



## Plant awareness in the hand

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### ABSTRACT

The human inability to notice plants and recognise their importance on Earth has been termed “plant blindness”. Among the main reasons (e.g., cultural and biological factors) underlying this phenomenon, the lack of visible movement of plants seems to be the main factor that makes plants less prominent to the human eye. Here, we tested the idea that observing plants moving on our time scale might change the way we attend to them. We combined single-pulse transcranial magnetic stimulation (TMS) and motor-evoked potential (MEP) recordings to assess the activation of observers' motor system during the observation of an action performed by either a pea plant or a human when approaching and grasping a pole. Control conditions involving a stationary hand or pea plant, a hand or pea plant rotating along their axes, and a hand grasping the pole in the style of a plant were also considered. The participants' sensitivity to the role and importance of plants for human life and other living organisms was assessed by means of an ad-hoc questionnaire. The results showed a specific effect of motor facilitation relative to baseline values when observing plants rotating and grasping, but not for plants standing still. Higher levels of motor activation may indicate a greater degree of effort in interpreting the observed action, when it is perceived as unfamiliar by the observer. An effort that can be reduced through awareness and knowledge of the role and importance of the green kingdom for life on Earth. Notably, people more sensitive to plants showed similar levels of motor activation when observing both plant and human actions.

### 1. Introduction

Plants make up about 80% of all biomass on Earth, surpassing humans and livestock in sheer mass (Bar-On et al., 2018). They are crucial in almost all ecosystems, contributing to climate hazard mitigation (Knapp, 2003; Ziska et al., 2009) and supporting humans and other animals by providing shelter, oxygen, and food. Despite this, people tend to overlook plants as living organisms (e.g., Pany et al., 2022), often viewing them as unassuming backdrops. This phenomenon is known as “plant blindness” (Amprazis & Papadopoulou, 2020; Wandersee & Schussler, 1999). Plant blindness, described by Wandersee & Schussler in 1999, is the inability of a person to perceive plants in their environment, acknowledge their importance in the biosphere or appreciate plants' esthetic and unique biological features. It also refers to the misguided anthropocentric view of plants as inferior to animals (Wandersee & Schussler, 1999). Since then, various other terms for plant blindness have been suggested including “plant unawareness”, “biodiversity naivety” or “plant awareness disparity” (Niemiller et al., 2021; Parsley, 2020). According to a recent review (Stagg & Dillon, 2022), the

most common characteristics of plant awareness disparity is a deficit of knowledge, followed by an attention or memory advantage for animals compared to plants, and low interest in plants. This language, however, attaches a negative connotation to those who experience these phenomena, and several educators have suggested alternative concepts to move from a deficit-focused concept to one that focuses on plants more holistically, such as ‘plant awareness’ (Bacon & Peacock, 2021; Stroud et al., 2022).

Among the main reasons behind plant awareness is a shortage of knowledge about plants. Life sciences curricula tend to be zoocentric or zoochauvinistic, suggesting that studying animals is more important than studying plants (e.g., Bozniak, 1994; Darley, 1990; Flannery, 1991; Hershey, 1996, 2002). School science textbooks, for instance, include more content on animals than on plants, as shown by the number and diversity of images, the quantity of text, and the number of animal examples of core biological concepts (Link-Pérez et al., 2010; Schussler et al., 2010). As a result, plants are often ignored and neglected by teachers, students, and the general public. Efforts to combat the lack of plant awareness through plant-focused education or experiences have

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recently been implemented with some success (e.g., Borsos et al., 2023; Pany et al., 2019). Some strategies include gamification (Borsos et al., 2023), and out-of-school learning experiences like visiting botanical gardens (Lindemann-Matthies, 2006) or utilizing digital tools in extra-curricular activities (Kissi & Dreesmann, 2018).

Apart from educational issues, other factors contribute to lack of plant awareness, including a failure to distinguish between the differing biology of plants and animals and the perceived slow lifecycles and behaviors of most plants that do not captivate our attention in the same way that animals do (New et al., 2007). Balas and Momsen (2014) adapted a technique from research in visual perception to provide empirical evidence that our attention is captured differently by plants than by animals. They capitalized on an established phenomenon in visual perception known as the “attentional blink”. “Attentional blink” occurs when a sequence of images is rapidly presented, and identifying the first target can temporarily hinder the detection of the second target. That is, when attentional resources are deployed on the first image, attention “blinks” and misses a closely presented second image. In particular, Balas and Momsen (2014) used this paradigm to objectively measure the extent to which people detect plants and animals in a quantitatively different way. Participants in their experiment were better in detecting the second target when the first target was a plant compared to when it was an animal, indicating that people may not pay attention to plants. Schussler and Olzak (2008) also found that adults are better in detecting animals than plants. In their study, they presented a series of pictures depicting plants and animals to psychology and botany undergraduate students. Following a brief distraction, students were asked to recall as many of the images as they could. The results showed that, despite being botany students, participants had better recall for animal images than plant images. This suggests that animals are more strongly encoded in memory than plants. However, a point worth noting is that recall tasks mainly adopted pictures showing a single plant or animal, thus limiting the possibility of understanding whether plant blindness would affect recall of elements in more complex naturalistic scenes. In this regard, Zani and Low (2022) recently conducted a memory task involving the simultaneous presentation of a plant item and an animal item. They found inferior recall of plants than animals, suggesting that plant blindness impacts the way adults process real-world scenes. Indeed, plant blindness appeared to affect the ability to encode complex scenes and to bind elements together to form richer memory representations.

