UNIVERSITÀ DEGLI STUDI DI PADOVA

Department of General Psychology

Master's Degree in Cognitive Neuroscience and Clinical Neuropsychology

Final Dissertation

Quantity-related ability in pea plants (*Pisum sativum* L.)

Supervisor:
Professor Castiello Umberto

Co-Supervisor:
Dr. Silvia Guerra

Candidate: **Esma Nur Doganbas**
Student ID number: **2071348**

Academic Year: 2023/2024

Peygamberimiz (s.a.v.), *"İlim Çin'de de olsa ona talip olun. Çünkü ilim her Müslümana farzdır."* (Beyhakî, Şuabu'l-İman-Beyrut, 1410, 2/253) buyurmuştur. O yüzden tezimi ilim yolunda vatanını ve sevdiklerini geride bırakmış bütün Müslüman öğrencilere ithaf ediyorum.

Acknowledgement

Firstly, I would like to thank my esteemed supervisor Professor Umberto Castiello, who inspired me with his academic research and passion for science.

I would like to express my sincere gratitude to my dear co-supervisor Professor Silvia Guerra, who never withheld her valuable advice and support throughout my internship and thesis process and who always made time for me in her academic intensity.

Finally, from the bottom of my heart I would like to say thank you for all professors in Cognitive Neuroscience and Clinical Neuropsychology program who have been happy to share their knowledge with us for two years and who have made great efforts to educate us, especially Professor Silvia Elena Benavides Varela, who gave me the opportunity to acquire a new passion, and Professor Antonino Vallesi, whose attitude I will always take as an example as an educator throughout my life, whom I did not have the opportunity to thank since I started such a challenging educational adventure.

Abstract

Contrary to common belief that plants are immobile, they in fact exhibit a variety of movements to increase their chance to survive. In addition to these mechanisms, they need to recognize their environment and have access to light, water, nutrients and support for climbing plants to adapt to their environment and grow successfully. Climbing plants have demonstrated kinematic features that prove the movement mechanisms they exhibit to reach support are purposeful. In this study, we focused on whether the pea plant, a climbing plant, exhibits quantity-related abilities, which are one of the cognitive abilities that require complex processes such as decision making against possible supports. In the experiment, we questioned how plants change their kinematic properties according to the numerical characteristics of the supports offered as they approach the support. Pea plants were tested in the presence of 3 supports on one side and a single support on the other side (different quantity condition – DQ) or in the presence of 2 supports on one side and 2 support on the other side (equal quantity condition – EQ) by means the three dimensional (3D) kinematical analysis. Results showed that in the DQ condition, where there were 3 supports on one side and a single support on the other side, the majority of plants directed their movements towards the side with more supports, while in the EQ condition plants randomly chose one of the four support available. Furthermore, results demonstrated that plants modulated the kinematics of their tendrils depending on the different distribution of the support in the environment showing a distinct motor behavior towards the more-numerous sets. In sum, findings provided preliminary evidence on the existence of quantity-related abilities in a neural organism such as plants.

Introduction

Numerical cognition refers to the concepts which underlines cognitive processes for understanding, processing, and using numerical information. It contains many aspects such as number sense, numerical representation, arithmetic processing and quantity discrimination. Skills in number cognition are important for animals and humans to survive and make more efficient and profitable decisions. Human beings since their birth use this information for their benefits. These abilities start to develop very early. Wynn (1992) showed that infants can recognize changes in objects sets. The studies conducted proved the existence of such abilities in animals as well. Abilities on numerical cognition can lead to survival and feeding strategies. Honeybees (*Apis mellifera*) can follow numbers up to 4 and use their ability while feeding (Chitta & Keiger, 1994), minnows fish prefers larger groups for their safety (Hagel & Helfman, 1991), or wolves decides on the most optimized number of flocks to make hunting advantageous (MacNulty et al., 2014).

In nature, living things who need numerical abilities to increase survival chance are not only human and animal. Plants need to monitor their environment by finding nutrients and resources and by recognizing possible allies or enemies. Although we suppose them as sessile organisms, to obtain abovementioned facilities plants need to carry out some movement that might not be catch with naked eye. Recently, it has been demonstrated that plants are not passive organisms and that they are able to perceive and respond to their environment and external stimuli properly (Baluška & Mancuso, 2009; Segundo-Ortin & Calvo, 2021). For instance, climbing plants can adjust their motor behavior (e.g., speed of their approach-to-grasp movement toward a support) according to different features of a potential support (e.g., thickness; Guerra et al., 2019). Furthermore, it has been demonstrated that when plants are faced with a choice scenario, plants are able to adapt one of several alternative plastic responses in a way that optimally corresponds

to environmental scenarios (Wang et al., 2023). However, in nature plants face several environmental elements such as neighboring plants which might be from the same kind or a different kind that possibly a potential enemy in resource competition, different potential support that have different qualifications cause struggle while attaching and level of nutrient which encourage them more actively in case of risk.

When all aspects are taken into consideration to enhance their chance of survival, plants should present some quantity related abilities that facilitates their competition with rivals to reach nutrients, water, and light. Movement abilities of plants that are proven by previous studies, observable and helping factor for understanding quantity related abilities of plants.

The present thesis aimed to investigate if plants present quantity related abilities and if so, how sophisticated are these abilities with respect to those observed in different animal species including human beings. Pea plants (*Pisum sativum* L.) were tested in two conditions, control and experimental conditions. In control condition two supports (2 vs.2, EQ condition) located both sides with the same distance (10cm). In experimental condition (DQ condition) three supports are located one side and single support located on the other side of the plant with the same distance. We have hypothesized that if plants are able to perceive the quantity of potential supports in the environment, then they will grow towards the side with more supports and be more likely to contact supports on the more-numerous sides. We further predicted that plants placed in an environment with unequal opportunity for support would exhibit a more-precise, cautious patterning, than movements for the condition in which an equal quantity of supports was present. This patterning would serve to better control the merger phase and minimize variability at contact. On the other hand, if *P. sativum* plants are not able to represent the quantity of potential supports, then we should observe similar kinematic behavior between the two conditions. Results showed plants

perceive the different distribution of support and modulate their kinematics based on the support distribution. According to the data obtained the plants perceive and process the different distribution of supports in the environment and as a result, they modulate the kinematics of their tendrils accordantly to increase their chances of survival by moving towards the side with more support.

In order to have a good understanding of the present study, the concepts of plant movement and behavior will be introduced and followed by a review of the scientific literature with the aim of illustrating and explaining plant movements, with particular emphasis on the distinction between movements produced by the apical part of the plant (i.e. stem, apex, tendrils) and those produced by the root system of the plant (Chapter 1). Then, the concept of number sense will be discussed, to understand numerical cognition of humans while starting from infancy the developmental trajectory will be presented with related literature and quantity related abilities of non-human animals will be demonstrated with various examples (Chapter 2). Current study that is aiming to question quantity related abilities of plants will be observed by testing on pea plants with experimental conditions (EQ and DQ). The research I have been involved in contains two conditions which are mentioned earlier, helping us to clarify by using kinematic analysis of our conditions. (Chapter 3). Finally, the results are discussed in the light of the scientific evidence that preceded the research (Chapter 4).

Chapter 1. Green Cognition: The Fine Line Between Action and Purpose

1.1. From Past to Present: Plant Intelligence & Cognition

Recent studies have been conducted not only to understand mechanisms underlying plant physiology but also their abilities that can be said to be cognitive. It is still a very debatable topic nowadays about the presence of cognition in organisms without a central nervous system (CNS) such as plants and batteries. Researchers like Alpi (2007) claim that there is a strict approach among cognition, that makes it difficult to look at plants as cognitive agents. Cognition is defined as processes including thoughts, actions and organizing one's own behaviors and giving a meaning to all these actions by processing, storing, and using information that is provided by environmental inputs (Neisser, 1967). This point of view is supported by the idea of the brain that is based on processing of sensory information and creation of appropriate behavioral response. Different from this perspective some researchers look at plant intelligence from the perspective of situated cognition. There are three different types of situated cognition. Embodied cognition focuses on the effects of body state and action on cognition outside the central nervous system (CNS). Extended cognition goes beyond this and focuses on the fact that cognition extends beyond the body and includes objects in the environment. The last one *enactivism* emphasizes that a cognitive system is an open and organizational system that explores its environment, meets its needs and goals by communicating with the environment, and uses sensory-motor abilities to do this (Castiello, 2021). Cheng (2018) pointed out that plants can be classified as cognitive creatures when viewed from these three different perspectives. To understand plant cognition, they examine the relationship between plants and their environment. They look at the concept of intelligence without the existence of the brain or a central nervous system. A recently developed discipline, plant cognition, aims to understand how plants perceive and process signals coming from the environment, to use

them as information to survive how they generate responses to this information (Calvo, 2017; Castiello, 2023). Evidence obtained from some recent studies showed that plants successfully perceive their environment and to achieve their purposes how they generate flexible responses suggesting that plants present all qualifications to be accepted as cognitive organisms (Trewavas, 2005; Baluška et al., 2006; Trewavas, 2007; Baluška & Mancuso, 2009). Theories supported by various and detailed studies support that plants have abilities such as sensory perception, self-recognition, information processing and learning (Baluška & Mancuso, 2009; Segundo-Ortin & Calvo, 2021). In fact, plants have a wide repertoire of behaviors that have a purpose and are exhibited to adapt to the environment (Baluška and Reber, 2019; Calvo et al., 2020; Trewavas et al., 2020), and that they do these to survive, like other living things. Such evidence is the most fundamental support for the intelligence and various cognitive abilities of plants. It has been demonstrated that plants communicate with other plants using volatile organic compounds (VOCs) secreted by leaves, flowers, fruits and the rest of the body of the plant. They also use VOCs as a defense mechanism against the herbivore threat (Dicke et al., 2003; Dicke & Baldwin, 2010).

Plants can perceive the presence of neighboring plants and recognize kin over strangers (Murphy & Dudley, 2009). For instance, the *Impatiens pallida* plant responds to the presence of non-kin plants (different family) by increasing stem elongation and branching, and leaves and root allocation. The process of kin recognition seems to rely on the emission and perception of root exudates (chemical compounds emitted by the roots; Biedrzycki et al., 2010) and/or on the leaves' photoreceptors (Crepy & Casal, 2015). Plants can detect the presence of neighboring plants by 'smelling' their 'odors'. For instance, the *Cuscuta pentagonata* can perceive, locate and choose the type of plant that offers better nutrition such as the tomato plant (Runyon et al., 2008).

Plants also exhibit predictive behavior, such as the *Lavatera cretica* plant starting to turn its body towards the sun at night to obtain resources and nutrients (Garcia Rodrigues & Calvo Garzon, 2010). Some behaviors may indicate that they learned from their previous experiences. In their experiment Bose (1906) gave a shock to *Mimosa pudica* and saw that after the shock leaves of the plant reached a maximum fall for 2 seconds and stayed in that position for 30 seconds. Then recovery begins slowly, and complete recovery takes 6 minutes. After this first trial, Bose repeated the shock seven times. One-third reduction observed in the leaf movements from 1st trial to 7th trial. So, it is understood that when *Mimosa pudica* encounters the same stimulus repeatedly, its response gradually decreases (Bose, 1906).

It has been mentioned that plants exhibit these behaviors to enhance their chances to survive. They can use different information they encounter while searching for food and integrate them (de Kroon et al., 2009). Studies on *Fragaria vesca* revealed that the plant uses the intensity of light as a clue to reach the light source (González et al., 2016; 2017). *Pisum sativum* exhibits different risk-taking behaviors in different environments depending on the density and availability of nutrients (Dener et al., 2016). Plants also display some complex abilities such as imitation (Williamson, 1982; Niu et al., 2018). *Boquila trifoliolata* mimics the leaves of its prospective supporter and does so before coming into physical contact with the supporter (Gianoli & Carrasco-Urra, 2014).

Various reductive and non-reductive theories have been put forward, most fundamentally on plant cognition and consciousness. While reductive theories argue that consciousness originates from physical mechanisms and chemical compounds, non-reductive theories argue that consciousness is the whole of communication with the environment (Segundo-Ortin & Calvo,

2021). While theories are still being debated their existence has long become completely undeniable in a context where cognition and consciousness of plants are discussed.

1.2. Plants on the Move

As its importance has been emphasized several times, although plants appear to be sessile, they focus on their environment and have various movement mechanisms (Guerra et al., 2019). It can be said that starting with research on animal cognition has been an entry point for understanding plant cognition. Linson and Calvo (2020) thought that it might be enlightening to compare the cognitive activities of the two in terms of their locomotion abilities. Researchers divided organisms according to their different energy demands, namely locomotive and non-locomotive; therefore, they stated that they had to use different strategies to meet different energy demands. Of course, their differences even at the cellular level cannot be ignored. Animals moved to meet their needs, but plants meet their energy needs through photosynthesis (Calvo et al., 2017). Locomotion is just one type of movement. Higher plants (angiosperms and gymnosperms), on which Darwin (1880) conducted many studies, show different movements from standard animal movements. Plants carry out these movements with the growth of their organs and the turgor changes in their cells unlike animal locomotion. These may be reversible or non-reversible movements. In this way, they adapt to their small environment (Hopkins & Hüner, 1995).

1.2.1. Types of Plant Movements

Plants, like animals, had to exhibit certain movements to survive. Unlike animals, this happens much more slowly in plants. And these movements occur because of some phenotypic changes, such as the lengthening and shortening of the leaves, roots and stems of the plants.

