for the winner) was 79.4%, whereas the probability of  $\beta > 0$  (i.e., the probability that the mean duration of the circumnutations was larger for the winner) was 20.6%.

### Center of the Circumnutation and Its Distance From the Stimulus

The center of the circumnutations and its distance from the stimulus between the winner ( $\mu_{\text{winner}} = 88.36 \text{ mm} \pm 6.82$ ) and the loser ( $\mu_{\text{loser}} = 115.33 \text{ mm} \pm 8.33$ ) condition was  $\beta = -27 \text{ mm}$  with a 95% uncertainty interval ranging from  $-48.2$  to  $-5.71 \text{ mm}$ . The probability of  $\beta < 0$  (i.e., center of the circumnutation was more distant from the stimulus for the loser than for the winner) was 99%, whereas the probability of  $\beta > 0$  (i.e., the probability that the center of the circumnutations was more distant from the stimulus for the winner) was 1%.

### Roots’ Surface Area

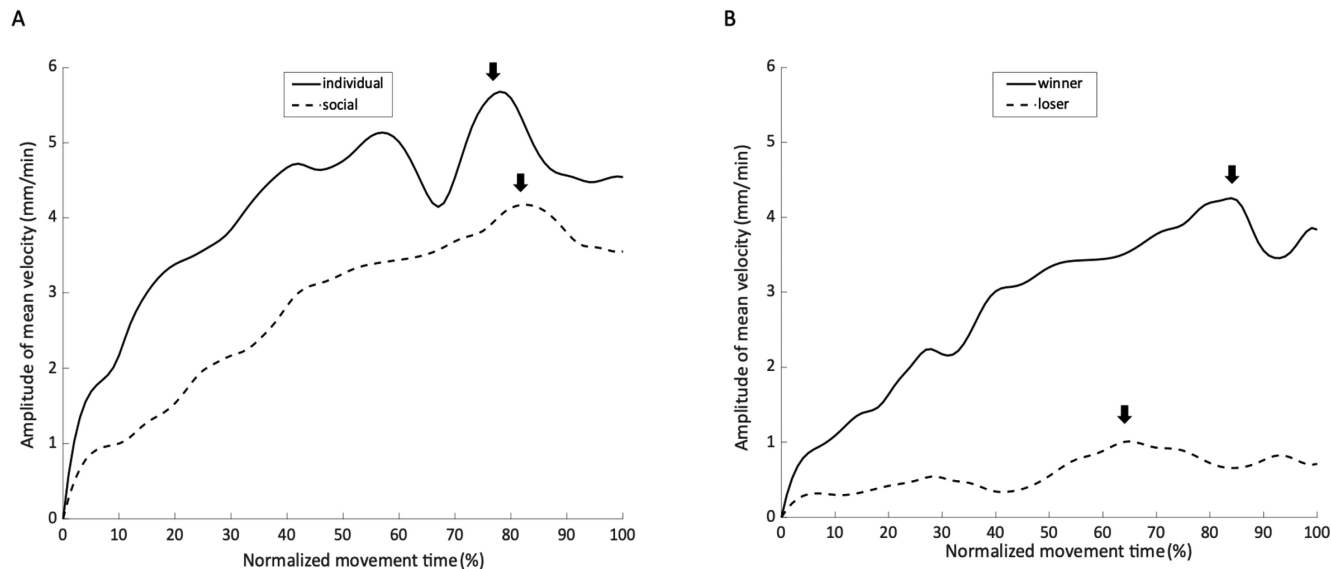
The RSA comparing the winner ( $\mu_{\text{winner}} = 16,657 \text{ cm}^2 \pm 3,113$ ) and the loser ( $\mu_{\text{loser}} = 16,711 \text{ cm}^2 \pm 5,754$ ) plants determined  $\beta = -0.0539 \text{ cm}^2$  with a 95% uncertainty interval ranging from  $-13.5$  to  $12.5 \text{ cm}^2$ . The probability of  $\beta < 0$  (i.e., the RSA was larger for the loser) was 50.1%, whereas the probability of  $\beta > 0$  (i.e., the RSA was larger for the winner) was 49.9%.

### Bayesian Correlation Analysis

The Bayesian correlations between the winner–loser dyad are outlined below. For the amplitude of mean peak velocity, correlation was moderately positive ( $r = .33$  [0.43, 0.90]) with a probability

**Figure 4**

Graphical Representation of the Amplitude of Mean Velocity for Representative Plants Acting Individually or Socially



*Note.* The amplitude and the time at which maximum velocity occurred for the individual and the social condition (A) and for the winner and the loser plants within the social condition (B). Arrows indicate the time occurrence of maximum peak velocity as a percentage of movement duration. Please note that the amplitude of peak velocity during circumnutation is higher, and it occurs earlier for the individual than for the social condition (A). It is higher for the winner than for the loser plant (B), and it occurs earlier for the loser than for the winner plant (B).

of 78.2%. For the percentage of movement time at which the peak of mean velocity occurred, correlation was moderately positive ( $r = .46$  [0.27, 0.94]) with a probability of 86.2%. For the mean duration of the circumnutations, correlation was moderately positive ( $r = .46$  [0.28, 0.95]) with a probability of 86%. For the center of the circumnutations and its distance from the stimulus, correlation was slightly negative ( $r = -.19$  [-0.84, 0.58]) with a probability of 65.9%. For the RSA, correlation was moderately positive ( $r = .46$  [-0.29, 0.93]) with a probability of 86.6%.