So far, plant awareness has been an area of limited research, with studies primarily focused on static images and no consideration of plants acting in the environment. Crucially, plants produce movements, and these movements can be too slow to be perceived with the naked eye, such as the helical organ movement (i.e., circumnutation movement) which is common in climbing plants (Darwin, 1875; Darwin & Darwin, 1880). In this respect, Forterre (2013) showed that plants do not attract people’s attention because they are too slow to be perceived. In fact, the animal characteristic that generates the most interest in humans is movement (Kinchin, 1999). Therefore, it appears that lack of plant awareness is inherently a complex phenomenon which may also include a motor component. Here we aim to test for the first time whether the degree of plant blindness/awareness can be measured at the motoric level. Our hypothesis is that displaying videos featuring plants exhibiting movement patterns akin to those commonly observed in animals would promote an enhanced awareness of (or attention to) plants. In particular, it would facilitate the mapping of plant movements into the observer’s motor repertoire, leading to motor resonance (Fadiga et al., 1995; for an example of attentional effect on motor resonance, see also Betti, Castiello, et al., 2019; Betti et al., 2018). To investigate this aspect, we implemented an action observation paradigm based on the evidence that the motor system is activated sub-threshold when we observe another person in motion, but not when we observe that person at rest (e.g., Urgesi et al., 2006). This kind of covert motor activation in response to observed actions has been investigated between conspecifics

(i.e., humans) and non-conspecific (i.e., other animals). For instance, White et al. (2014) measured the corticospinal excitability of individuals’ hand muscles while they watched grasping actions performed by a human, a robotic arm, a rat, and an elephant. Their results indicate a facilitatory effect for non-conspecific actions (White et al., 2014). That is, the corticospinal excitability (CSE) of subjects’ hand muscles was greater during the observation of a grasping action performed by an elephant and a rat, and lower for actions performed by a human and a robotic effector. Amoruso and Urgesi (2016) also found that individuals with long-lasting familiarity with dogs showed similar levels of motor activation for human and canine grasping actions. This effect suggests that humans can resonate at a motoric level also to non-human actions and that activation of the human motor cortex may be related to a general process of inferring goals from observed dynamics, particularly when the observer has been familiarized with them (see also Buccino et al., 2004). An associative mechanism (i.e., the correlation of perceptual and action-related components; Catmur et al., 2007) may explain the occurrence of motor activation during the observation of non-conspecific actions. It is also crucial to note that motor resonance does not occur when observing moving objects or moving water (e.g., waterfall; Avenanti et al., 2013; Urgesi et al., 2006). Therefore, motor resonance appears to be closely related to the perception of a biological movement. In the present study, we investigate whether a moving plant is capable of activating a motor response in the observer, thus determining a similarity with agents of other species. As the motor facilitation triggered while watching an action has significant implications for the way we perceive and represent the world (e.g., Wilson & Knoblich, 2005), we propose to extend this research paradigm to the investigation of plant blindness. That is, here we combined single-pulse transcranial magnetic stimulation and motor-evoked potential recording of a hand muscle of the observer (i.e., the first dorsal interosseous muscle, FDI) to explore the activation of the observers’ motor system during the observation of an action performed by a pea plant, namely the elliptical movements made around their axes of elongation by pea plants (i.e., circumnutation; Darwin and Darwin, 1880) when approaching and grasping a potential support. To date, recent evidence suggests that during the approach to a potential support, pea plants preshape their tendrils (i.e., modified leaves used by plants to climb a potential support) by following the same kinematic principles underlying a human hand reaching towards and grasping an object (Bonato et al., 2023; Ceccarini et al., 2020, 2021, Guerra et al., 2019, 2021, 2022, Wang et al., 2023).

With this in mind, videos displaying grasping actions toward a pole performed either by a human or by a pea plant were shown to individuals. Control conditions implying a still hand or a still pea plant, and a hand or a pea plant rotating along their axes were also considered (i.e., non-goal-directed behavior). A further control condition was set showing a hand which mirrored the approach and grasp movement performed by the pea plant to balance the direction and the amount of movement displayed among the two actions. We thought that if plant blindness stems primarily from the idea that plants do not move while animals do, then the presentation of moving plants with the same time scale as a human movement should cause a corticospinal activation. In addition, we administered an ad-hoc questionnaire to measure the individual’s sensitivity to plants and to correlate results with the corticospinal activation detected during the observation task. In other words, our conjecture is that displaying videos featuring plants exhibiting movement patterns akin to those commonly observed in animals would promote an enhanced awareness of (or attention to) plants, leading to motor resonance (Fadiga et al., 1995). Alternatively, if plant movement cannot be associated with our behavioral repertoire, then it would not be possible to exploit our motor system to motorically map moving plants, and plant blindness effects should emerge as an absence of corticospinal activation for plant movement.

## 2. Method

### 2.1. Participants

Thirty-two healthy Italian adult participants (males 16; females 16), aged 19–29 years (mean age  $24.37 \pm 2.78$  years), took part in the study. All participants were right-handed, as assessed with the Edinburgh Handedness Inventory (EHI; Oldfield, 1971), with normal or corrected-to-normal visual acuity. Participants were screened for TMS exclusion criteria (Rossi et al., 2009; Wassermann, 1998). The study was approved by the University of Padua Ethics Committee and carried out in accordance with the Declaration of Helsinki (Protocol Number: 4733). Written informed consent was obtained prior to the experiment. No discomfort or other adverse effects were reported during the experiment.