Although these movements of plants do not serve purposes such as escape or hunting, as in animals, they serve to perceive the threat from outside and to reach the possible source. For example, the *Mimosa pudica* L. plant rapidly closes its leaves when there are touched by an external stimulus perceived by the plant as dangerous. The *Cressa cretica* orients his body towards the direction of the sunrise to catch the sunlight (Garcia Rodrigues & Calvo Garzon, 2010).

Plant movements are divided into two categories: tropic movements and nastic movements. Tropic movements occur in response to the stimuli the plant receives from the environment. The stimuli from the environment can be exemplified as light and gravity, on which the basic growth and development of the plant largely depends. Nastic movements, on the other hand, are movements that are determined beforehand, regardless of the presence of a stimulus. The direction of these movements is determined by the structure and position of the engines performing the movements (Bhatla & Lal, 2023).

Tropic Movements. The Tropism movements of plants began to be examined and researched in more detail. It was stated that plant roots make negative and positive tropism movements to respond to external stimuli in biotic and abiotic forms, and that this may be a mechanism like the sensory-motor circuit in animals (Gilroy, 2008). Positive movements are defined as movements towards the stimulus, and negative movements defined as movements away from the stimulus (Bhatla & Lal, 2023).

Phototropism is the general name for the movements of the plant using light as a reference and, the plant's elongation directed towards the light; allows the plant to obtain sufficient light for photosynthesis in the upper part and to capture optimum water and nutrients in the root part. It includes the movements of the plant's leaves, flowers, and stem to change their direction according

to the light. Plants respond to the changing conditions of the environment they are in while also trying to continue growth and development. Photoreceptors are a way plants use to understand what is happening in their environment; they optimize the quality of light and the germination of the seed or reproduction by adapting to the characteristics of the light. Studies on some plants, such as *Avena sativa* and *Zea mays* L., have shown that they have a common photoreceptor - called phototropin. Phototropins are absorbed peaks in blue-light and UV-A rays. These receptors, which we call phototropins, enable certain movements such as the distribution of chloroplasts on the plant, the opening and closing of stomata, and some reactions resulting from blue light, depending on the light intensity. Detailed studies have been carried out on a mutant version of *Arabidopsis thalina* that cannot respond to phototropic stimuli. Asymmetric exposure of the plant to light causes differential growth, which leads to unilateral accumulation of the growth hormone in plants, which we call auxin. The unilateral distribution of auxin by phototropin is caused by the deterioration in the protein that transports auxin, called PIN1. Tested on *Brassica oleracea* with 20% less light on one side (Bhatla & Lal, 2023). When phototropic responses, or the elongation of the plant's organs, occur in a direction towards the light source, this is called positive phototropism. When the organs of the plant grow away from the light source such as the root system, this is an example of negative phototropism (Liscum et al., 2014). As is known, roots live in the dark. When they are placed in a bright environment, they try to escape from the light by exhibiting a reverse phototropism (Baluška et al., 2009). In their study with *Arabidopsis* roots, Laxmi and his colleagues (2008) found that if the roots of the plant were exposed to light, the roots grew larger to move away from the light. Light is perceived by the root as a stress stimulus, the same reactions are given to high amounts of salt, and the plant creates an escape plan by stimulating the scent body (Baluška et al., 2009). Research on negative phototropism - the growth of plant scents away

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from light - dates to Darwin (1880). The discovery of blue light receptors such as PHOT1 has led to an understanding of how signal transmission occurs in this tropism (Wan et al., 2008).

Although the tropism on which the most research has been conducted is gravitropism - the growth of the plant in response to gravity - it is thought that not fully understood (Baluška et al., 2009). Gravity affects all living things, as well as the growth and movements of plants. Gravitropism is the growth of plants in different ways under the influence of gravity. Gravitropism helps shoots grow towards the light source and obtain the necessary resources for photosynthesis, while roots grow towards the soil, keeping the plant skeleton stable, and reaching water and other nutrients that can be taken from the soil. Gravitropism is not a process that happens quickly and ends quickly; it requires certain steps. Gravity is first perceived, and the stimulus is transformed into a physiological signal to be transmitted throughout the plant. Then, this signal is transmitted from the point where it is perceived to the ends of the roots and shoots where the reaction will occur, and it reveals the curvature reaction in these places (Masson et al., 2002).

Charles Darwin (1880) noted that roots and trunks respond to gravity differently. He showed in his studies that roots exhibit positive gravitropic response and grow in the direction of gravity, while stems exhibit negative gravitropic response and move in the opposite direction of gravity (Darwin & Darwin, 1880). The growth of plant roots in the direction of gravity via gravitropism can be explained by the fact that auxin, which can be simply explained as a growth hormone, moves from the root of the plant to the lower parts and concentrates there. The auxin concentrated here suppresses growth in this direction and ensures elongation at the tip of the roots. The resulting directional growth explains the downward appearance of plant roots (Band et al., 2012). The exact opposite can be observed in shoots. As the shoots grow, auxin concentrates towards the bottom of the shoot and suppresses possible growth in the upper part. Thus, the lower

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parts start to grow more towards the upper parts. The further growth of the lower parts cause growth and elongation at the upwardly curved ends. Statocyst cells are cells that undertake the task of sensing gravity, thanks to the starchy structure they contain. Since starch is heavier than the cytoplasm, it affects the position of the organelles within the cell and causes an asymmetrical appearance. Recently, the 'position hypothesis', which suggests that their positions in the plant are effective rather than their weight, has become accepted. In the gravitropic response, auxin distributes laterally. This causes greater growth in the lower part of the shoot. (Bhatla & Lal, 2023).

Another type of tropism is the hydrotropism that is the movement of a plant towards water. Plants can detect water according to the humidity level of the environment they are in, or a change in the current water level. Hydrotropism is a positive tropism that ends with growth or movement. It is very crucial for plants, because it helps to broaden the chance to obtain water that is the one of the most important sources for plants to survive. Hydrotropism is used by plants to reach humid parts of the soil by bending their roots (Gul et al., 2023). Studies on hydrotropism date back to the studies conducted by Charles Darwin and Francis Darwin in the 1880s. According to their observations, the opening and closing of plant stomata was affected by the humidity of the air or water stress (Baluška et al., 2009).

Nastic movements. Nastic movements are movements that are genetically programmed in the plant and do not have a specific direction, affected by growth and the change in turgor balance within the plant. Movements directed from the inside of the plant cause the buds to swell and open. The movement of leaves and flowers in response to external factors such as light and temperature is called paratonic movements (Bhatla & Lal, 2023). Nastic movements are also present in plant organs such as leaves, where the same growth is not observed in all parts. Upward growth is called

hyponastic, and downward growth is called epinastic. For example, epinastic growth is observed in the leaves of tomato seedlings growing in irrigated soil. In the hashish plant, the flower stalk shows epinastic growth when growing downwards in the form of a hook, and when the flower opens, it shows hyponastic growth (Bhatla & Lal, 2023).

What we call nyctinastic movements are reversible turgor changes that regulate the rhythmic movements of the plant in the day and night cycle and create sleep responses. During the day, the plant remains in a vertical or horizontal open position, and at night it moves to a closed position. The movements of the plant according to temperature are called thermonastic movements. The flowers of *Liliaceae* and *Iridaceae* react to the increase in ambient temperature by opening their flowers and closing them. Plants exhibit thigmonast movements in response to touch. *Mimosa pudica* is one of the most prominent examples of this. When the plant is touched, this is detected by the pulvinus, and this message is carried by the sieve tubes. It causes the transport of Aba (abscisic acid) and the ions it controls and their diffusion in the upper region of the pulvinus, causing K+ ions and water to fill into the spaces. The swelling in the upper parts of the pulvinus is lost. The leaves return to their previous position by transferring the K+ ion to the cells and regaining turgor (Bhatla & Lal, 2023).

Circumnutation. Charles Darwin and his son Francis Darwin (1880) included extensive and comprehensive research on the movements of plants in their book *The Power of Movement in Plants*. In this book, they observed many plant movements in different environments, experiments or ordinary living conditions, and talked about the properties of many movements and classified them, but they said that the basis of all of them was the movement called circumnutation movement, which was previously called 'rotating nutation' by Sachs. Circumnutation was created

by combining the Latin words circus, meaning 'circle', and nutation, meaning 'sway'. It is the name given to the rhythmic, long-short periods, elliptical or completely irregular movements that occur in many organs of the plant such as hypocotyl, coleoptile, epicotyl, stem, shoot, tendril, petiole or root (Stolarz, 2009).

It has been reported by many researchers that circular movements are observed in most plants (E.g., Hart, 1990; Kiss et al., 2007). Although it is generally recorded that there are elliptical movements, the movements can also be circular or irregular. Darwin reported that recorded movements could be right-handed or left-handed (1875). Namely direction might be clockwise or counterclockwise. *Arabidopsis thalina* shows clockwise pattern while it is in short period of movement and counterclockwise pattern while it is in long period of movement (Schuster & Engelman, 1997).

The amplitude of circumnutation can vary widely depending on the type of the plant. It has been observed in the *Helianthus* that the circumnutation movement also shows changes within the plant itself. The plant exhibited a circumnavigation that sometimes lasted less than an hour, sometimes lasted several hours, and was mixed with circadian cycles (Stolarz et al., 2008; Stolarz, 2009). On the other hand, the *Arabidopsis* exhibited two types of oscillations. One consisted of long periods (LPNs) lasting 1 to 8 hours and the other consisted of short periods (SPNs) lasting 20 to 60 minutes. The basis of these movements lies in the asymmetrical development seen in the plant (Schuster & Engelman, 1997).

There are three hypotheses put forward about the underlying cause of the circumnutation movement. One of them suggests that this movement is of internal origin, that is, it is endogenous, the other suggests that it is caused by gravity, that is, it occurs as a response to an external stimulus and is exogenous, and the third one suggests that these two are effective together (Israelsson &

Johnsson, 1967; Brown et al, 1990; Johnsson, 1997; Mugnai et al., 2007). According to Darwin's claim, unlike other plant movements, internal control lay behind this plant movement (Darwin, 1880). More recent studies observing the development of plants in a zero-gravity environment in space also support this hypothesis (Brown, 1993; Correll & Kiss, 2008; Stolarz, 2009; Whippo and Hangarter, 2009). Today, the hypothesis that internal control and gravitropism underlie oscillatory movements (Brown, 1993; Johnsson, 1997) but that these are effective independently of each other is accepted. The purpose of circumnutation movement was clearly explained by Darwin. Shoots and tendrils of climbing plants perform nutation movement and seek mechanical support for the plant to grow. The upper parts of the plant that perform nutation continue to perform circumnutation movement until they find a suitable support to hold on to (Darwin & Darwin, 1880).

1.2.2. The case of climbing plants

Climbing plants are also known as climbers, this special type of plants cannot carry their own weights, so they need a support to anchor, ascend vertical surfaces and reach the light. They are characterized according to their climbing methods such as twining stems, tendrils and root climbers. Their adaptation allows them to reach sources they need to grow and survive. Twining stems climb by wrapping around a support and they are the most common types in climber, wisteria and beans are examples of this kind (Chen et al., 2023). Climbers that use tendrils can easily attach slender supports; the most common example is pea plant (*Pisum sativum*) which is the subject of our current study too. Some climbers use their roots to climb, this strategy might be useful to climb large-diameter objects (Lehnebach et al., 2022). Climbers use different strategies that provide them

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to grow and survive in diverse environments, by facilitating to reach sources for living and growing.

Climbing plants need to find external support upon which grow and reach the greatest exposure to the light (Garbin et al, 2012; Putz, 1984). Some characteristics of the support such as the size affect the clasping movement of climbing plants (Hegarty, 1991). Some theoretical and practical studies have shown that the plant loses its attachment ability when the diameter of the support exceeds a certain point (Putz, 1984; Putz & Holbrook, 1991; Neukirch & Goriely, 2006). Darwin's studies on *Wisteria sinensis* (Sims) showed that the plant could not hug a 15 cm wide support (Darwin, 1875). The extent of support for different climbing plants varies greatly (Gianoli, 2015). A study with two different twining lianas showed that plants succeeded at different rates when faced with supports of different diameters, a result that is paralleled when the same plant is faced with supports of different sizes (Peñalosa,1982).

Environmental factors have an impact, at least to some extent, on the circumnutation motion and the response to the support. For example, Gartner (1991) stated that the growth of shrubs and vines depends on the presence of support. Darwin (1875) reported that *Phaseolus coccineus* L. could not connect to an 8-10 cm support in a bright test environment but could do so under sunlight. Perhaps related to this, a study comparing twining plants in temperate and subtropical climates revealed that the presence of twining plants in subtropical climates was higher (Durigon et al., 2014).

Although Atala and Gianoli (2008) showed that genetic variation can influence the response to the presence of support through their experiments on *Convolculus* spp. and *Ipomoea* spp., within-species studies on *I purpurea* (L.) Roth showed that the effect of the maternal family

within a species does not affect the response to the presence of support (Gianoli & Gonzáles-Teuber, 2005).

It has been understood that the rough structure of tree barks also affects the behavior of climbing plants (Putz, 1980; Campbell et al., 2005; Campanello et al., 2007). Although it is thought that the structure of the tree bark is to prevent liana invasion (Talley et al., 1996; Carsten et al., 2002), it has been observed that vine invasion cannot be prevented in trees that shed a lot of bark (Carsten et al., 2002; Carrasco-Urra & Gianoli, 2009). Another study showed that roughness of the tree bark in rainforests is beneficial to the climber (Carsten et al., 2002). In his study with kidney bean seedlings, Darwin observed that their axial bending increased during climbing when they encountered rough stems (1880).