## General Discussion

In the present study, we investigated for the first time whether the kinematical pattern of the reach-to-grasp movement in plants is influenced by the kind of intention driving their movement, namely individual or social. Results revealed specific motor patterns for individually intended actions and actions motivated by a social intention. Pea plants plan and execute actions differently depending on the intention underlying them.

In general, these results may be interpreted as evidence of the influence of intentions on kinematics. Here, we demonstrate for the first time that in plants, intentions are reflected in the kinematics, so that actions embedded in different contexts show different kinematic characteristics. We shall discuss these differences in kinematics at two levels. First, we shall focus on the differences between the individual and the social conditions. Second, within the social condition, we shall consider the differences between the winner and the loser plant.

## Individual Versus Social Actions

When comparing individual and social actions, movement time and the mean duration of the circumnutations were longer for the social

than for the individual condition. And, the maximum velocity reached by the tendril during circumnutation was lower for the social than for the individual condition. This signifies a more cautious kinematic patterning for the social situation. This is understandable given that for climbing plants, grasping a potential support is a one-off attempt; if they do not seize the support firmly and properly, they may not survive. These results are suggestive of a more careful honing phase when the goal is nested within a social interaction and they are in line with human studies showing a more careful movement when acting within a social context (Becchio et al., 2008a; Sartori et al., 2009). Of relevance, this occurs despite the shape, size, and location of the support for the individual condition matched the location, shape, and size of the support for the social condition. And, more importantly, this occurs despite no physical difference occurred in the reach-to-grasp phases across the two conditions. All in all, these observations suggest that differences in intentions are reflected in the kinematics.

When animals “intend” to do something, they enact their directedness toward by moving their muscles. Plants, instead, generate action potentials and synthesize proteins, which are responsible for the direction of growth (Baluška, 2010). This directionality, along with its deliberate regulation, is relevant to explain the present findings in terms of intentionality. Plant and animal behaviors are the outcomes of the goals underlying intentional compartments. In phenomenological terms, each type of plant perception expresses a mode of its intentionality: directedness toward the light in photosensitivity, directedness toward sources of heat in thermosensitivity, as well as toward (or away from) self and/or others. In each of these cases, it is not just a question of perceiving, but also of interpreting signals and making decisions in a nonautomatic manner in the face of at times conflicting conditions. Intentionality here assumes the more colloquial sense of deliberate purposeful behavior.

Some may say that this conceptual framework does not work for plants because, in order to act in a goal-directed manner, they should be able to construct a representation of the environment, including potential supports. And it goes without saying that many argue a priori that cognition is impossible in plants (Adams, 2018). According to classical views, mental representations are created by a number of neurophysiological mechanisms in the brain that are activated after perceptual processing occurs. The events activating mental representations take place, according to this view, in the following order: physical signals are received through the perceptual systems and transmitted to the brain, then the physical signals are translated into mental representations (e.g., concepts, intentions) with the mind in charge of processing them, finally the motor system operationalizes the mind's will.

This explanation of mental representations does not take plants as cognitive agents into consideration since they lack a brain and a centralized nervous system (CNS) where mental states and representations can be localized. However, scholars favoring the enactivist and extended cognition theories maintain that cognition is not-just-in-the-head and goes beyond the constraints of the body. They challenge the notion of representational content by taking into consideration extraneural bodily structures and the environment (Chemero, 2009; Clark, 2008; Gallagher, 2005; Hutto & Myin, 2012, 2017; Noë & Noë, 2004; Thomasson, 2007). According to Gibson (2014), for example, cognitive activities do not necessarily depend on mental representations but on affordances, defined as structural supports or resources the environment offers. What an organism perceives of an object is not only its physical properties but also its affordances, in other words, what it can do with them (Gibson, 2014). The key to understanding affordance is that it is relational and characterizes the suitability of the environment to the organism, which means that it depends on their current intentions and capabilities. The notion of intention is crucial here because the same environment can provide various affordances. The finding that plants select the most relevant affordance for satisfying their needs suggests that they are endowed with some forms of selective attention, as recently theorized by Parise et al. (2022).

For those subscribing to the extended cognition theory, the environment plays an active role in cognitive processes which are not confined to the CNS or to the body (Clark, 2008). According to this theory, cognition extends beyond the physical boundaries of the organism into its environment and is inclusive of objects that are not part of the body. According to Parise et al. (2020), plants might extend their cognitive processing into their environment by actively modifying the rhizosphere and the soil directly influenced by root secretions, as well as shaping the root microbiome to the microbial community of the roots. It has been seen, for example, that the accumulation of exudates between obstacles and the roots is related to the plant's perception of obstacles in the soil, causing inhibited root growth in the direction of the accumulated exudates (Falik et al., 2005).