### 2.2. Experimental stimuli

Seven greyscale video clips were used as experimental stimuli (see Fig. 1 and supplementary material). The human video clips were filmed from a frontal point of view with the use of a Canon Legria HFM36 (Tokyo, Japan) mounted on a tripod. All videos included the effector at rest before the action, followed by a rotation or a grasp of the object. The model was instructed to minimize any time variations between the start and the grasp. The grasp occurred approximately 1.665 ms after video onset. The pea plant movement was recorded by means of an infrared camera which took a picture every 180 s (total number of frames: 119, total duration: 21,420 s, average velocity: 0.006 mm/s). The wooden pole was coloured in red to increase the tendrils' contrast with the background (Fig. 1C–F). The movement was then presented within a time window of 4.5 s (average velocity: 30 mm/s), so that the time window was the same for both the pea plant and the hand movements. For all the video clips, the animation effect was obtained by presenting

each frame for 33 ms in series. All last frames lasted 600 ms. The order in which the videos were presented was randomized for each participant. The inter-stimulus interval between videos was 10-s. The first 8 s of rest were accompanied by a message urging participants to keep their hands as still and relaxed as possible. Subsequently, in the last 2 s of rest, a white fixation cross on a black background appeared at the center of the computer screen. The experimental conditions were:

- i) Still condition: a static picture of either a hand (Fig. 1A) or a pea plant (Fig. 1D).
- ii) Rotation condition: a video of either a hand (Fig. 1B) or a pea plant (Fig. 1E) rotating around their central axis (i.e., circumnutation).
- iii) Grasping condition: a video of a reach-to-grasp movement performed by either a hand (Fig. 1C) with the thumb opposing the index and middle fingers (i.e., the most appropriate grasp type according to object size, shape and orientation; Feix et al., 2016; Lee & Jung, 2014) or a pea plant (Fig. 1F) on a wooden pole (60 cm height, 3 cm diameter) placed at a distance of 120 mm from the starting position.

Given that the kinematics characterizing plant and human reach-to-grasp movements differs (i.e., pea plants do circumnutate in the reaching phase while humans do not), in addition to the three main conditions (Still, Rotation, Grasping), we decided to have an additional control condition to better compare the plant and the human reaching phase. We then filmed a Plant-style Grasping condition, having a reach-to-grasp movement performed by a hand with comparable goals and comparable motion features with respect to the grasping movement performed by the pea plant. That is, the human model simulated the movement of the pea plant by performing circular movements during the reaching phase.

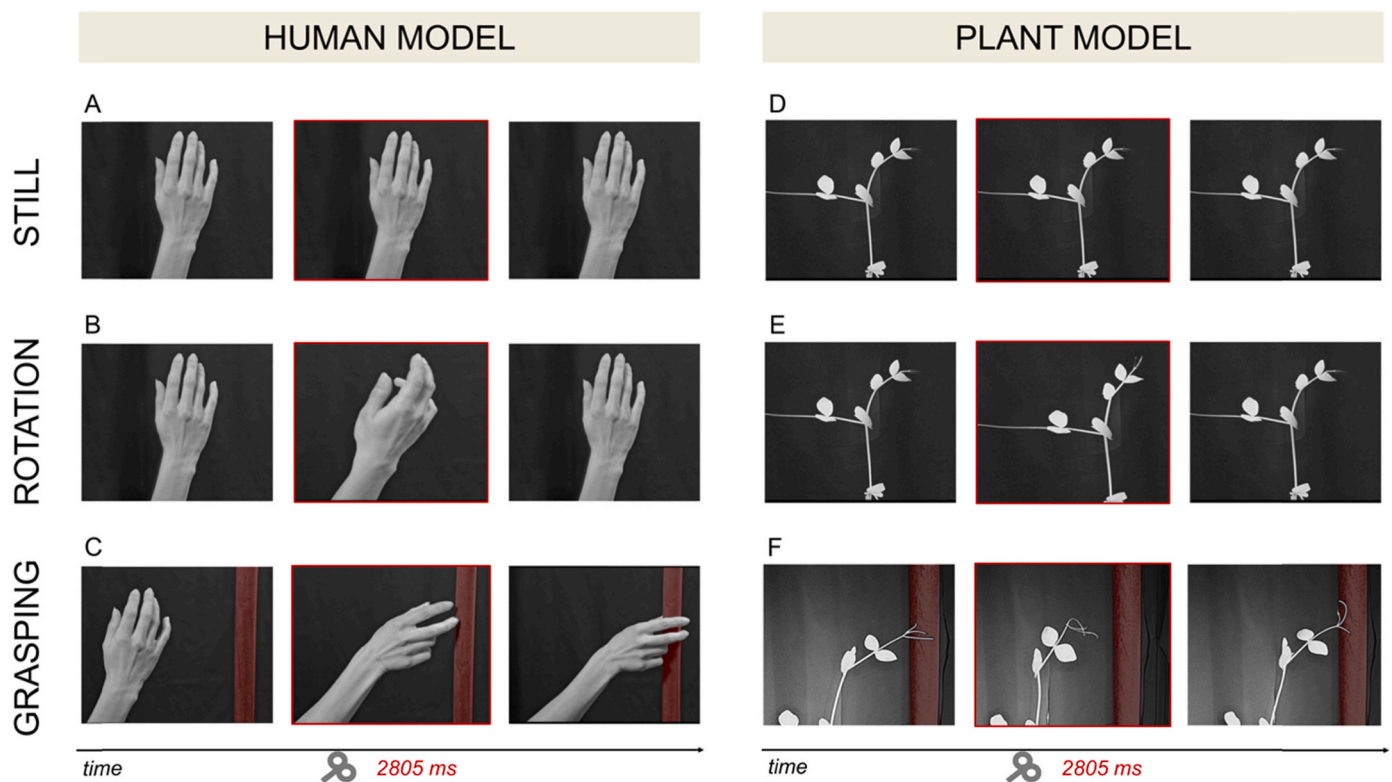


Fig. 1. The video clips used in the present study showing a human hand (left) or a pea plant (right). (A) A static picture of a hand (Still); (B) a hand rotating along its axis (Rotation); (C) a reach-to-grasp movement toward a wooden pole (Grasping); (D) a static picture of a pea plant (Still); (E) a pea plant rotating along its central axis (Rotation); (F) a reach-to-grasp movement toward a pole by a pea plant (Grasping).