The only advantage of climbing plants that they can climb is not only that they get rid of the shadows of tall plants, but also that they get away from herbivores on the ground (Gianoli, 2015). Studies on vines that are damaged when they cannot find support also prove this (Gianoli & Molina-Montenegro, 2005). The identity of the support tree also has an impact on the herbivore's behavior (Sasal & Suarez, 2011). In parallel with what the adaptive climbing hypothesis claims, it has been observed that the climbing of vines with damaged leaves increases. The study conducted on *Convolvulus arvensis* L. proved that climbing occurs in both sun and shade, but parallels photosynthesis under the shade (Gianoli & Molina-Montenegro, 2005). This may be parallel to the increased need for resources in low light conditions (Gianoli, 2015). Water stress caused a negative effect on the climbing behavior of the plant (Atala et al., 2011). Researchers suggested that trichomes facilitate climbing by acting as a hook in I. purpurea (Silk & Holbrook, 2005). But I. purpurea is also affected by water stress in the same way (Atala et al., 2011).

Kinematic behaviors of the climbers have been subjected to several studies. Studies help us to understand the different behavioral strategies to approach and clasp an external support. One of the most important questions has been asked by Guerra and their colleagues (2019) who investigate whether climbing plants take consideration of the facilities of possible support and arrange accordingly their movements by means of the three dimensional (3D) kinematical analysis. *Pisum sativum* L. plants were tested in three experiments, in the first one there was no stimulus and stimulus conditions, in the second one there was thin and thick support conditions and in the final one, a group of plant were presented with the 2D picture of 3D thin support whereas a group were presented with 2D picture of thick support. Results showed that plants were able to perceive the presence or the absence of a potential support in the environment and to module the kinematics of their tendrils properly. When support detected circumnutating tendrils were changing their direction toward the detected support, and their pattern of growth. This can be seen as a proof of their sophisticated movements in the presence of a goal. Furthermore, in presence of potential support with different diameter (i.e., thin or thick support) plants were able to module the kinematics of their tendrils in term of velocity and aperture. In specific, the movement velocity was lower, and the aperture of the tendrils more contained in the presence of the thick support compared to the thin one. Difference kinematic results between thin and thick support is the result of the plants' ability to extract among the graspable properties of varied supports (Guerra et al., 2019). Researchers reported that since thicker support is more energy demanding, the pattern for thick and thin support conditions therefore plants needed to slow down their movement and contained the aperture of their tendrils to preserve energy and execute a more precise and firmer grip upon the support. Based on the study, it was observed that plants can modify their movements in a sophisticated way towards a target when they set a target, changing their growth direction

according to different features of the target. These results may indicate that plants grow flexibly using sensory information and have control over their movement direction. Another study by Wang and colleagues (2023) investigated how pea plants (*Pisum sativum* L.) adapt their movement in the situation of choosing between supports of different diameters by means of 3D motion analysis system. The results indicate that the way pea plants move can vary depending on whether they are presented with one or two potential supports. Furthermore, when presented with a choice between thin and thick supports, the plants showed a distinct preference for the former than the latter. The present findings shed further light on how climbing plants make decisions regarding support-searching and provide evidence that plants adopt one of several alternative plastic responses in a way that optimally corresponds to environmental scenarios.

Several kinematic experiments (Bonato et al., 2024; Ceccarini et al., 2020a;b; Guerra et al., 2019; 2021; 2022; 2024; Wang et al., 2023) aimed to understand whether plants show goal-directed anticipatory behavior like animals and whether they make a motor plan according to the features of the plant's support and environmental conditions. Recent evidence has shown that plants are able to perceive their environment and respond to it properly. It has been understood from studies conducted on plants that elongate their roots by limiting the resources of rival plants (Maina et al., 2002; Gruntman & Novoplansky, 2004), that they make decisions based on the different possibilities offered by the environment. The underground root systems of the plant and the shoots above the ground act as organs searching for the necessary nutrients for the plant and are the subject of studies on plant intelligence and intentionality (Maina et al., 2002; Marder, 2012, Wang et al., 2021). According to Marder (2012), plant structures that perform this searching function show that plants do not have a passive function towards their environment, but rather exhibit goal-directed behavior. The question of whether the behavior of plants can be this

complicated and intelligent has been investigated from many perspectives and presented with evidence, but it also brings with it some other questions. One of these is the basic question of my study, whether plants have a quantity-related ability. Indeed, discrimination ability represent the most basic type of numerical competence, and it concerns the capability to discriminate which of quantities are greater in size. This ability allows organisms to enhance their change to survive by avoiding predators and/or by maximizing the food foraging strategies. Importantly, this ability is observed among different animal species including human beings. But, what about brainless organisms such as plants? To date few evidence has investigated this issue in the green kingdom. Therefore, further studies are needed before we can claim that plants exhibit quantity discrimination abilities and if so, how sophisticate they are in relation to those observed in different animal species. In this view, examining the studies conducted on plant cognition and understanding the types and scope of movements, it is necessary to understand the numerical abilities of various animal species, especially humans, to form the basis of the research.

Chapter 2. Numerical Cognition in Human and Non-human Animals

2.1. Number Sense

All living beings have capabilities to survive in nature. These capabilities are more complex in the entities who are in the most recent in the evolutionary tree namely, homo sapiens, humans. Lots of humans' cognitive abilities have been discovered in the last centuries, which are varying in a wide range from higher order cognitive abilities to lower order cognitive abilities such as planning, problem solving, logical thinking, attention, memory, social cognition, perceptual abilities and so on (O'Brien & Shapiro, 1968; Hagen and Hale, 1973; Cole & Loftus, 1987; Aslin & Smith, 1988; Garfield et al., 2001; McCormack & Atance, 2011; Keen, 2011; Tecwyn et al., 2014). One of the most important questions about human cognition is the ability to represent numbers and the origins and nature of this capacity (Lipton & Spelke, 2003). According to the explanation of many researchers, adult human's number representation and mathematical thinking abilities depend in some sense on their feelings based on approximate numerical quantities or number sense (Dehaene, 1997).

'Sense of number' is one of these cognitive functions and origin of numerical abilities. In other words, 'sense of number' is defined as humans' intuitively or instinctively understanding, perceiving and representing numerosity. Mathematical operations such as number discrimination, counting, calculating, and arithmetic to be done requires a sense of number and representation of numerosity. Adults' mathematical system stands upon two basic components one of them is 'number sense' of approximate numbers and the other is having a symbolic capacity to express and relate magnitudes that they receive and mathematical operations (McCrink and Wynn, 2007). However, adults perceive and represent numbers in two different ways and their manipulations vary accordingly. These two core systems are tracking small numbers as individual objects and

reaching precise conclusions, on the contrary, estimating large numbers imprecisely, this is summarized as approximate number sense (Fiegenson et al., 2004). In respect of this number representation is a core function both for 'number sense' of approximate numbers and to calculate mathematical operations.

This representation and manipulation of small and large numbers is used to judge numerosity. Numerosity judgment may vary depending on the format of the stimuli that is received from outside. This ability is one of the abilities which requires number sense, is not unique to humans at all; we can observe this among a lot of non-human beings. Starting from humans' numerical abilities, commonalities shared between species will be discussed during this and next chapters.

2.2. Number Concept

To begin, it is worth mentioning several external studies in which some researchers tested people's counting abilities from infancy and from birth by presenting numerical sequences in different modules such as visual and auditory. One of the most fundamental studies on number estimation belongs to Jevons (1871). Jevons randomly threw the black beans in his hand into a white round cardboard box placed on a black background, regardless of their number, and asked the participants to guess how many beans were in the box. During the experiment, both the participants' predictions and the number of beans were noted. The number of black beans that participants estimated varied between 3 and 15. After the experiment, he compared the actual numbers, and the numbers predicted by the participant. Results showed that participants did more errors in predictions when looking at larger numbers. Additionally, as the estimated numbers grew, so did the variability of the estimate. For all numbers predicted, the distribution of the prediction

was around the mean of the prediction. This was a clear clue for the approximate decision on the number estimate. In short, it summarized in its most basic form the rules underlying the mechanisms that people use when guessing numbers.

Kaufman and colleagues (1949) pointed out that the accuracy of estimating small numbers was high, supporting previous studies, which was consistent with the study of Jevon (1871). They showed that young children were also more successful at guessing and manipulating small numbers, which was a degree of evidence of the ability to subsidize them. In the following years, more attention was paid to studies on children and infants. Starkey and Cooper Jr.'s (1980) research investigated children's counting abilities in an environment that inhibits verbal counting. This was clearly seen by the presence of subsidy in addition to verbal counting in young children, confirming Kaufman and his colleagues (1949).

Starkey and Cooper (1980) made a study aimed to investigate if infants can discriminate, represent, and remember small numbers of sets. Results revealing a possible influence of perceptual counting capacity highlights this process. In the ongoing process, the difference between small and large numbers began to emerge. Antell and Keating (1983) focused on infants' numerical discrimination ability between two different sets of numbers: small numbers and large numbers. They tested forty healthy newborn babies in two different conditions: sets of dots with either 2 vs 3 or 4 vs 6 blocks. The habituation/violation of expectation paradigm moved towards the 2 to 3, but not to the larger cluster of 4 to 6. If habituation had to be defined briefly, it could be said as follows; Habituation means that the response to a stimulus gradually decreases and this decrease is not due to adaptation (Segundo-Ortin & Calvo, 2021). On the other hand, to violate the expectation, a result that is very different from the participant's possible expectation is presented, as Wynn did in his study (1992). Results showed that infants were not able to distinguish between

large numbers (i.e., 4 vs 6 dots). However, Starkey et al. (1990) revealed in their study that the development of early numerical abilities is independent of the emergence of language, the development of complex cognitive abilities and cultural experience, which clarified the fact that numerical abilities are seen even in almost newborn infants. To explain this, they conducted a series of experiments. In the first experiment, based on the knowledge that infants are more likely to count homogeneous objects than heterogeneous objects (Gast, 1957), they tried to understand whether this counting ability of infants is also valid for homogeneous objects. As a result of the first experiment, they concluded that infants perceive multiplicity not only when the elements are the same but also when they are different. In the second experiment, to activate auditory abilities, two screens on which two different number sequences were presented were presented to the infants, along with an auditory stimulus compatible with one of these two sequences. The infants' preferences were for the number sequence with which the sound was compatible. Except for the two experiments they conducted for control purposes, in their last experiment, infants were first shown two screens where two different number sequences were presented, and then different number sequences were presented to the infants. As a result of the experiment, it was seen that infants could understand the numerical match even if the numerical sequences presented in different modes were not simultaneous (Starkey et al., 1990).

In this matter, Van Oeffelen and Vos (1982) limited the verbal counting abilities of adults and presented the dots as stimuli to the participants in sets of two, matching them in different proportions. They found that participants could distinguish between two sets of numbers that differed by at most 1.15. This was one of the first studies showing that counting ability in adults is ratio dependent. Ratio dependency of numerical discrimination is the law that states that the ability of animals to distinguish numbers from each other depends on the ratio of the numbers

presented to each other. This law was put forward based on Weber's Number Representation Laws (Nieder, 2020). When studies continued adults, it was observed that adults could still estimate large numbers when subjected to tests that restricted their verbal counting abilities (Cordes et al., 2001). This was different from the results of experiments done on infants. The reasons for this will be examined in depth in the later stages of the chapter.

According to Dehaene (1997), there is evidence of the existence of the use for the representation of numbers in the approximate number system, when even adults trained in mathematical abilities are asked to perform according to numbers presented in words or Arabic format. The finding underscores a common understanding of multiplicity in animals and humans. If we look at how this approximate number develops, we must look at it from childhood, even infancy. In line with the purpose of the studies, one should be aware of the limitations of working with babies who do not speak language and have limited physical abilities. Researchers focused on two specific paradigms to test infants' abilities to habituation and violation of expectation. They assumed that babies' attention would be attracted and aroused by increasing novelty in the experimental environment. In the following chapter, starting from the children's ability to distinguish numbers, step by step, we will focus on how the numerosity ability is shaped developmentally during lifetime.

The first studies in the literature aiming to understand babies' quantity discrimination abilities show that we cannot make a distinction as to whether babies discriminate discrete numbers or continuous variables come into play (Feigenson, 2004). It has been observed that when continuous variables such as total surface area, continuous length, and display size are limited, babies fail to distinguish larger numbers such as 8 vs 16 (Xu & Spelke, 2000). While the first of the two separate core systems in the brain is responsible for numerical representations, the second

system is responsible for non-numerical continuous variables and discrete number representation (Feigenson, 2004). Naturally, when continuous variables are controlled, the representation of large number sequences becomes difficult and babies cannot acquire information about these number sequences (Brannon et al., 2004). Interestingly, when non-numerical continuous variables and discrete number representations are tested against each other using habituation and violation of expectation paradigms, babies are seen to respond according to continuous variables (Clearfield & Mix, 1999; Fiegenson et al., 2002).

Therefore, in studies trying to understand the numerical abilities of babies, it is necessary to control these to ensure that babies do not acquire information from non-numerical continuous variables. For example, Xu and Spelke (2000) conducted a series of experiments in their study and presented number sequences to babies as dots. The authors made sure that the brightness, contour length, display density, element and display size of the dots were the same and that the babies were not affected by them while performing the task (Xu & Spelke, 2000). In another study, when presenting dot arrays to babies, researchers equated the total occupied area and the differences between the brightness of the elements in different dot arrays to eliminate the possibility of continuous variables explaining the responses (Hyde & Spelke, 2011). In most of the studies I will discuss below, researchers controlled for brightness, overall space, and area and made sure they kept them equal throughout the experiment to make sure they did not influence their child's ability to count discrete numbers (Xu & Spelke 2000; Lipton & Spelke, 2003).