Enactivism posits that the dynamic interaction between organisms and their environment is a kind of action-oriented cognition (Gibson, 2014; Gibson, 1966; Maturana & Varela, 1980; Varela, 1991) eschewing representationalism (Hutto & Myin, 2012). Cognition is not a matter of representing the environment, but rather the active exploration of an environment by an organism, known as "sense-making" (Carvalho & Rolla, 2020). In this perspective, plants can be considered as cognitive agents and the challenges

linked to the mental representation theory are circumvented (Calvo Garzón & Keijzer, 2011; Carello et al., 2012; Castiello, 2021; Maher & Sias, 2017). Carvalho and Rolla (2020) proposed an enactivist-ecological approach according to which complex cognitive capacities such as ones involving representations are deeply rooted in the basic processes that enable biological organisms to survive and maintain their integrity in a dynamic environment. The approach offers a base upon which the theory of cognition in single-cell organisms, plants, animals, and humans can be constructed.

Once we have put aside a representational approach, plant behavior can be interpreted in a different light. Plants can act in an "intentional" goal-directed manner in a form of cognition in which the plant and the stimulus (i.e., the support) interacted as a single unit. The environment, in this case, could be considered part of the plants' intention as it approached the support it intended to grasp.

### Winner Versus Loser

Plants are limited in their ability to choose their neighbors, but they are able to orchestrate a wide spectrum of social behaviors that increase their prospects to survive under various ecological settings. Indeed, through the perception of neighbors, plants are able to anticipate probable interactions and modify their behaviors to maximize their long-term gains (Novoplansky, 2009). Put simply, they need to make "educated" social decisions under various ecological circumstances.

In the present study, we put plants in a social situation to unveil a modulation of their behavior under a context that at first sight may appear competitive. The winner plant exhibited a higher velocity during circumnutation and a closer proximity to the stimulus for a longer time, waiting for the right conditions to unfold a firm attachment. As happens for competitive tasks in animals, the action for the winner is characterized by higher velocity and a time-saving approach that minimizes behavioral efforts (Lehner et al., 2011). In contrast, the action for the loser individual is characterized by a submissive behavior with a lower velocity of reaction: a pattern that could be explained in terms of the "Theory of the games" (von Neumann & Morgenstern, 1944). By "game" or "contest" is meant an encounter between two individuals. Individuals will choose their resources to maximize their fitness (Smith, 1982). The best choice will depend on what other individuals are doing (Smith, 1982). In the present study, the two plants, albeit they share the same conditions of light, resources, soil, and access to the support, manifest different but complementary behaviors. The one that grasps the support shows a perfect opposite kinematical pattern of the one that fails to attach to the support. This signifies that for plants, as for animals, the best strategy in terms of time and energy-saving depends on what others are doing. The loser plants start to orient their behavior far from the support as soon as the defeat is perceived, so that they can invest more energy in a new search.

But is this kind of behavior a true manifestation of a competitive attitude? An answer to this question comes from the analysis performed on the RSA. Remember that plants may become territorial by proliferating roots with the intent of directly discouraging intrusions from other individuals for access to resources (Dudley & File, 2007; Falik et al., 2005). Thus, plants are expected to demonstrate a mosaic of competitive behaviors for the same or different resources. In this view, we might have expected the roots' area for

the winner plants to be greater than that for the loser plants. However, no differences were detected, suggesting that we are not in the presence of a competitive situation. Rather, the two individuals share available resources and act in concert for the apparent benefit of one of them (Parise et al., 2022). We propose that plants employ an adaptive perception for action process based on an anticipatory “intentional” behavior that is relevant to the future environment within which the plants eventually will function in Ballaré et al. (1987) and Novoplansky et al. (1990). This principle is ubiquitously important for any decision-making system, yet it is especially crucial in social settings where the behavior of each part is inherently dependent on the responses of its counterparts (Maina et al., 2002; Smith, 1982).

### Conclusions

We have identified new conditions for the study of the covert mechanisms underlying the control of action. In particular, the present study demonstrates that, in aneural organisms, such as plants, just like those with nervous systems, the planning and execution of a goal-directed action is modulated with respect to the intention driving it. The adoption, on the basis of the task demands, of a specific intention (individual vs. social) translates into an identifiable, measurable kinematic pattern which, even during the planning phase, is different from the kinematic pattern of the same action motivated by a different intention.

All of these findings support the idea that plants are capable of distinct social intentions and take action accordingly, exactly as humans do. We can truthfully say that based on the findings outlined here, plants do seem to possess the ability to perceive other plants’ actions and to process them in a way that enables them to react optimally. They open questions that only a few years ago might have been considered absurd. Some of these are: to what extent can plants intentionally plan their movements? Is plant movement affected in any way by the behavior of their plant neighbors? Does the intention to interact socially involve basic processes that are shared with animals, or are they plant-specific? A fascinating frontier awaits, in short, for psychologists attempting to break the code of intentionality across taxa.

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