### 2.3. Transcranial magnetic stimulation (TMS) and motor evoked potentials (MEPs) recordings

Single-pulse TMS was administered to the hand region of the left primary motor cortex (M1) using a 70 mm figure-of-eight coil connected to a Magstim Bistim2 stimulator (Magstim Co., Whitland, UK). The coil was held tangentially on the scalp at a 45-degree angle relative to the interhemispheric fissure, with the handle pointing laterally and caudally (Brasil-Neto et al., 1992; Mills et al., 1992). The optimal scalp position (OSP) for the target muscle, that is the position where MEPs with maximal amplitude are recorded with minimal stimulation intensity, was identified by delivering single TMS pulses at fixed intensity while moving the coil of 0.5 cm around the target area until the best position was reached. The OSP was marked on a tight cap the participant wore. MEPs were acquired from the first dorsal interosseous (FDI) muscle of the right hand. The resting motor threshold (rMT) was determined by applying ten consecutive pulses at the minimum stimulation intensity required to produce, in the relaxed contralateral FDI muscle, MEPs of more than 50  $\mu$ V in the 50% of the trials (Rossini et al., 1994). rMT ranged from 28 to 62% (mean 42%; SD = 5.96) of the maximum stimulator output. The stimulation intensity was then set at 120% of the rMT to record a clear and stable MEPs signal throughout the experiment (ranged from 34 to 74%; mean 51%; SD = 7.11). During the experimental sessions the coil was held by a tripod and continuously checked by the experimenters to maintain a constant positioning with respect to the marked OSP. MEPs were recorded through a pair of Ag/AgCl electrodes (1 cm diameter) placed in a belly-tendon montage. After the skin was cleaned, electrodes with a small amount of water-soluble EEG conductive paste were placed and fixed on the target positions. The active electrode was placed over the belly of the muscle, determined by palpation during maximum voluntary contraction, and the reference electrode was placed over the proximal interphalangeal juncture. The ground electrode was placed on the participant's right wrist. The skin impedance, evaluated at rest prior to beginning the experimental session, was considered of good quality when below the threshold level (5 kOhm). The electrodes were connected to an isolable portable ExG input box linked to the main EMG amplifier for signal transmission via a twin fiber optic cable (Professional BrainAmp ExG MR, Munich, Germany). A high-pass filter of 20 Hz and a low-pass filter of 1000 Hz were applied to the raw myographic signal, which was amplified prior to being digitalized (5 kHz sampling rate) and stored on a computer for off-line analysis. EMG signals were recorded with Brain Vision Recorder software (Brain Products GmbH, Munich, Germany).

### 2.4. Importance of plants questionnaire (IPQ)

Participants were requested to fill the Importance of Plant questionnaire (IPQ) after attending the experimental session. The IPQ is an ad-hoc questionnaire, not yet validated, designed to assess the role and importance of plants for human life and other living organisms. Nevertheless, the reliability (i.e., Cronbach's alpha) of our questionnaire was calculated as a minimum level of validation ( $\alpha = 0.73$ ). The IPQ consists of ten items (in Italian; see Supplementary materials), namely: (i) life would be impossible without plants; (ii) trees are very important in urban centres because they provide shade and for their natural freshness; (iii) municipal authorities should take care of urban greenery; (iv) plants use solar energy; (v) plants produce oxygen (vi) environmental pollution affects plant life; (vii) plants are very important for medicine; (viii) plants should be introduced in cities to increase their attractiveness; (ix) plants are also affected by diseases; (x) plants absorb carbon dioxide and help to regulate the climate. IPQ was developed based on previous questionnaires on plant awareness disparity (Fančovičová & Prokop, 2010; Marmaroti & Galanopoulou, 2006; Pany et al., 2022; Parsley et al., 2022; see Supplementary Material). Participants scored each item using a Likert-type scale ranging from 1 (strongly disagree) to 5 (strongly agree). Positive and negative items were used in

the scale, negative items were scored in the reverse order (e.g., point 5 equates point 1).

### 2.5. Procedure

Participants were tested individually in a single experimental session lasting 1 h and 30 min. Participants were seated in a comfortable armchair in front of a 19" computer screen (i.e., resolution of 1920 x 1080 pixels, refresh rate of 60 Hz) at a distance of 80 cm; their right arm was positioned on a pillow and their head on a fixed head rest. Participants were requested to remain still and relaxed during the entire experimental session. A single TMS pulse was released during each video presentation at the timing of 2805 ms and MEPs from the right hand FDI muscle were acquired. This timing corresponds to the time the human model reached the maximum hand grip aperture before getting in contact with the red pole (Fig. 1C). Concerning the plant model, the electromagnetic pulse was delivered when the tendrils (i.e., modified leaves used by the plant to clasp potential supports) reached the maximum aperture (Fig. 1F). A total of 105 MEPs (7 conditions  $\times$  15 repetitions) were recorded for each participant during video presentation. Prior and after the experimental block, each participant's baseline corticospinal excitability was assessed by acquiring 15 MEPs while they passively watched a white fixation cross on a black background presented on the computer screen. The average MEPs amplitudes recorded during the two baseline periods (i.e., 30 MEPs in total) was used to set each participant's individual baseline for data normalization procedures and to test for facilitation/inhibition relative to baseline under the experimental conditions. For baseline recording, an inter-pulse interval lasting 5.25 s was adopted between trials. During this interval participants were reminded to remain fully relaxed for 5 s and a fixation cross was presented for the remaining 0.25 s. The presentation of a fixation cross before each trial ensured that participants always started the trial by observing the videos from a neutral position. At the end of the experimental phase, a brief open-ended interview followed, in which the participant was asked about the impressions he/she felt while watching the videos. The experimental task was designed and run with the use of E-prime software (Psychology Software Tools, version 2.0).

### 2.6. Data analysis

Data were analyzed offline using Brain Vision Analyzer software (Brain Products GmbH, Munich, Germany) for EMG data and the R software package (R package version 4.2.2; R Core Team, 2013) and JASP 0.16.3 (JASP Team, 2022) for statistical analysis. The MEPs peak-to-peak amplitude (mV) for the FDI muscle was determined as a measure of participants' corticospinal excitability. MEPs amplitude that deviated more than three standard deviations (SD) from the mean for each experimental condition (outliers), and trials in which muscle pre-activation in a time window preceding of 100 ms the TMS pulse was recorded were excluded from the data analysis (<5%). A paired sample *t*-test (two-tailed) was used to compare the amplitude of MEPs recorded during the two baseline periods carried out at the beginning and at the end of each block. This comparison is useful to ascertain that modulations in MEPs amplitudes are due to the experimental manipulation and not to other influences. In addition, to assess possible differences between experimental conditions with baseline data (i.e., facilitation/inhibition), paired sample *t*-tests (two-tailed) were performed.