Xu and Spelke (2000) while looking at previous evidence for infants' discrimination ability on small numbers they wanted to conduct an experiment for large numbers. Sixteen participants participated in the study, half were female, and the other was males whose mean age is six months-old. Participants were habituated to 8 vs 16 elements. Six test trials consisting of 8 vs 16 elements

were represented. In conclusion infants looked longer to unfamiliar numerosity. Infants discriminate between 8 vs 16 elements. On their second experiment, the ratio reduced 1:3. As noted previously, when infants presented with small numbers 2 vs 3, they became successful at discriminating however when they presented with large numbers (4 vs 6) they were not successful (Starkey & Cooper, 1980). In the second experiment, participants were habituated to 8 vs 12 elements. Six test trials consisting of 8 vs 12 elements were represented. This experiment resulted with the evidence that when the distance between numbers is reduced no evidence found discrimination of infants amounts to different sets. Infants were sensitive to 1:2 ratio for small-number discrimination, again this study proved that infants could discriminate between large-numbers which are distant from each number ratio of 1: 2 but not for the number ratio of 1:3.

Lipton and Spekle (2003) investigated whether infants' performance in tests in which they discriminated proportionally ratio of the set sizes depended on their abstract understanding of approximate numerical magnitude. They repeated the experiment of Xu and Spelke (2000) by replacing the stimuli in the experiment with sensory stimuli and making numerical changes but with the same ratios (1:2 and 1:5) with 6-month-old babies. In a separate experiment, they examined whether 9-month-old babies could distinguish between sets of 8 and 12 and sets of 8 and 10. Their first experiment showed that infants were able to discriminate stimuli with a ratio of 1:2, but not being able to discriminate with a ratio of 1:3 (as previously observed by Xu and Spelke, 2000). Thus, they saw that these ratios were valid for the infants' discrimination abilities in both visual-spatial and auditory-temporal sequences. The results of the other experiment showed that 9-month-old babies could also distinguish stimuli with a ratio of 2:3 but not between 8 and 10, which showed the limits of their abilities. The fact that the proportional discrimination ability in 9-month-old infants differed compared to 6-month-old infants not only shows that the numerical

discrimination ability develops throughout infancy, but also is consistent with the claim that this mechanism is based on a common cause with adults and that it emerges in the early period when verbal counting and arithmetic abilities have not yet developed (Lipton & Spelke, 2003).

According to Xu and Spelke (2000), there was a reason why children could easily distinguish differences in small proportions when distinguishing small numbers (Antell & Keating, 1983; Starkey et al., 1990; Starkey & Cooper, 1980), but this proportional difference was limited to 1:2 when distinguishing large numbers. When infants are shown fewer objects or events, they try to follow each event separately, depending on their attention mechanisms or similar mechanisms. This tendency of infants to individually represent a small number of objects and their preference-based responses to perceptual variables can be explained. When many objects are presented to them, their ability to keep track of objects of different individuality becomes inadequate and they may focus on collections rather than individual representations. These tendencies can be explained by successful responses to numbers in which perceptual variables are controlled. Infants' sensitivity to multiplicity requires a 1:2 ratio difference - future studies will focus more on how different ratios give results - and if they can distinguish up to 3 objects regardless of the proportional difference in their ability to track individual objects (Xu & Spelke, 2000). As seen in adults, it is seen that rate differences come into play in infants' numerical discrimination abilities, and when infants represent numbers, the variability is proportional to the numerical size, as in Weber's law (Gallistel & Gelman, 1990). In most experiments in which children's numerical abilities were measured, children were presented with a small number of objects. In addition, many of the experiments conducted for adults and children have suggested that the mechanism used to distinguish a small number of objects is related to the ability to form

individual representations of a small number of presented objects, rather than the ability underlying the number sense (Lipton & Spelke, 2003).

If we look at more recent studies, we see that there is a lot of curiosity about newborn infants' understanding of numerical concepts across different modalities. Specifically, Izard and his colleagues (2009) studied the ability of newborn infants to distinguish large numbers of objects cross-modally in three experiments. They used audio and visual stimuli and looked at their results in congruent and incongruent number sequences. They noticed that newborn infants react to abstract numerical values, even if they have different modalities and versions. Infants could distinguish between stimuli when the difference was a ratio of 1:3.

2.3. Development of Numerical Ability

As with human adult understanding of numbers, infants (Coubart et all., 2013) and animals (Nieder, 2020) have ability to estimate numerosity in an approximate way. According to Weber's law, numerical values that are close to each other are difficult to discriminate against, but discrimination ability gets better with the increase of the distance numbers that are compared. This effect is called the 'numerical distance effect'. When adults are asked to compare two numbers, they do better when the numbers are farther apart (Dehaene et al., 1990). Quantity discrimination that is represented by Weber's Law is parallel with the internal approximate number system (ANS).

Izard and Deheane (2008) started with the hypothesis that every perceived numerical value is encoded in an internal continuum and the continuum is called a number line. In their research, they claim that this number line was scaled logarithmically, making use of Fechner's laws. In fact, it has been claimed by many researchers that this number line is logarithmic rather than linear (Dehaene, 2003). They did not try to prove this in their studies, they just proceeded based on this

hypothesis. According to their hypothesis, when n is perceived as a multiplicity, an activation occurs on this logarithmic number line, with the average being log(n). The distribution around log(n) is assumed to be Gaussian with constant width w. This equation used to measure children's number representations is called the internal Weber fraction. Izard and Deheane (2008) gave an example as follow to make this explanation clear. If w = 0.20, the activation evoked by the perceived multiplicity of n will form a table between these logarithmic values with a probability of 0.7 [log (n 20%), log (n + 20%)]. For example, when the multiplicity is 10, 70% of the chances are in the range [log (8), log (12)].

Now it is necessary to touch upon the connection between Weber's laws and the logarithmic relationship of the number line. Assuming that the logarithmic function equation is applied to each number consecutively, as mentioned above, it can be easily observed that a logarithmic compression occurs. This compression shows that the overlap between numbers increases as the numbers grow. This may be an explanation for why numbers that are close to each other become more difficult to distinguish as the numbers specified in Weber's laws get larger (Piazza et al., 2010). However, the discriminability of numbers varies depending on the width of the Gaussian distributions. The width of the distribution is measured by the "internal Weber fraction" and this measures the precision of the internal representation. The internal Weber fraction calculated in this way varies significantly from infancy to adulthood (Halberda et al., 2008; Izard et al., 2009).

The Weber fraction is used to measure the "acuity" of abundance estimates made with the Approximate Number System. According to Weber's laws, when the difference between two separate numbers is divided by the reference size, the difference obtained is called the Weber fraction (Nieder, 2020). While this fraction is small, it indicates that number acuity is high, while the growth of this fraction indicates that number acuity is low (Piazza et al., 2010). In multiplicity

comparison tests, two n values are presented to the participant; one of these n values is the reference number and the other is the variable number. The participant is asked which value is greater and the predictions are scaled logarithmically. Another logarithmic scale is obtained by dividing the logarithmic values of the reference number by the logarithmic values of the variable numbers. This is the scale that allows us to obtain the Weber fraction. While increasing this fraction reduces "number acuity", decreasing this value reduces "number acuity". The radical change of the inner Weber fraction we mentioned above throughout life shows how "number acuity" changes throughout life.

In their study, Piazza, and his colleagues (2010) examined people in three different age groups who showed typical development (i.e., preschool children, school-age children, and adults). In the non-symbolic numerical comparison test, they present 16 or 32 dots used as references inside two white discs, and on the other, they present non-reference numbers. While non-reference numbers 12, 13, 14, 15, 17, 16, 19, 20 are used for reference number 16. For the reference number 32, non-reference numbers 24, 26, 28, 30, 34, 38, 40 are offered. The size of the area covered by the dots and the size of the dots were kept constant in the trials. The researchers did not want non-numerical variables to affect the participants' performance. Participants were asked to estimate which number in the box was larger without counting the dots. Then, when the participants' predictions and the ratio of the reference numbers were logarithmically scaled, the Weber fraction values of 10-year-old children and adults, starting from kindergarten children, were obtained. It was observed that the Weber fraction was gradually decreasing. This showed that "number acuity" increases from childhood to adulthood.

2.4. Commonality Among Species

As clearly explained at the beginning abilities are related with survival needs of living beings. Survival is not a requirement specific to humans. Animals must struggle to survive by adapting to their environment and developing different abilities. The abilities of primates, mammals, birds, fish, and many non-human animals to use numerical information have been tested and supported by different studies over many years (Reznikova & Ryabko, 2011; Agrillo, 2014; Agrillo, 2017; Nieder, 2020). Two scientists have put forward various laws for number representation: Weber and Fechner (Hoagland, 1930). Weber fraction was mentioned before. This is a fraction that Weber introduced by deducing it from Weber's laws.

These two core systems are widespread and usable across many different genres: small numbers can be clearly traced and understood as individual objects, and large numbers can be approximated and manipulated (Feigenson et al., 2004). Animals can approximately estimate numbers. This has previously been observed in animals tested both in trained and natural environments. We can look at the results of the study in which rats were trained and tested to press the press lever a target number of times. When the standard deviation of the trials in which the mice were expected to press the button as many times as the target number during the test was taken, the researchers noticed that the mice made more imprecise estimations as the numbers increased (Platt & Johnson, 1971). Studies have shown that primates can represent numbers approximately on the number line. Rhesus monkeys (*Macaca mulatta*) are trained to order elements from one to four in ascending order, then two different numerosity from five to nine are presented to the monkeys. When they look at the results, they see that the choices made by the monkeys depend on numerical ratios. The ratio of the difference between numbers is a limit for monkeys in distinguishing those numbers (Brannon & Terrace, 2000). At the same time, animals

represent small numbers as separate individuals, just like humans. Hauser and colleagues (2000) show rhesus monkeys two different series of apple slices in different locations. While monkeys can easily choose large numbers when asked to choose between 1 vs 2, 2 vs 3, 3 vs 4; When asked to choose between a series of 3 vs 8 and 4 vs 8 apples, their choice was entirely based on luck.

Weber's law of 'numerical distance effect' serves some survival cognitive capacities; distant quantities are easy to distinguish. This is consistent behaviorally. Animals need food to live and while they are struggling to find food, they need to keep their energy as possible, so they should decide to take food which gives them significant energy; more food means more energy for them. Nonetheless animals can benefit from their ability to discriminate against absolute small numbers. For example, Stancher and their colleagues (2015) conducted free choice experiments with frogs and examined their choice between different numbers of prey. While three and six patches, and four vs eight patches could be distinguished from each other among large numbers, three and four patches could not be significantly distinguished from each other by the frogs. However, Weber suggested that as the numbers to be distinguished become larger, the ability to distinguish them becomes less and less accurate. This rule is called the 'numerical size effect'. For example, in the study conducted by Stancher and his colleagues (2015), frogs could distinguish between two and four meals. He could not successfully distinguish between four and six meals.

Finally, to distinguish between two different clusters, the numerical distance between them must increase, that is, the ability to distinguish between these quantities is 'ratio dependent'. Ratio dependency can be presented with two different cognitive capacities that can be adapted to animals. First, the further apart two different quantities are, the more easily they can be distinguished, which is more behaviorally consistent. Because distinguishing between different numbers of foods is important to preserve energy, there is not much disadvantage in not being able

to choose between two different foods that are like each other. The second cognitive benefit is that it is proportionally beneficial for animals to be able to distinguish between small numbers more clearly than between large numbers. For example, if he can discriminate between one or two foods and choose two foods, he chose the one that is proportionally twice as large. But not being able to clearly distinguish between ten or eleven foods does not cause much loss proportionally (Nieder, 2020).

According to Weber, the function representing numbers expands in proportion to the increasing size of the imaginary number line where numbers are represented in our brain. Based on this, animals can distinguish between small numbers more easily but have difficulty distinguishing between large numbers. Fechner took a different approach. According to him, numbers are plotted on a nonlinear, compressed logarithmic scale, so that the functions are symmetric and have equal variance. Its formulation is explained by Fechner as follows: 'the subjective sensation of magnitudes is the logarithm of the objective sensation' (Nieder, 2020).

2.4.1. Animal Examples for numerical abilities

As changed in Nieder's (2020) review, researchers used different methods to understand how animals react to numerical cues. First, they observed their relationships with their environment and saw whether they used their numerical information. They tested their hypotheses by presenting different experimental manipulations during playback experiments. Finally, free choice experiments conducted in their natural habitat or in the laboratory were used to measure animals' reactions to numerical cues. In addition, due to some methodological limitations, it may not be possible to fully understand whether animals respond to concrete continuous quantities or abstract numerical quantities.

Control of these non-numerical quantity factors is critical for such studies. Because quantity can be definite and countable values, as well as continuous and uncountable values. While continuous quantities are more concrete and direct values that can be fed from more sensory experiences and data. Numerical quantities are more concrete values that do not have any meaning for sensory input. If left unchecked, numerical quantities can be affected by continuous quantities. For example, Nieder (2020) gave the following example to clarify this issue; six red apples cover twice as much red area as three red apples and are quite distinguishable, but not because of numerical values, but because of the area covered by red. Another factor that comes into play when experimenting on animals is the unpredictable motivation of the wild animal choosing between two quantities. Finally, since recent studies ask whether one of the two quantities is more than the other, they can only provide clues as to whether animals use numerical information (Nieder, 2020).