MEPs were then normalized computing a ratio between mean MEPs amplitude values recorded during each experimental condition and during the two baseline periods (MEP ratio = MEP<sub>obtained</sub>/MEP<sub>baseline</sub>). A repeated-measure ANOVA (rmANOVA) with the type of model (human or plant) and movement performed (still, rotation or grasping) as within-subject factors was performed on MEP amplitudes of the FDI muscle. The partial eta square (partial- $\eta^2$ ) value was calculated as an estimate of effect size. In the presence of significant interactions, Bonferroni-corrected post-hoc comparisons were performed. To control



for the effect of the amount of perceived motion on corticospinal excitability modulation while observing a grasping action performed by a plant or a human model, paired sample t-tests (two-tailed) were used to compare the amplitude of MEPs recorded during the observation of the plant and human grasping with the human grasping plant-style movement. The Pearson correlation coefficient was used to assess the relationship between the score of the PBQ and the MEPs values for each experimental condition. The significance threshold was set at  $p < .05$  for all statistical analyses.

### 3. Results

The mean raw MEPs amplitudes recorded at the beginning and at the end of the experimental session were not significantly different ( $877.13$  vs.  $717.77 \mu\text{V}$ ;  $t_{31} = 1.49$ ;  $p = .147$ ). Therefore, TMS per se did not induce any nonspecific change in corticospinal excitability that could have biased the results.

The comparison between raw MEP data for each condition and baseline values showed that MEPs were facilitated during the observation of the rotation of a human hand ( $t_{31} = 2.07$ ;  $p = .047$ ), as well as during the rotation ( $t_{31} = 2.2$ ;  $p = .036$ ) and grasping ( $t_{31} = 2.09$ ;  $p = .045$ ) of a plant. No significant facilitation emerged during the observation of a stationary plant ( $t_{31} = 1.47$ ;  $p = .150$ ) or a stationary human hand ( $t_{31} = 0.97$ ;  $p = .339$ ). A lack of facilitation for the human grasping condition was also shown ( $t_{31} = -0.52$ ;  $p = .610$ ; see Fig. 2).

#### 3.1. Human versus plant: same goal, but different motion features

The normalized MEP amplitudes of the FDI muscle during the observation of a gesture performed by a human (Fig. 1A, B, C) or a plant (Fig. 1D, E, F) were compared. Results showed a significant main effect of the type of model (Human vs. Plant;  $F_{1,31} = 6.250$ ;  $p = .018$ ;  $\text{partial-}\eta^2 = 0.168$ ), a significant main effect of the type of action (still, rotation or grasping;  $F_{2,62} = 3.232$ ;  $p = .046$ ;  $\text{partial-}\eta^2 = 0.094$ ), together with the interaction between the type of model and type of action ( $F_{2,62} = 3.652$ ;  $p = .032$ ;  $\text{partial-}\eta^2 = 0.105$ ; Fig. 3). Post-hoc contrasts revealed that FDI MEP amplitude was lower when participants observed a grasping gesture performed by the human model compared to a rotation gesture performed by either a human ( $p = .008$ ) or a plant ( $p = .019$ ), and lower than a grasping gesture performed by a plant ( $p = .011$ ). No other significant differences emerged.

#### 3.2. Human versus plant: same goal and same motion features

The normalized MEP amplitude of the FDI muscle recorded during

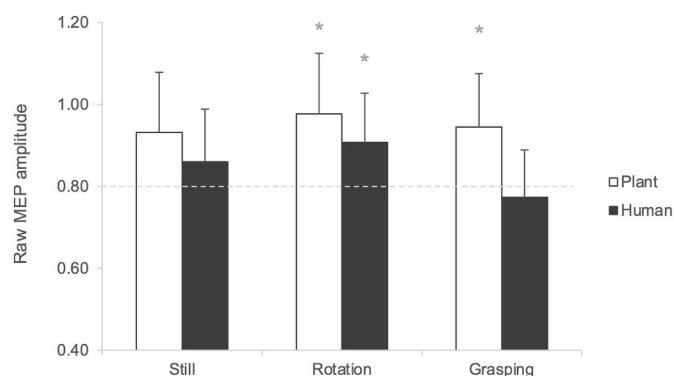


Fig. 2. Graphical representation of the mean values for the raw MEPs amplitude of the FDI muscle when participants observed a still, rotation or a grasping gesture performed either by a plant (white) or a human (black) model. The dashed bar represents the mean raw MEP amplitude for baseline data. The error bar represents the standard error of the mean. Asterisk indicate a significant difference ( $p < .05$ ) between condition and baseline data.

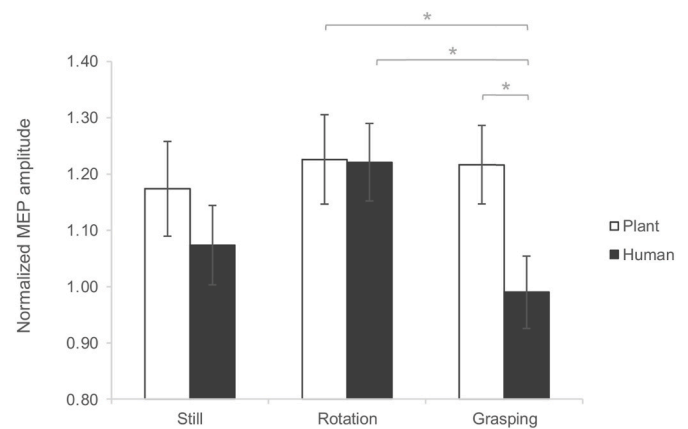


Fig. 3. Graphical representation of the mean values for the MEP amplitude of the FDI muscle when participants observed a still, rotational or a grasping gesture performed either by a human (black) or a plant (white) model. The error bar represents the standard error of the mean. Asterisks indicate significant differences ( $p < .05$ ) between conditions.

the observation of a reach-to-grasp movement performed by either a human or a plant model having the same goal (i.e., to grasp the red pole) and similar motion features (i.e., the model simulated the reaching movement of a plant by performing circular movements during the reaching phase) were compared. No significant differences were observed when comparing the grasping gestures performed by a human model mimicking a plant (i.e., grasping plant-style) and a plant model ( $t_{31} = -1.72$ ;  $p = .094$ ; Fig. 4A).

#### 3.3. Human: same goal and different motion features

The normalized MEP amplitude of the FDI muscle recorded during the observation of a reach-to-grasp movement performed by a human model having the same goal (i.e., to grasp the pole) but different motion features (i.e., plant-style vs. prototypical grasping) were compared. A significant facilitation emerged when the observed gesture was mimicking a plant (i.e., grasping plant-style, Fig. 4B;  $t_{31} = 2.06$ ;  $p = .048$ ).

#### 3.4. Human versus plant: impact of sensitivity to plants on motor resonance

To assess whether sensitivity to plants might influence motor resonance, the relationship between the scores to a questionnaire aimed at testing sensitivity to plants and MEPs values for the FDI muscle in each experimental condition were assessed by means of the Pearson correlation coefficient test. Results showed a significant negative correlation between MEPs amplitudes of the FDI muscle and the questionnaire scorings for all experimental conditions, except for the condition in which participants observed a still hand. For the remaining conditions, MEPs of the FDI muscle decrease in amplitude as the questionnaire scores increases (Fig. 5).

## 4. Discussion

In the present study, we investigated the corticospinal activation following the observation of videos depicting actions performed either by a human or by a pea plant. In general, we found that the level of corticospinal excitability was higher than the baseline when a grasping and a rotating plant was observed compared to a still plant. And that people more sensitive to plants showed similar levels of motor activation when observing both plant and human actions. To our knowledge, this is the first study reporting such effect on motor activation in response to the observation of actions performed by plants. We therefore support the

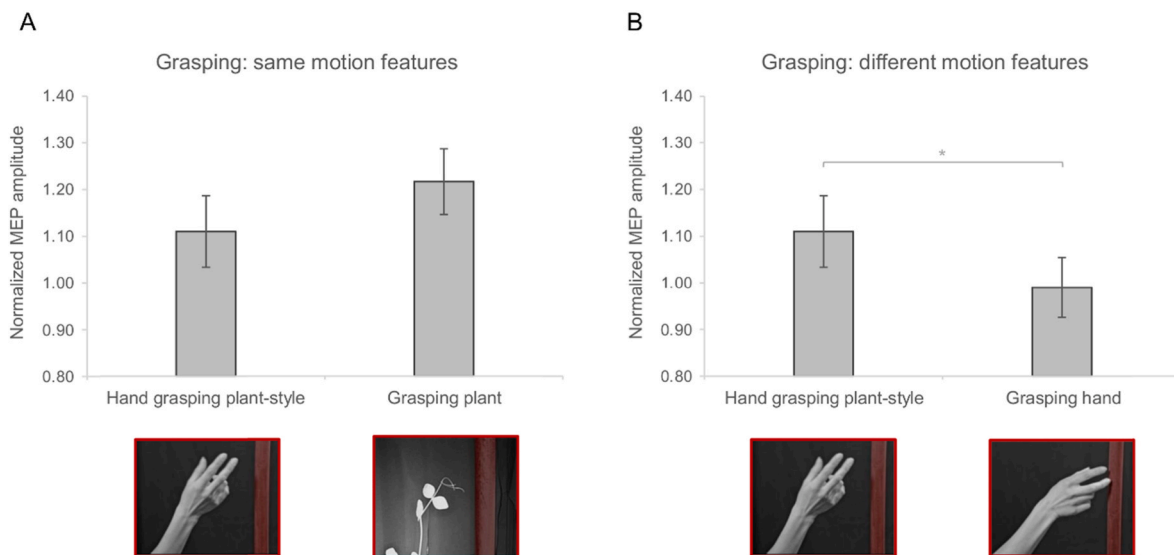


Fig. 4. Graphical representation of the comparison between normalized MEP amplitudes acquired during the observation of a grasping gesture performed by a human model mimicking a plant and (A) a plant model, or (B) a canonical grasping movement performed by a hand. Asterisks indicate significant differences ( $p < .05$ ) between conditions.

inclusion of a motor component in the definition of plant blindness (Achurra, 2022; Parsley, 2020; Wandersee & Schussler, 1999).

In terms of generalized motor activation, our findings are in line with previous studies involving the observation of actions performed by non-conspicuous (Amoruso & Urgesi, 2016; White et al., 2014) and extend this literature by showing that this “tuning” is not restricted to human or other animal actions, but also accounts for actions performed by plants. The similar activation of the motor cortex found for both the plant-style hand grasping and the grasping plant may be related to a general process of inferring goals from observed dynamics (Cross et al., 2012; Engel et al., 2008; Fiorio et al., 2010; Gazzola et al., 2007; Gowen & Poliakoff, 2012; Petroni et al., 2010). Support to this contention comes from several studies showing the activation of motor system areas during observation of recognizable actions performed by other agents and species (for review see Kemmerer, 2021). In this view, the observed motor activation effect may reflect the attribution of goal/intention to the plant’s action. In other words, individuals might have coded the plants’ actions at the goal or outcome level (i.e., grasping the pole).