Taking all these presented conditions into consideration, many studies have been carried out to prove that different animals use numerical cues for different vital reasons. These are under different headings, as Nieder (2020) classifies them in his study; it can be explained as results obtained using different experimental methods from animals.

The most important of these is foraging, which is one of the methods used by people to feed and live for a long time. Krebs and his colleagues (1974) found the optimal foraging theory correct in their study. According to the optimal foraging theory, when animals compare with two or more food options, they can choose the option with more food. It is difficult to control non-numeric values for foodstuffs (Nieder, 2020).

Another important ability required for animals to continue their vital activities is to determine the path. Navigation ability is very important, especially for animals that travel long distances (Nieder, 2020). Chittka and Keiger (1995) conducted a study on honeybees (*Apis*

mellifera). Bees were trained along four identical landmarks spaced evenly apart in a 300-meter-long setup; the substance, which has nutritional properties for bees, was placed between the third and fourth points. It was observed that bees depend on landmarks when estimating the distance to food. Following this study, we can look at a more recent study conducted by Dacke and Srinivasan (2008) on honeybees. At first, bees were trained by giving them food rewards when they passed certain milestones. While the distance of the food reward was changed during the trials, the number of landmarks was kept the same throughout training, and it was found that the bees could count to four objects. Bees trained with this method were able to count stimuli they had never encountered before.

One other crucial requirement for animals to survive is to hide from predators. Many animal species do this by joining large groups. Larger groups naturally offer more hiding opportunities. Naturally, Hagel and Helfman (1991) thought that animals that had to choose between two groups would choose the larger group. Based on this assumption, they hypothesized that fathead minnows would choose the larger of the two groups facing them when threatened by largemouth bass. With or without predator threat, fathead minnows chose the larger flock group. When they are under the threat of predators, they make faster decisions and avoid small groups. Pritchard and colleagues (2001) conducted experiments on zebrafish in the following years. They manipulated the temperature of the water while waiting for the zebrafish to choose between four different schools. They found that if the water temperature was the same in the presence of the test fish and the school, the test fish preferred the larger school. They hypothesized that this experiment could give different results by decreasing or increasing the temperature of the water in the parts of the apparatus where schools of fish of different sizes are located. And they suggested that it was one of the different mechanisms that fish could use when distinguishing sizes of shoals.

Another area where knowledge of numbers may be actively required is in the hunting of animals. Just as very large groups may be needed to hunt; Very large groups can become inefficient, where not every member of the group can participate, remaining passive, and only some contributing to the hunt. Therefore, an optimum number of participants is required for hunting, since neither very large groups nor small groups are functional (Nieder, 2020). MacNulty and colleagues (2014) also mentioned this in their study on the hunting behavior of wolves and stated that large groups are not as successful as small groups in hunting due to decreased cooperation. Until this conclusion, they had tested whether wolves determined the number of members joining the group according to the difficulty and size of the prey hunted. Knowing that in previous studies, Yellowstone wolves (*Canis lupus*) formed groups of 2-6 individuals while hunting deer; They wanted to see how many groups of people they formed while hunting bison. They measured the link between rapture success and the size of wolf groups. And they concluded that the groups that successfully hunted bison were between 9-13 individuals. This study was consistent with the hypothesis that wolves can cooperate with more individuals when hunting larger prey.

One of the other points where number knowledge is used critically is mating. Mating is necessary for living things to survive and produce new generations. Carazo and colleagues (2012) created their hypothesis by suggesting that mealworm beetles (*Tenebrio molitor*), like many other insect species, can predict large numbers based on numerical cues during their reproductive behavior. During their studies on male and female mealworms that were ready to mate; They presented the male mealworms with one to four other male mealworm competitors during different trials. And at the end of the study, they concluded that, in proportion to the increasing number of male mealworm competitors, the time it took for mealworms to protect their pairs after mating was

longer. They argued that these data were good evidence for the true numerical prediction abilities of mealworm beetles, and that when they compared the positive results of experiments on other insect species, they also stated that they supported the hypothesis that vertebrates and invertebrates share the same core systems for the representation of non-verbal numbers.

Chapter 3. Current Research

The current study was carried out to investigate the existence of quantity related abilities in plants. Here, pea plants were tested in two different conditions: a control condition in which two supports (2 vs. 2) were placed on both sides of the plant at the same distance (10 cm) with an equal distance between the plants (8 cm) and an experimental condition in which three supports were positioned at an equal distance from each other (8cm) on one side of the plant, and one support was positioned at an equal distance from the plant (10cm) on the other side.

3.1. Subjects

Twenty-four snow peas (*P. sativum* var. saccharatum cv Carouby de Maussane) were used as the study plants (see Table 1). Healthy-looking pea seeds were selected, placed in pots, and maintained under the conditions specified below. The plants were randomly assigned to the control and experimental condition as half and a half.

Table 1. Sample description

Equal quantity condition	
N°	12
Distance from the poles	10 cm
Age	18.5 d (± 8.25; Range 13–46)
Different quantity condition	
N°	12
Distance from the poles	10 cm
Age	21 d (± 10; Range 10–53)

Note. The age, which is expressed in days, refers to the median, while median absolute deviation is noted in parentheses.

3.2. Experimental condition

The stimuli were identical wooden poles with a height of 50 cm (i.e., 7 cm the grounded part and 43 cm above part of it) positioned at 10 cm from the plant's and 8 cm from each other (Figure 1A, B). Sets of support were distributed to each side of the growing environment with either equal quantities on each side (2 vs. 2; Figure 1A) or different quantities (1 vs. 3; Figure 1B).
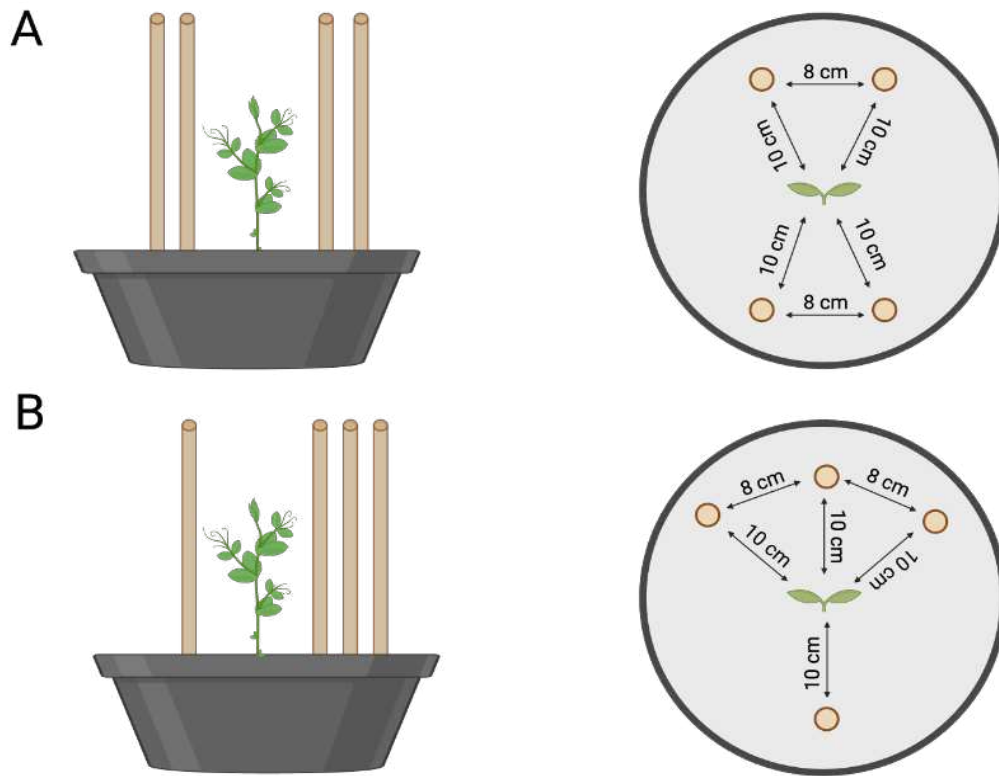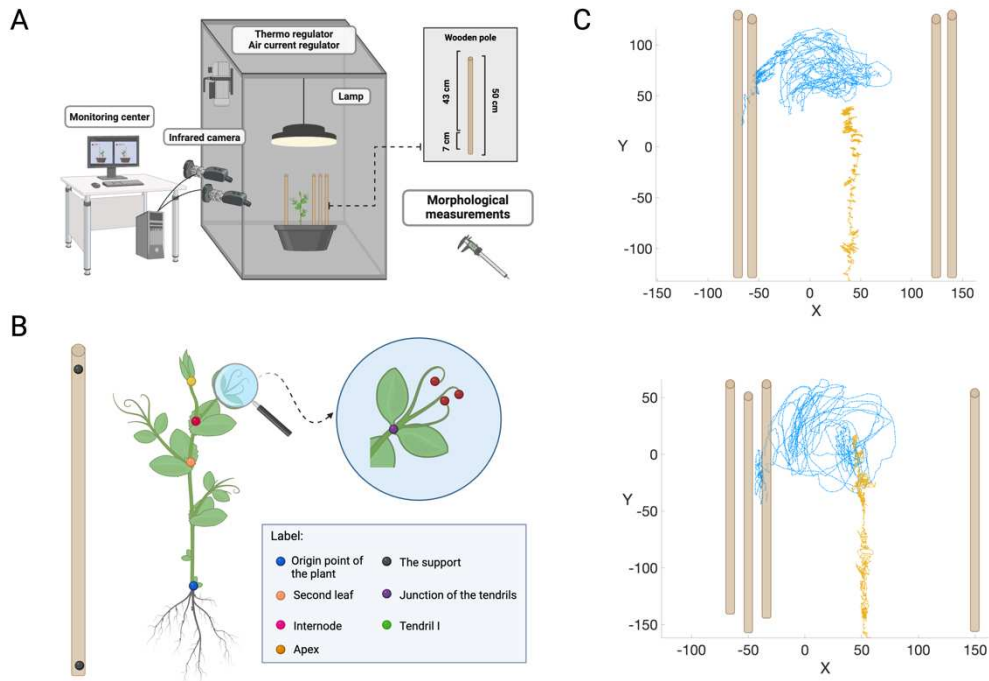

Figure 1. Graphical representation of the experimental conditions in which *P. sativum* plants germinated and grew, with an equal quantity distribution of the support (A; 2 *vs.* 2 support – EQ condition) or a different quantity distribution of supports (B; 3 *vs.* 1 support – DQ condition). Supports were placed around the plant at a distance of 10 cm from the center and 8 cm from each other.

3.3. Germination and Growth Condition

Silica sand (type 16SS, size 0.8/1.2 mm, weight 1.4) was filled into cylindrical pots (D 30 cm, height 20 cm). At the beginning of each experiment, pots were watered and fertilized using a

half-strength solution culture (Murashige and Skoog Basal Salt Micronutrient Solution; 10x, liquid, plant cell culture tested; SIGMA Life Science). Afterwards, the pots were watered as needed with tap water three times a week. Seeds were soaked in water for 24 hours, and then placed in absorbent paper for 5 days to germinate. Once the seeds germinated, healthy seedlings of the same height were chosen and potted. Once the seedling germinated, it was placed at the center of the pot and at 10 cm from each support. Each pot was placed in a growth chamber (Cultibox SG combi 80x80x160 cm; Figure 2A) so that the seeds germinated and grew under controlled conditions. The temperature of the room was adjusted to 26 °C so that the plants could grow under controlled conditions. For this, the room extractor fan was surrounded by a thermo-regulator (TT125; 125 mm diameter; maximum 280 MC/H ventilation) and there was an inlet ventilation fan (Blauberg Tubo 100 - 102m3/h). This dual fan combination offered a constant airflow rate into the grow rooms with air residence times of approximately 60 seconds. The fan is positioned so that movements caused by the fan have no effect on the movements of the plants. Plants were incubated with an 11.25-h photoperiod (5:45 - 17:00) under a cool white LED lamp (V-TAC innovative LED lighting, VT-911-100W, Des Moines, IA, USA) positioned 50 cm above each plant. enlarged. The Photosynthetic Photon Flux Density corresponding to 50 cm below the lamps above each seedling was 350 µmolph/(m2s) (quantum sensor LI-190R, Lincoln, Nebraska USA). The walls of the room were covered with reflective Mylar® film, allowing for even distribution of light. This method was the same for all single plants in separate growth chambers in the growth room.

Figure 2. A) Graphical representation for the DQ condition. **B)** Graphical representation of the anatomical landmarks of interest (the apex, the junction of the tendrils, and the tips of the tendrils). Five reference points were also considered: the origin of the plant, the second leaf, the internode and the lowest and the highest point of the support. **C)** Representative trajectories for the apex and the tendril's movement of the grasping leaf for the EQ and DQ conditions. The axes x and y refer to the sagittal and vertical axis in mm, respectively. Note that the plant perceives the supports in the DQ condition; it directed its approach and grasp movement toward the side of the pot with more supports available.