#### 4.1. Sensitivity to plants

An important aspect of the present study is a motor facilitation during the observation of a rotational movement of either a human hand or a plant, as well as during the grasping of a plant, when compared to baseline values. Participants may need a greater degree of interpretive effort when observing unfamiliar actions, that reflects in increased corticospinal activity (e.g., Betti et al., 2019; Buccino et al., 2004). The motor system being more recruited when sensory information is incomplete (D’Ausilio et al., 2012). This motor-driven process would help to disambiguate the goal of the action through anticipatory mechanisms (Amoruso & Finisguerra, 2019; Betti et al., 2022).

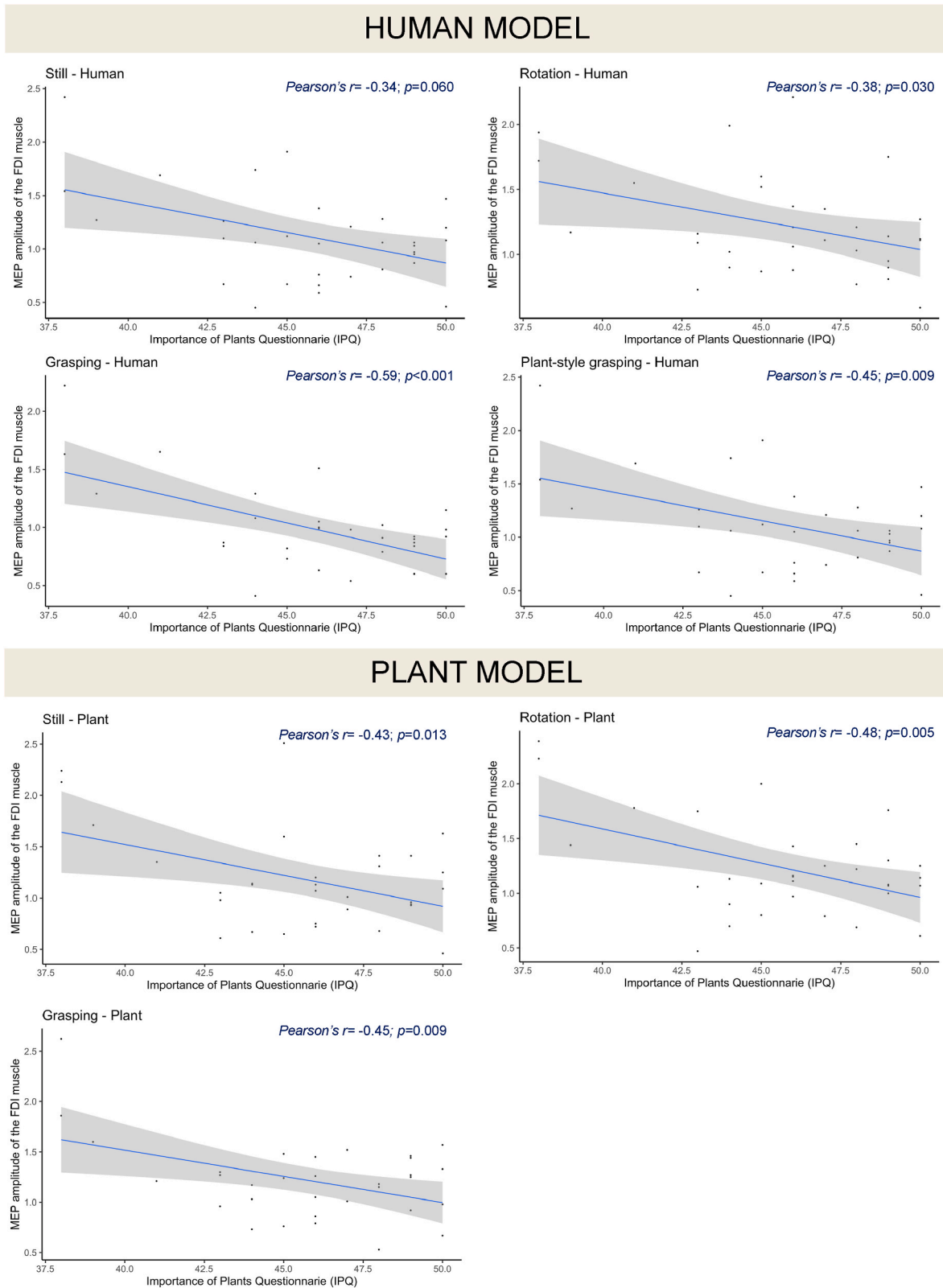
The reduction in MEP amplitude for the prototypical grasping action is a novel finding in the action observation literature (but see Betti et al., 2019; Naish et al., 2014) and could indicate a paradigm effect. In the framework of a “plant study”, the one movement (i.e., the prototypical hand grip) perceived as unrelated to the paradigm might have changed the way the hand grip was coded (for a review of factors influencing action observation, see Kemmerer, 2021). From an action-oriented predictive coding approach, an empirical Bayesian inference process might have created top-down priors that helped reduce uncertainty in the observation of plant and plant-style movements at the expense of the

prototypical grasping action (Amoruso & Finisguerra, 2019). Rens et al. (2020) recently found that when observers’ expectations were violated, their mirror responses were reduced. Specifically, motor resonance is eradicated when an observed grasping action deviates from what is expected (Craighero et al., 2014; Gangitano et al., 2004; Rens et al., 2020; Senot et al., 2011; for other relevant studies see Obhi & Hogeveen, 2010; Ondobaka et al., 2015). Indeed, in our study we found a statistically significant decrease in corticospinal excitability comparing a hand performing a prototypical grip with a plant-style grasping.

The lack of facilitation for the prototypical human grasping condition, on the other hand, could suggest a task-related inhibitory effect: as grasping actions are performed quite automatically dozens of times in daily life, but participants were asked to remain as still as possible, a muscular deactivation may have been triggered to keep the hand fixed on the hand rest and to avoid imitation reactions (i.e., a mechanism to suppress the observation-evoked response codes from generating overt muscle activity; Betti et al., 2023; Coxon et al., 2006; Duque et al., 2017; Villiger et al., 2011). Naish et al. (2014) formulated a corticospinal inhibition hypothesis linked to action observation in an influential review. Corticospinal inhibition would act as a dam to restrain the impulse to move or to respond, i.e. to execute the automatically triggered action. Remember that humans have much greater visual familiarity and direct motor experience with human actions than with any other moving stimuli, including other species’ biological movements, and this might have led to the task-related inhibition.

In this light, an important result supporting the inhibitory hypothesis is the negative correlation between MEP amplitudes and the IPQ scores. Considering that greater familiarity induces greater inhibition, it is not surprising that individuals who acknowledge the importance of plants exhibit lower MEP amplitude. We propose that a greater impulse to imitate - generated by observing familiar actions - needs greater inhibition (Betti et al., 2023). Empathy might also be the key to understand why higher scores in the Importance of plants questionnaire (IPQ) are associated with similar motor output (i.e., decreased CSE) for both plants and human movements, as they were perceived to be similar. Empathy has been already associated to modulations in motor activation (Lepage et al., 2010; see also Balding & Williams, 2016 for considerations on empathy and plant blindness).

To our knowledge, this is the first study reporting such effect on motor activation in response to the observation of actions performed by plants.



**Fig. 5.** Graphical representation of the relationship between the amplitude of MEPs of the FDI muscle and the Importance of Plant Questionnaire (IPQ) for each experimental condition. \* =  $p < .05$ ; \*\* =  $p < .01$ .

#### 4.2. Plant-style vs. human-style grasping

Our results show that the primary motor cortex was more active during the observation of a hand performing a plant-style grasping

action than during the observation of a hand performing a prototypical grasping action. This effect might be due to the effort required to interpret an unfamiliar action (see above). Novel movements demand more attention compared to familiar movements (an effect known as

odd ball effect) and require more activation for recognition and learning of the new motor pattern. The fronto-parietal regions of the perception-action system are in fact mostly recruited during the observation of meaningless than meaningful actions (Hétu et al., 2011). In line with this study, the data presented here on the observation of plant-style grasping movements provide the literature with new information regarding the effect of observing unfamiliar actions on corticospinal activation.

#### 4.3. Plant awareness and the educational context

Broader implications of the present findings are concerned on how conceptual knowledge is somewhat organized in our brain. Do animals and plants fall into the same partition? It has been hypothesized that in our brain there is a categorical distinction for animals, plants and artifacts (Caramazza & Shelton, 1998). A categorization that subsequently has been compressed in the literature into animates and inanimates. In this respect, it has been reported that animates are better remembered than inanimates, but the study did not include plants (Nairne et al., 2013). To date, studies on animates versus inanimates do not specifically compare plants versus animals but the majority of them use fruits (e.g., Jackson & Calvillo, 2013) and flowers (e.g., Guerrero & Calvillo, 2016) as the only images of plants. Therefore, it is fundamental to enrich the animacy dimension, which refers to the state of being alive and animate, with plants movements. We need to determine the necessary and sufficient properties of ‘animated’ plants that allow for a rapid and successful recognition of plants by our brain.

The results of studies conducted on samples of students of different ages agree that they show greater interest in studying animals than in studying plants (Wandersee, 1986), a preference attributable primarily to the fact that animals move. Indeed, the concept of life appears to be intimately related to movement. Plants are seen as background characters for the animals which live out their dynamic lives (Balding & Williams, 2016; Yorek et al., 2009). However, plants also move and manifest behaviors very similar to those observed in animals (Simonetti et al., 2021). What solutions can be proposed to address globally a problem as pervasive as the lack of plant awareness? This effect is indeed common, but not inevitable (Stagg & Dillon, 2022). The most forward-looking answer is therefore to “start at the grassroots,” i.e., education: it is necessary to raise teachers’ awareness of plant and channel students’ attention with hands-on experiences (e.g., “The Pet Plant Project”; Krosnick et al., 2018) that can foster the development of positive and respectful behaviors, knowledge, and attitudes toward the environment (Fančovičová & Prokop, 2011; Stagg & Dillon, 2022). Balas & Momsen suggested that our visual system process plants in a manner that may contribute to lack of plant awareness (Balas & Momsen, 2014). They argued that educators should focus on materials that increases plant awareness to overcome these inherent perceptual limitations (Balas & Momsen, 2014). Making the movement of plants explicit and manifest, as well as enhancing awareness toward plants - as we did in this study - produced an effect at the level of motor activation. The visual familiarity effect found in people most sensitive to plants may reflect the attribution of a goal/intention to plant action and highlight the enormous potential of observational learning. Our results might be explained by embodied cognition theories as an automatic involvement of the corticospinal system induced by the observation of a movement reproducible by the observer (Buccino et al., 2004; Craighero et al., 2016). An intense visual experience of the actions performed by plants can engage the observer’s motor system and increase our motor resonance with the green world. From this perspective, we propose that having people “see” plant movement could be a feasible way to reduce lack of plant awareness.

To conclude, lack of plant awareness is inherently a complex phenomenon. The cultural underpinnings of plant blindness have been well recognized; here, we add to a growing body of research documenting a physiological component. Further studies that will clarify how the

human brain perceives and attends to plants can help to take concrete steps toward increasing plant awareness.

#### Declaration of competing interest

The authors declare no conflict of interest.

#### CRediT authorship contribution statement

**Silvia Guerra:** Conceptualization, Data curation, Writing – original draft. **Sonia Betti:** Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Writing – original draft. **Luisa Sartori:** Conceptualization, Writing – original draft. **Giovanni Zani:** Conceptualization, Writing – original draft. **Umberto Castiello:** Conceptualization, Funding acquisition, Project administration, Resources, Supervision, Validation, Writing – original draft, Writing – review & editing.

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#### Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.jenvp.2024.102246>.

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