3.4. Video Recording and Data Analysis

A pair of RGB-infrared cameras (i.e. IP 2.1 Mpx outdoor varifocal IR 1080P) positioned 110 cm above the floor, 45 cm apart, were used to record stereotypic images of plants in each growth chamber. These two recording cameras were connected to a wireless router (e.g. D-Link Dsr-250n) with 10 ports, which was connected to a PC via Ethernet cables, and the frame acquisition and recording process was controlled by the CamRecorder software (Ab.Acus s.r.l.,

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Milan, Italy). To make it easier to distinguish the background and some anatomical points of the peas (e.g., shoots), some parts of the walls of the boxes were covered with black felt velvet, and the wooden stimulators were also painted black using charcoal. Using the MATLAB Camera Calibrator Application, the intrinsic, extrinsic and lens distortion parameters of each camera were estimated. To infer depth, 20 different photographs were taken of a chessboard (squares edge 18 mm, 10 columns, 7 rows) from different angles and under natural, non-direct light. The chessboard used for single camera calibration was placed in the middle of the growth chamber for stereo calibration. Photographs were taken by two cameras to determine the parameters of stereo calibration. The cameras captured one frame simultaneously every 3 minutes (frequency 0.0056 Hz) to comply with the experimental protocol. To reconstruct the 3D trajectory of each marker, their positions on the two camera images were used frame by frame in a special software developed by MATLAB (Ab.Acus s.r.l., Milan, Italy). The leaf stage that coiled the support was considered in the analysis for both the 'different quantity' condition – DQ (i.e., 3 *vs.* 1 support) and the 'equal quantity' condition – EQ conditions (i.e., 2 *vs.* 2 supports). The initial frame was defined as the frame in which the tendrils started to develop, and they were clearly visible from the apex. The end of the movement was defined as the frame in which tendril(s) started to wrap around the support. Landmarks at the anatomical landmarks of interest of the plants - namely the apex, the junction of the tendrils, and the tips of the tendrils - were inserted post-hoc (Figure 2 B). Markers were also positioned on the support (i.e., on both the lowest and the highest point of the support), the origin of the plant, the second leaf and the internode as reference points (Figure 2 B). The tracking procedure was carried out automatically throughout the time course of the motion sequence using the Kanade-Lucas-Tomasi (KLT) algorithm. The position of the markers was

manually controlled frame by frame by the experimenter. Triangulation of the 2D trajectories obtained from both cameras was used to calculate the 3D trajectory of each marker (Figure 2 C).

3.5. Dependent variables

The dependent variables specifically tailored to test our topic based on previous studies (Bonato et al., 2023; Ceccarini et al., 2020a, b; Guerra et al., 2019; 2021; 2022; Simonetti et al., 2021; Wang et al., 2023a; b) were:

i.   The spatial trajectories of the landmarks considered: this measure provides a way for quantifying circumnutation in both qualitative and quantitative terms.

ii.   The movement time (min): the interval between the beginning and the end of the movement.

iii.   The maximum velocity of the tendrils (mm/min): the maximum peak of velocity of the tendrils during circumnutation.

iv.   Time of maximum tendrils velocity (%): the time at which the tendrils reached the maximum velocity.

v.   The end point variability (min): the standard deviation of the Euclidean distance between the final position of the tip of the tendrils and the reference marker located upon the potential support.

3.5. Statistical analysis

Data analyses were computed in the R environment (R studio, 2020). Data from kinematical measurements (see section 3.5 Dependent variables) were analyzed by means of the lmer (Bates, 2015) function to perform linear mixed effect models with condition (i.e., EQ and

DQ) as a between factor and plant's ID as a random factor. The tendrils of each plant were considered in the analysis and the total number of observations considered for each model was equal to 72. The significance level was set at $p < 0.05$.

3.6. Results

3.6.1. Qualitative Results

For all the experimental conditions, each organ of the plant (e.g., the tip of the tendrils) showed a growing movement pattern characterized as circumnutation (Figure 2 C), which aims to find a potential support in the environment. Once the plant detected and perceived the support, strategically modified the trajectory of its tendrils that started to bend toward the support to approach and clasp it. Plants selected randomly between 4 supports in the EQ. In the DQ condition, the majority (9 of the 12 plants) of the plant directed their movements toward the side with 3 supports, while only 3 plants moved towards the side with the single support.

3.6.2. Kinematic Results

Movement time

No significant difference in the movement time was observed between conditions (EQ=3295.60; DQ= 3389.55; $\chi2$=1.077; p=.299; df=1; Marginal R^2=.009; Conditional R^2 = .448; Figure 3).
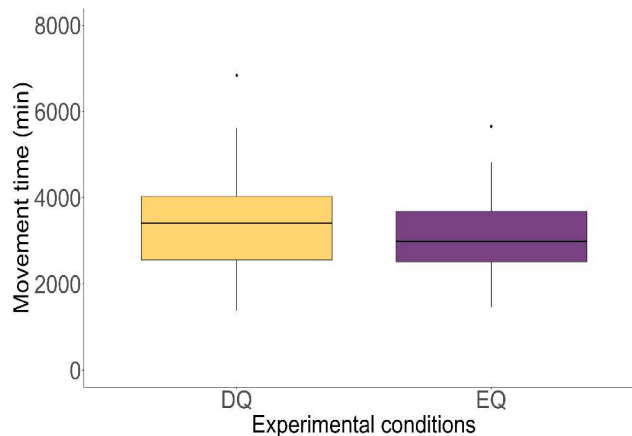
Figure 3. Box plots representing the difference between the EQ (i.e., violet box) and the DQ (i.e., yellow box) in the movement time.
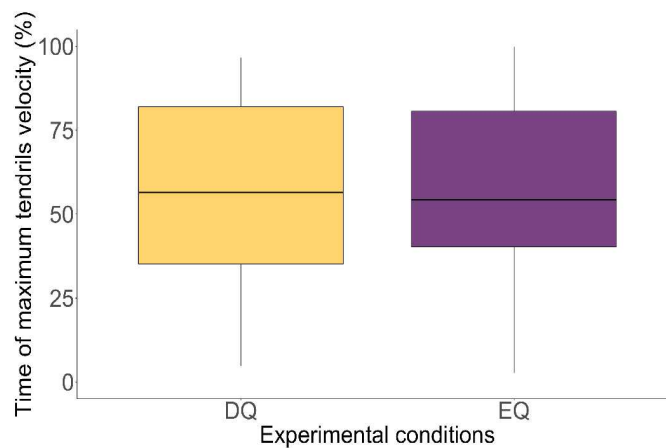
Maximum tendrils velocity (mm/min)

Significant difference in the maximum tendril's velocity was observed between conditions (EQ=14.42; DQ= 10.05; $\chi2$=6.233; p=.012; df=1; Marginal R^2=.042; Conditional R^2 = .541; Figure 4).
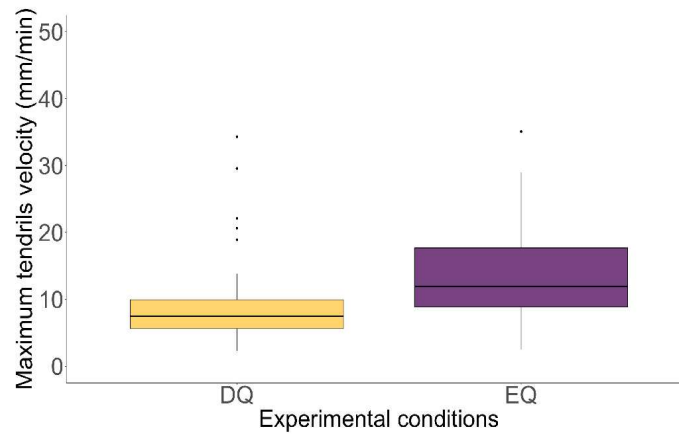
Figure 4. Box plots representing the significant difference between the EQ (i.e., violet box) and the DQ (i.e., yellow box) in the maximum tendril velocity.

*Time of maximum tendrils velocity (%)*
No significant difference in the time maximum tendrils velocity was observed between conditions (Mean: EQ=56.82; DQ= 55.87; $\chi2$=.077; p=.782; df=1; Marginal R^2=.001; Conditional R^2 = .236; Figure 5).

Figure 5. Box plots representing the significant difference between the EQ (i.e., violet box) and the DQ (i.e., yellow box) in the time of maximum tendril velocity.

Endpoint variability (mm)

Significant difference in the endpoint variability was observed between conditions (Mean: EQ=256.63; DQ= 180.32; $\chi2$=26.653; p=<.001; df=1; Marginal R^2=.139; Conditional R^2 = .648; Figure 6).
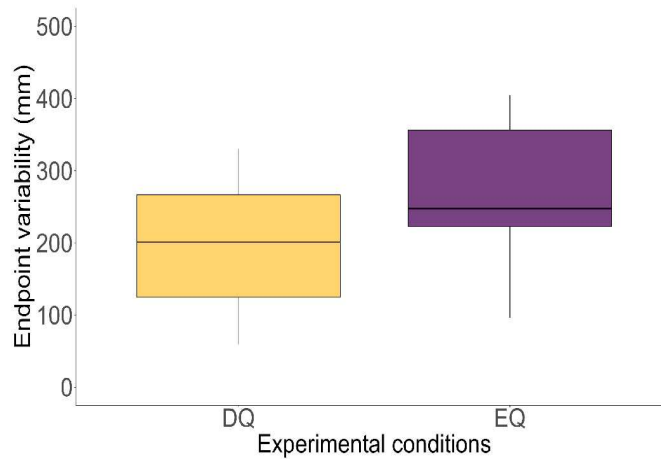
Figure 6. Box plots representing the significant difference between the EQ (i.e., violet box) and the DQ (i.e., yellow box) in the endpoint variability.

Chapter 4: Discussion and conclusions

In the present thesis pea plants were exposed to different numbers of supports (DQ – 3 vs 1 support and EQ – 2 vs 2 supports) aiming to understand quantity related abilities of pea plants, by observing kinematic patterns of plants' reaching and grasping movements. Qualitative results showed that the majority of the plants (9 of 12) in DQ condition moved toward the side which had more supports than the other side while in EQ condition plants randomly reached one of the supports on both sides. Furthermore, kinematical results showed that the maximum tendrils velocity (mm/min) was higher in EQ condition and there was higher variability in terms of endpoints (mm). While no significant differences were observed in the peak of maximum tendrils velocity (%) and in the movement time (min).

Results showed that when plants acted in an area with a large number of supports on one side, a small number on the other (DQ), they slowed down their movement and showed less variability in the point of contact of the tendrils with the support more so than when acting in an area with equal opportunities for attachment (EQ). In the presence of a different distribution of opportunities in the environment, pea plants must make an anticipatory choice towards the side which is more likely to support them. The strategy adopted by the plants is an energy consuming process resulting in both a high energy expenditure and consumption of adenosine triphosphate (ATP; Putz, &. Holbrook, 1991). Therefore, the reduction of movement velocity during the approaching movement may allow plants to preserve energy for the clasping phase and to execute a more precise grip upon one of the three potential supports (Ceccarini et al., 2020a; b; Guerra et al., 2019). For the EQ condition, no selection strategy is required, and their movement can be faster and with less precision. Concerning the temporal component of the plant's movement, no significant differences were observed for the peak of maximum velocity (%) and the movement

time (min) even if the velocity of the tendrils increased. Results can be discussed in the light of the isochrony principle, which is the spontaneous tendency to increase the velocity of a movement as a function of the linear extent of its trajectory, to maintain approximately constant execution time (Wang et al., 2023; Viviani &. McCollum, 1983). These results suggest that plants are able to evaluate the quantity of elements in their environment and modulate their behavior accordingly. Unlike many studies in the literature, the current study questioned whether plants have a quantity-related ability based on pea plants. It clearly states that the plant modifies its movements and actively controls its kinematic properties flexibly after receiving and processing sensory information from outside; it can be said that the fact that the plant clings to the support that is in the direction where there is more support among the different support options presented to it (DQ condition; 3 vs. 1) is an indication that plants, may have the ability to process quantity-related information in a similar manner of those observed in different animal species (Reznikova & Ryabko, 2011; Agrillo, 2014; Agrillo, 2017; Nieder, 2020).

References

Agrillo, C., Miletto Petrazzini, M.E. & Bisazza, A. (2014). Numerical acuity of fish is improved in the presence of moving targets, but only in the subitizing range. *Animal Cognition 17*, 307–316. https://doi.org/10.1007/s10071-013-0663-6

Agrillo, C., Miletto Petrazzini, M. E., & Bisazza, A. (2017). Numerical abilities in fish: A methodological review. *Behavioural Processes, 141*, 161–171. https://doi.org/10.1016/j.beproc.2017.02.001

Alpi, A., Amrhein, N., Bertl, A., Blatt, M. R., Blumwald, E., Cervone, F., Dainty, J., De Michelis, M. I., Epstein, E., Galston, A. W., Goldsmith, M. H., Hawes, C., Hell, R., Hetherington, A., Hofte, H., Juergens, G., Leaver, C. J., Moroni, A., Murphy, A., … Wagner, R. (2007). Plant Neurobiology: No brain, no gain? *Trends in Plant Science*, *12*(4), 135–136. https://doi.org/10.1016/j.tplants.2007.03.002

Antell, S. E., & Keating, D. P. (1983). Perception of numerical invariance in neonates. *Child Development*, *54*(3), 695–701. https://doi.org/10.2307/1130057

Aslin, R. N., & Smith, L. B. (1988). Perceptual development. Annual Review of Psychology, 39(1), 435–473. https://doi.org/10.1146/annurev.ps.39.020188.002251

Atala, C., & Gianoli, E. (2008). Induced twining in Convolvulaceae climbing plants in response to leaf damage. *Botany*, *86*(6), 595-602.

Atala, C., Cordero, C., & Gianoli, E. (2011). Drought and leaf damage limit the search for support in the climbing plant Ipomoea purpurea (L.) Roth (Convolvulaceae). Gayana Botanica, 68(2), 207-212.

Baluška, F., & Mancuso, S. (2009). Plants and animals: Convergent evolution in action? *Plant-Environment Interactions*, 285–301. https://doi.org/10.1007/978-3-540-89230-4_15

Baluška, F., & Reber, A. (2019). Sentience and consciousness in single cells: how the first minds emerged in unicellular species. *BioEssays*, *41*(3), 1800229.

Baluška, F., Mancuso, S., Volkmann, D., & Barlow, P. (2009). The 'root-brain' hypothesis of Charles and Francis Darwin. *Plant Signaling &Behavior*, *4*(12), 1121–1127. https://doi.org/10.4161/psb.4.12.10574

Baluška, F., Volkmann, D., Hlavacka, A., Mancuso, S., & Barlow, P. W. (2006). Neurobiological view of plants and their body plan. *Communication in Plants*, 19–35. https://doi.org/10.1007/3-540-28516-4_2

Band, L. R., Wells, D. M., Larrieu, A., Sun, J., Middleton, A. M., French, A. P., Brunoud, G., Sato, E. M., Wilson, M. H., Péret, B., Oliva, M., Swarup, R., Sairanen, I., Parry, G., Ljung, K., Beeckman, T., Garibaldi, J. M., Estelle, M., Owen, M. R., … Bennett, M. J. (2012). Root gravitropism is regulated by a transient lateral auxin gradient controlled by a tipping-point mechanism. *Proceedings of the National Academy of Sciences*, *109*(12), 4668–4673. https://doi.org/10.1073/pnas.1201498109

Bhatla, S.C., Lal, M.A. (2023). Plant Movements. *Plant Physiology, Development and Metabolism. Springer*. https://doi.org/10.1007/978-981-99-5736-1_29

Biedrzycki, M. L., Jilany, T. A., Dudley, S. A., & Bais, H. P. (2010). Root exudates mediate kin recognition in plants. *Communicative & Integrative Biology, 3*(1), 28–35. https://doi.org/10.4161/cib.3.1.10118

Bonato, B., Simonetti, V., Guerra, S., & Castiello, U. (2024). Artificial and biological supports are different for pea plants. Plant Signaling & Behavior, 19(1). https://doi.org/10.1080/15592324.2024.2355739

Bose, J. C. (1906). *Plant response as a means of physiological investigation*. Longmans, Green and Company.

Brannon, E. M., & Terrace, H. S. (2000). Representation of the numerosities 1–9 by rhesus macaques (macaca mulatta). *Journal of Experimental Psychology: Animal Behavior Processes*, *26*(1), 31–49. https://doi.org/10.1037/0097-7403.26.1.31

Brannon, E. M., Abbott, S., & Lutz, D. J. (2004). Number bias for the discrimination of large visual sets in infancy. Cognition, 93(2). https://doi.org/10.1016/j.cognition.2004.01.004

Brown, A. H. (1993). Circumnutations: From Darwin to space flights. Plant Physiology 101: 345–348

Brown, A. H., Chapman, D. K., Lewis, R. F., & Venditti, A. L. (1990). Circumnutations of sunflower hypocotyls in satellite orbit. *Plant Physiology*, *94*(1), 233–238. https://doi.org/10.1104/pp.94.1.233

Calvo, P., Gagliano, M., Souza, G. M., & Trewavas, A. (2020). Plants are intelligent, here's how. *Annals of botany*, *125*(1), 11-28.

Calvo, P., Sahi, V. P., & Trewavas, A. (2017). Are plants sentient? *Plant Cell & Environment, 40(*11), 2858–2869. https://doi.org/10.1111/pce. 13065

Campanello, P. I., Garibaldi, J. F., Gatti, M. G., & Goldstein, G. (2007). Lianas in a subtropical Atlantic Forest: host preference and tree growth. *Forest Ecology and Management, 242*(2-3), 250-259.

Campbell, C. J., Aureli, F., Chapman, C. A., Ramos-Fernández, G., Matthews, K., Russo, S. E., ... & Vick, L. (2005). Terrestrial behavior of Ateles spp. *International Journal of Primatology, 26*, 1039-1051.

Carazo, P., Fernández-Perea, R., & Font, E. (2012). Quantity estimation based on numerical cues in the mealworm beetle (Tenebrio Molitor). *Frontiers in Psychology*, *3*. https://doi.org/10.3389/fpsyg.2012.00502

Carrasco-Urra, F., & Gianoli, E. (2009). Abundance of climbing plants in a southern temperate rain forest: host tree characteristics or light availability?. *Journal of Vegetation Science, 20*(6), 1155-1162.

Carsten, L. D., Juola, F. A., Male, T. D., & Cherry, S. (2002). Host associations of lianas in a south-east Queensland rain forest. *Journal of Tropical Ecology, 18*(1), 107-120.

Castiello, U. (2021). (Re)claiming plants in comparative psychology. *Journal of Comparative Psychology, 135*(1), 127–141. https://doi.org/10.1037/com0000239

Castiello, U. (2023). Plant Intelligence from a comparative psychology perspective. *Biology, 12*(6), 819. https://doi.org/10.3390/biology12060819

Ceccarini, F., Guerra, S., Peressotti, A., Peressotti, F., Bulgheroni, M., Baccinelli, W., Bonato, B., & Castiello, U. (2020). Speed–accuracy trade-off in plants. Psychonomic Bulletin & Review, 27(5), 966–973. https://doi.org/10.3758/s13423-020-01753-4

Ceccarini, F., Guerra, S., Peressotti, A., Peressotti, F., Bulgheroni, M., & Baccinelli, W. et al. (2020). On-line control of movement in plants. *Biochemical And Biophysical Research Communications*, *564*, 86-91. https://doi.org/10.1016/j.bbrc.2020.06.160

Chen, P.H., Chung, A.C., Lin, H.C., Yang, S. Z. (2023). Climbing strategies of Taiwan climbers. *Bot Stud* 64, 26. https://doi.org/10.1186/s40529-023-00399-4

Cheng, K. (2018). Cognition beyond representation: Varieties of situated cognition in animals. *Comparative Cognition and Behavior Reviews, 13*, 1–20. http://dx.doi.org/10.3819/CCBR.2018.130001

Chittka, L., & Geiger, K. (1995). Can honey bees count landmarks? *Animal Behaviour*, *49*(1), 159–164. https://doi.org/10.1016/0003-3472(95)80163-4

Clearfield, M. W., & Mix, K. S. (1999). Number versus contour length in infants' discrimination of small visual sets. Psychological Science, 10(5), 408–411. https://doi.org/10.1111/1467-9280.00177

Cole, C. B., & Loftus, E. F. (1987). The memory of children. In Children's eyewitness memory . *New York, NY: Springer US*, 178-208.

Cordes, S., Gelman, R., Gallistel, C. R., & Whalen, J. (2001). Variability signatures distinguish verbal from nonverbal counting for both large and small numbers. *Psychonomic Bulletin & Review*, *8*(4), 698–707. https://doi.org/10.3758/bf03196206

Correll, M. J., and J. Z. Kiss. (2008). Space based research on plant tropisms. In S. Gilroy and P. K. Masson [eds.], Plant tropisms, 161–182. Blackwell, New York, New York, USA.

Coubart, A., Izard, V., Spelke, E. S., Marie, J., & Streri, A. (2013). Dissociation between small and large numerosities in newborn infants. *Developmental Science*, *17*(1), 11–22. https://doi.org/10.1111/desc.12108

Crepy, M. A., & Casal, J. J. (2015). Photoreceptor-mediated kin recognition in plants. New Phytologist, 205(1), 329-338.

Dacke, M., & Srinivasan, M. V. (2008). Evidence for counting in insects. *Animal Cognition*, *11*(4), 683–689. https://doi.org/10.1007/s10071-008-0159-y

Darwin CR. (assisted by Darwin F.) The Power of Movements in Plants. 1880; John Murray, London (http://darwin-online.org.uk/).

Darwin, C. (1875). *The movements and habits of climbing plants*. John Murray.

De Kroon, H., Visser, E. J., Huber, H., Mommer, L., & Hutchings, M. J. (2009). A modular concept of plant foraging behaviour: the interplay between local responses and systemic control. *Plant, Cell & Environment*, *32*(6), 704-712.

Dehaene, S. (1997). *The number sense: How the mind creates mathematics*. Oxford University

    Press, USA.

Dehaene, S. (2003). The neural basis of the weber–fechner law: A logarithmic mental number

    line. *Trends in Cognitive Sciences*, *7*(4), 145–147. https://doi.org/10.1016/s1364-

    6613(03)00055-x

Dehaene, S., Dupoux, E., & Mehler, J. (1990). Is numerical comparison digital? Analogical and

    symbolic effects in two-digit number comparison. *Journal of Experimental Psychology:*

    Human Perception and Performance, *16*(3), 626–641. https://doi.org/10.1037/0096-

    1523.16.3.626

Dener, E., Kacelnik, A., & Shemesh, H. (2016). Pea plants show risk sensitivity. *Current*

    Biology, *26*(13), 1763-1767.

Dicke, M., & Hilker, M. (2003). Induced plant defences: from molecular biology to evolutionary

    ecology. *Basic and Applied Ecology*, *4*(1), 3-14.

Dicke, M., & Baldwin, I. T. (2010). The evolutionary context for herbivore-induced plant volatiles:

    beyond the 'cry for help'. *Trends in plant science*, *15*(3), 167-175.

Durigon, J., Miotto, S. T., & Gianoli, E. (2014). Distribution and traits of climbing plants in

    subtropical and temperate S outh A merica. *Journal of Vegetation Science, 25*(6), 1484-

    1492.

Feigenson, L., Dehaene, S., & Spelke, E. (2004). Core Systems of number. *Trends in Cognitive*

    Sciences, *8*(7), 307–314. https://doi.org/10.1016/j.tics.2004.05.002

Gallistel, C. R., & Gelman, R. (1990). The what and how of counting. *Cognition*, *34*(2), 197–199. https://doi.org/10.1016/0010-0277(90)90043-j

Garbin, M. L., Carrijo, T. T., Sansevero, J. B., Sánchez-Tapia, A., & Scarano, F. R. (2012). Subordinate, not dominant, woody species promote the diversity of climbing plants. *Perspectives in Plant Ecology, Evolution and Systematics*, *14*(4), 257–265. https://doi.org/10.1016/j.ppees.2012.03.001

Garcia Rodriguez, A., & Calvo Garzon, P. (2010). Is cognition a matter of representations? Emulation, teleology, and time-keeping in biological systems. *Adaptive behavior*, *18*(5), 400-415.

Garfield, J. L., Peterson, C. C., & Perry, T. (2001). Social Cognition, language acquisition and the development of the theory of mind. *Mind & Language, 16*(5), 494–541. https://doi.org/10.1111/1468-0017.00180

Gartner, B. L. (1991). Structural stability and architecture of vines vs. shrubs of poison oak, Toxicodendron diversilobum. *Ecology, 72*(6), 2005-2015.

Gianoli, E. (2015). The behavioural ecology of climbing plants. *AoB plants*, *7*, plv013.

Gianoli, E. & González-Teuber, M. (2005) Environmental heterogeneity and population differentiation in plasticity to drought in Convolvulus chilensis (Convolvulaceae). *Evolutionary Ecology, 19*, 603–613.

Gianoli, E., & Carrasco-Urra, F. (2014). Leaf mimicry in a climbing plant protects against herbivory. *Current Biology*, *24*(9), 984–987. https://doi.org/10.1016/j.cub.2014.03.010

Gianoli, E., & Molina-Montenegro, M. A. (2005). Leaf damage induces twining in a climbing plant. *New Phytologist, 167*(2), 385-390.

Gilroy, S. (2008). Plant Tropisms. *Current Biology*, *18*(7). https://doi.org/10.1016/j.cub.2008.02.033

González, A. P. R., Chrtek, J., Dobrev, P. I., Dumalasová, V., Fehrer, J., Mráz, P., & Latzel, V. (2016). Stress-induced memory alters growth of clonal offspring of white clover (Trifolium repens). *American Journal of Botany*, *103*(9), 1567-1574.

González, A. P. R., Dumalasová, V., Rosenthal, J., Skuhrovec, J., & Latzel, V. (2017). The role of transgenerational effects in adaptation of clonal offspring of white clover (Trifolium repens) to drought and herbivory. *Evolutionary Ecology*, *31*, 345-361.

Gruntman, M., & Novoplansky, A. (2004). Physiologically mediated self/non-self discrimination in roots. *Proceedings of the National Academy of Sciences, 101*(11), 3863-3867.

Guerra, S., Peressotti, A., Peressotti, F., Bulgheroni, M., Baccinelli, W., D'Amico, E., ... & Castiello, U. (2019). Flexible control of movement in plants. *Scientific Reports*, *9*(1), 16570.

Guerra, S., Bonato, B., Wang, Q., Ceccarini, F., Peressotti, A., & Peressotti, F. et al. (2021). The coding of object thickness in plants: When roots matter. *Journal Of Comparative Psychology*, *135*(4), 495-504. https://doi.org/10.1037/com0000289

Guerra, S., Bonato, B., Wang, Q., Peressoti, A., Peressoti, F., Baccinelli, W., Bulgheroni, M., Castiello, U. (2022). Kinematic Evidence of Root-to-Shoot Signaling for the Coding of

Support Thickness in Pea Plants. *Biology 11*(3), 405. https://doi.org/10.3390/biology11030405

Guerra, S., Bruno, G., Spoto, A., Panzeri, A., Wang, Q., Bonato, B., Simonetti, V., Castiello, U. (2024). Ascent and Attachment in Pea Plants: A Matter of Iteration. *Plants, 13*(10), 1389. https://doi.org/10.3390/plants13101389

Gul, M. U., Paul, A., S, M., & Chehri, A. (2023). Hydrotropism: Understanding the impact of water on plant movement and adaptation. *Water*, *15*(3), 567. https://doi.org/10.3390/w15030567

Hagen, J. W., & Hale, G. A. (1973). The development of attention in children.

Halberda, J., Mazzocco, M. M., & Feigenson, L. (2008). Individual differences in non-verbal number acuity correlate with maths achievement. *Nature, 455*(7213), 665–668. https://doi.org/10.1038/nature07246

Hart, J. W. (1990). *Plant tropisms: and other growth movements*. Springer Science & Business Media.

Hauser, M. D., Carey, S., & Hauser, L. B. (2000). Spontaneous number representation in semi–free–ranging rhesus monkeys. Proceedings of the Royal Society of London. Series B: *Biological Sciences, 267*(1445), 829–833. https://doi.org/10.1098/rspb.2000.1078

Hegarty, E. E. (1991). Leaf litter production by lianes and trees in a sub-tropical Australian rain forest. *Journal of tropical ecology, 7*(2), 201-214.

Hopkins, W. G., & Hüner, N. P. (1995). *Introduction to plant physiology*. John Wiley & Sons.

Hyde, D. C., & Spelke, E. S. (2011). Neural signatures of number processing in human infants: Evidence for two core systems underlying numerical cognition. *Developmental Science*, *14*(2), 360–371. https://doi.org/10.1111/j.1467-7687.2010.00987.x

Israelsson, D., & Johnsson, A. (1967). A Theory for Circumnutations in Helianthus annuus. *Physiologia Plantarum*, *20*(4).

Izard, V., & Dehaene, S. (2008). Calibrating the mental number line. *Cognition*, *106*(3), 1221–1247. https://doi.org/10.1016/j.cognition.2007.06.004

Izard, V., Sann, C., Spelke, E. S., & Streri, A. (2009). Newborn infants perceive abstract numbers. *Proceedings of the National Academy of Sciences*, *106*(25), 10382–10385. https://doi.org/10.1073/pnas.0812142106

Jevons, W. S. (1871). The power of numerical discrimination. *Nature*, *3*(67), 281–282. https://doi.org/10.1038/003281a0

Johnsson, A. (1997). Circumnutations: Results from recent experiments on Earth and in space. *Planta*, *203*(S1). https://doi.org/10.1007/pl00008103

Kaufman, E. L., Lord, M. W., Reese, T. W., & Volkmann, J. (1949). The discrimination of visual number. *The American Journal of Psychology*, *62*(4), 498–525. https://doi.org/10.2307/1418556

Kiss, J. Z., Kumar, P., Bowman, R. N., Steele, M. K., Eodice, M. T., Correll, M. J., & Edelmann, R. E. (2007). Biocompatibility studies in preparation for a spaceflight experiment on plant tropisms (TROPI). *Advances in Space Research, 39*(7), 1154-1160.

Krebs, J. R., Ryan, J. C., & Charnov, E. L. (1974). Hunting by expectation or optimal foraging? A study of patch use by chickadees. *Animal Behavior*, *22*, 953–964. https://doi.org/10.1016/0003-3472(74)90018-9

Laxmi, A., Pan, J., Morsy, M., & Chen, R. (2008). Light plays an essential role in intracellular distribution of auxin efflux carrier PIN2 in Arabidopsis thaliana. *PloS one, 3*(1), e1510.

Lehnebach, R., Poul-Victor, C., Courric, E., Rowe, N.P. (2022). Microspines in tropical climbing plants: a small-scale fix for life in an obstacle course, *Journal of Experimental Botany 73*(16), 5650-5670.

Linson, A., & Calvo, P. (2020). Zoocentrism in the weeds? Cultivating plant models for cognitive yield. *Biology and Philosophy, 35*(5), 49. https://doi.org/10.1007/s10539-020-09766-y

Lipton, J. S., & Spelke, E. S. (2003). Origins of number sense. *Psychological Science*, *14*(5), 396–401. https://doi.org/10.1111/1467-9280.01453

Liscum, E., Askinosie, S. K., Leuchtman, D. L., Morrow, J., Willenburg, K. T., & Coats, D. R. (2014). Phototropism: Growing towards an understanding of plant movement. *The Plant Cell*, *26*(1), 38–55. https://doi.org/10.1105/tpc.113.119727

MacNulty, D. R., Tallian, A., Stahler, D. R., & Smith, D. W. (2014). Influence of group size on the success of wolves hunting bison. *PLoS ONE*, *9*(11). https://doi.org/10.1371/journal.pone.0112884

Maina, G. G., Brown, J. S., & Gersani, M. (2002). Intra-plant versus inter-plant root competition in beans: avoidance, resource matching or tragedy of the commons. *Plant Ecology, 160*, 235-247.

Marder, M. (2012). Plant intentionality and the phenomenological framework of plant intelligence. *Plant signaling & behavior, 7*(11), 1365-1372.

Masson, P. H., Tasaka, M., Morita, M. T., Guan, C., Chen, R., & Boonsirichai, K. (2002). Arabidopsis thaliana: A model for the study of root and shoot gravitropism. *The Arabidopsis Book*, *1*. https://doi.org/10.1199/tab.0043

McCormack, T., & Atance, C. M. (2011). Planning in young children: A review and synthesis. *Developmental Review*, 31(1), 1–31. https://doi.org/10.1016/j.dr.2011.02.002

McCrink, K., & Wynn, K. (2007). Ratio abstraction by 6-month-old infants. *Psychological Science*, *18*(8), 740–745. https://doi.org/10.1111/j.1467-9280.2007.01969.x

Mugnai, S., Azzarello, E., Masi, E., Pandolfi, C., & Mancuso, S. (2007). Nutation in plants. *Rhythms in Plants*, 77–90. https://doi.org/10.1007/978-3-540-68071-0_4

Murphy, G. P., & Dudley, S. A. (2009). Kin recognition: Competition and cooperation in *impatiens* (balsaminaceae). *American Journal of Botany*, *96*(11), 1990–1996. https://doi.org/10.3732/ajb.0900006

Neukirch, S., & Goriely, A. (2006). Twining plants: how thick should their supports be?. In Proc. 5th Plant Biomechanics Conf..

Nieder, A. (2020). The adaptive value of numerical competence. *Trends in Ecology & Evolution*, *35*(7), 605–617. https://doi.org/10.1016/j.tree.2020.02.009

Niu, Y., Sun, H., & Stevens, M. (2018). Plant camouflage: ecology, evolution, and implications. *Trends in ecology & evolution*, *33*(8), 608-618.

O'Brien, T. C., & Shapiro, B. J. (1968). The development of logical thinking in children. *American Educational Research Journal, 5*(4), 531-542.

Peñalosa, J. (1982). Morphological specialization and attachment success in two twining lianas. *American Journal of Botany*, *69*(6), 1043-1045.

Piazza, M., Facoetti, A., Trussardi, A. N., Berteletti, I., Conte, S., Lucangeli, D., Dehaene, S., & Zorzi, M. (2010). Developmental trajectory of number acuity reveals a severe impairment in developmental dyscalculia. *Cognition*, *116*(1), 33–41. https://doi.org/10.1016/j.cognition.2010.03.012

Platt, J. R., & Johnson, D. M. (1971). Localization of position within a homogeneous behavior chain: Effects of error contingencies. *Learning and Motivation*, *2*(4), 386–414. https://doi.org/10.1016/0023-9690(71)90020-8

Pritchard, V. L., Lawrence, J., Butlin, R. K., & Krause, J. (2001). Shoal choice in zebrafish, Danio rerio: The influence of shoal size and activity. *Animal Behaviour*, *62*(6), 1085–1088. https://doi.org/10.1006/anbe.2001.1858

Putz, F. E. (1980). Lianas vs. Trees. *Biotropica 12*. 224-225

Putz, F. E. (1984). How trees avoid and Shed Lianas. *Biotropica*, *16*(1), 19. https://doi.org/10.2307/2387889

Putz, F. E., & Holbrook, N. M. (1991). Biomechanical studies of vines. *The biology of vines,* 73-97.

Reznikova, Z., & Ryabko, B. (2011). Numerical competence in animals, with an insight from ants. *Behaviour, 148*(4), 405–434. https://doi.org/10.1163/000579511x568562

Runyon, J. B., Mescher, M. C., Felton, G. W., & De Moraes, C. M. (2010). Parasitism by cuscuta pentagonasequentially induces JA and SA defence pathways in tomato. *Plant, Cell & Environment, 33*(2), 290–303. https://doi.org/10.1111/j.1365-3040.2009.02082.x

Sasal, Y., & Suarez, M. L. (2011). Insect herbivory in climber–host shrubs associations: Benefit or detriment?. *Austral Ecology, 36*(7), 814-820.

Schuster, J., & Engelmann, W. (1997). Circumnutations of Arabidopsis thaliana seedlings. *Biological Rhythm Research*, *28*(4), 422–440. https://doi.org/10.1076/brhm.28.4.422.13117

Segundo-Ortin, M., & Calvo, P. (2021). Consciousness and cognition in plants. Wiley Interdisciplinary Reviews: *Cognitive Science, 13*(2), e1578.

Silk, W. K., & Holbrook, N. M. (2005). The importance of frictional interactions in maintaining the stability of the twining habit. *American journal of botany, 92*(11), 1820-1826.

Stancher, G., Rugani, R., Regolin, L., & Vallortigara, G. (2015). Numerical discrimination by

    frogs (bombina orientalis). *Animal Cognition*, *18*(1), 219–229.

    https://doi.org/10.1007/s10071-014-0791-7

Starkey, P., & Cooper, R. G. (1980). Perception of numbers by human

    infants. *Science, 210*(4473), 1033–1035. https://doi.org/10.1126/science.7434014

Starkey, P., Spelke, E. S., & Gelman, R. (1990). Numerical abstraction by human

    infants. *Cognition*, *36*(2), 97–127. https://doi.org/10.1016/0010-0277(90)90001-z

Stolarz, M. (2009). Circumnutation as a visible plant action and reaction: physiological, cellular

    and molecular basis for circumnutations. *Plant signaling & behavior, 4*(5), 380-387.

Stolarz, M., Krol, E., Dziubinska, H., & Zawadzki, T. (2008). Complex relationship between

    growth and circumnutations in *helianthus annuus* stem. *Plant Signaling &*

    Behavior, *3*(6), 376–380. https://doi.org/10.4161/psb.3.6.5714

Talley, S. M., Lawton, R. O., & Setzer, W. N. (1996). Host preferences of Rhus radicans

    (Anacardiaceae) in a southern deciduous hardwood forest. *Ecology, 77*(4), 1271-1276.

Tecwyn, E. C., Thorpe, S. K. S., & Chappell, J. (2014). Development of planning in 4- to 10-

    year-old children: Reducing inhibitory demands does not improve performance. *Journal of*

    Experimental Child Psychology, 125, 85–101. https://doi.org/10.1016/j.jecp.2014.02.006

Trewavas A. (2005). Plant intelligence. *Naturwissenschaften, 92,* 401-13.

Trewavas, A. (2007). Response to Alpi et al.: Plant neurobiology–all metaphors have value. *Trends in Plant Science*, *12*(6), 231-233.

Trewavas, A., Baluška, F., Mancuso, S., & Calvo, P. (2020). Consciousness facilitates plant behavior. *Trends in Plant Science*, *25*(3), 216-217.

van Oeffelen, M. P., & Vos, P. G. (1982). A probabilistic model for the discrimination of visual number. *Perception & Psychophysics*, *32*(2), 163–170. https://doi.org/10.3758/bf03204275

Viviani, P., & McCollum, G. (1983). The relation between linear extent and velocity in drawing movements. *Neuroscience*, *10*(1), 211–218. https://doi.org/10.1016/0306-4522(83)90094-5

Wan, Y. L., Eisinger, W., Ehrhardt, D., Kubitscheck, U., Baluska, F., & Briggs, W. (2008). The Subcellular Localization and Blue-Light-Induced Movement of Phototropin 1-GFP in Etiolated Seedlings of Arabidopsis thalianaw. *Molecular Plant*, *1*(1), 103-117.

Wang, Q., Guerra, S., Ceccarini, F., Bonato, B., & Castiello, U. (2021). Sowing the seeds of intentionality: Motor intentions in plants. *Plant Signaling & Behavior, 16*(11), 1949818.

Wang, Q., Guerra, S., Bonato, B., Simonetti, V., Bulgheroni, M., & Castiello, U. (2023). Decision-making underlying support-searching in pea plants. *Plants, 12*(8), 1597. https://doi.org/10.3390/plants12081597

Wang, Q., Barbariol, T., Susto, G. A., Bonato, B., Guerra, S., & Castiello, U. (2023). Classifying circumnutation in pea plants via supervised machine learning. *Plants*, *12*(4), 965. https://doi.org/10.3390/plants12040965

Whippo, C. V., and R. P. Hangarter. (2009). The sensational power of movement in plants: A Darwinian system to study the evolution of behavior. *American Journal of Botany 96*, 2115–2127.

Williamson, G. B. (1982). Plant mimicry: evolutionary constraints. *Biological Journal of the Linnean Society*, *18*(1), 49-58.

Wynn, K. (1992). Addition and subtraction by human infants. *Nature*, *358*(6389), 749–750. https://doi.org/10.1038/358749a0

Xu, F., & Spelke, E. S. (2000). Large number discrimination in 6-month-old infants. *Cognition*, *74*(1), B1–B11. https://doi.org/10.1016/s0010-0277(99)00066-9