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Motor Intentions in Plants:
A Kinematic Perspective with a Touch on Chemistry

Coordinator: Prof. Lucia Regolin
Supervisor: Prof. Francesca Pazzaglia
Co-Supervisor: Prof. Umberto Castiello

Ph.D. student: Bianca Bonato

Ai miei genitori Ermella e Nico,

al loro amore per i boschi,

tra i quali mi hanno cresciuta.

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Table of contents

CHAPTER 6: CRACKING THE CODE OF SOCIAL BEHAVIOUR IN PEA PLANTS: THE ROLE OF STRIGOLACTONES………………………………………..121

Synopsis

In order to survive, all biological systems continuously retrieve information from their environment and use this information in order to effectively adapt to it (Kovac, 2007). The Darwinian wars will most likely favour those who can best mastery the environment. In Warwick (2001) words: *"The success of a species depends on it performing well (surviving and producing offspring, i.e., fitness) in its own particular environment and intelligence plays a critical part in this success"*. Nevertheless, if we are asked to name an intelligent organism, no one would mention a pea plant. Humans tend to assign intelligence to organisms that move. In fact, we are used to assigning intelligence to organisms that move about on their own (Castiello, 2023); in other words, we tend to assume that organisms that move in certain spatio-temporal conditions have intentions and thus possess some form of intelligence (Llinas, 2002).

Advances in empirical research, have finally demonstrated not only how plants continuously monitor numerous parameters from the environment, but also how the sensory information obtained is integrated into adaptive responses and complex plant behaviour (Trewavas, 2003; Dicke et al., 2003; Bais et al., 2004; Braam, 2005; Baldwin et al., 2006; Brenner et al., 2006; Barlow, 2008; Baluška & Mancuso, 2009) and how these complex behaviours imply adaptive, flexible and goal-directed movements (Guerra et al., 2019, 2021, 2022; Ceccarini et al., 2020a,b). These considerations are at the core of the present thesis, which aims to systematize the intentionality underlying the motor processes observed. In particular, the focus of the present thesis is re-locating the cognitive characteristics and intentional actions of plants in their social framework, to claim that also plants are eusocial organisms. It is impossible not to consider entire woods, forests, fields as big social superorganisms. The ability to possess *"a sense of self"* and interact with other organisms, is one of the highest abilities conquered through the evolution and commonly ascribed to certain animals only. In this thesis, my aim is to demonstrate that plants not only are able to perceive their neighbours, but also to implement different kinds of motor intentionality depending on an individual or social context requiring cooperative and competitive attitudes.

The first part of the thesis (Chapter 1) will provide a description of recent theories that includes aneural organisms in the realm of cognition (i.e., embodied cognition, extended cognition, enactivism, autopoietic cognition, basal cognition). These will provide the theoretical framework for discussing my data.

The following part (Chapter 2) will focus on the evolution of sociality across taxa, with specific references to three social behaviours that are at the core of the experimental part (i.e., competition, cooperation and communication).

The next section (Chapter 3) will offer a description of the different types of movements observed in plants with specific reference to the approach-to-grasp movements performed by climbing plants. An overview of the methods and techniques used for studying these movement will be provided.

The thesis then goes on to discuss the experimental work. At the outset of Chapter 4, I shall describe in detail the material and methods, which are common to all experiments. Then, in the first experiment (Chapter 5), I shall investigate different motor intentions exhibited by pea plants (*Pisum sativum*; from now on *P. sativum*) on the basis of individual or social contexts. For the individual condition, one plant was potted to grow in isolation and act to grasp a potential support. For the social condition, two plants were potted together with the same potential support in the middle, equidistant from each other. This set up permitted to investigate whether plants can act with either individual or social kind of intentions despite the action to perform and the object to grasp are the very same. In particular, the study also systematizes a different kind of behaviour and motor response for the two plants acting in the dyad, suggesting a possible competitive attitude between them.

In Chapter 6, I will provide a possible chemical explanation of the behaviour observed, by using mutant plants lacking the perception or production of strigolactones (SLs from now on) and then I tested different combinations with all the possible genotypes. The results showed different success of grasping depending on the combination, and so, depending on the SLs mutations of plants. This work offers a touch on chemistry, to make the first step on cracking the chemical code of social motor intentionality in plants.

A further experiment (Chapter 7) will offer another evidence of social behaviour in plants, this time in terms of cooperative attitudes. To better explain, two plants were potted together without any support in the environment. This brought plants to coordinate their movements in order to intertwine as to support each other in the absence of a potential support. They built a braided structure to climb towards the light. These results show how a shared intentionality is possible in aneural organisms.

Finally, in Chapter 8, I will describe an empirical work on the distinction between competitive and cooperative actions in pea plants, investigating the level of accuracy that guides these movements. Secondary movements (i.e., sub-movements) were analysed in order to have a quantification of the accuracy required to acting in either cooperative or competitive situations.

Altogether these experiments showed that *P. sativum* plants can plan a movement based on different context, providing evidence of motor intentionality in aneural organisms. Indeed, *P. sativum* plants not only acknowledged the presence of a neighbour in the environment, but also scaled the kinematics of their tendrils in both temporal and spatial terms based on different social contexts.

Finally, in Chapter 9, a general discussion outlining the theoretical implications of these findings will be provided. Importantly, my results provide evidence of motor intentions in plants performed with individual and social attitudes.

The ability of plants to reflect their sociality in the way they move, is an important step to better understand the evolution of sociality *across taxa*. Shedding light on the mechanisms with which aneural organisms adapt in the environment and communicate with other beings, provide exciting new insights regarding the evolution of the link between cognition and action along the intricated tree of life.

PART I

THEORETICAL FRAMEWORK

Chapter 1

Cognition beyond the brain

> *"Living systems are cognitive systems, and living as a process is a process of cognition."*
>
> *Maturana & Varela, 1980*

The purpose of this chapter is to provide a possible theoretical framework within which to discuss the experimental results of the present thesis, suggesting that plants are suitable candidates to be described as cognitive agents in a non-metaphorical way. In this perspective, plants appear to behave in ways that are adaptive, flexible, anticipatory and "*goal-directed"* (Trewavas, 2009; 2014; 2017; Gianoli, 2015; Raja et al., 2020; Castiello, 2020; Castiello & Guerra, 2021; Parise et al., 2021; Wang et al., 2021; Bonato et al., 2023). Taking this into account it remains to be understood *how* (through which behavioural strategies) these organisms can autonomously modify, and sometimes even improve their responses to various environmental challenges (Sultan, 2015). *Cognition* is an umbrella term that has been commonly referred to the animal kingdom, but in the present chapter I offer a theoretical *excursus* on the concept of cognition and how it could be applied to all the living beings capable of flexible adaptation to the environment. Cognition, and the evolution of minds is an across taxa phenomenon *"from bacteria to Bach"* to echo Dennett's work (Dennett, 2017), that inevitably includes also plants.

1.1 What is cognition?

This is one of the many hanging questions that needs an answer. While the processes that gave rise to this concept go back thousands of years, and in some regards millions of years, it first became a topic to think about at the birth of modern science in the seventeenth century (Dennett, 2017).

Renè Descartes, the seventeenth-century French philosopher was very curious about human mind. He called it *res cogitans*, and he was impressed by this *thinking thing* with miraculous competence. He concluded that minds are not simply matter, but they are made of things that humans learn through introspection and that didn't have to obey the laws of physics, articulating this view as "Cartesian dualism" (Dennett, 2017). This hypothesis crossed the boundaries of the investigation of what the mind is, and what makes a mind a *cogitans* thing, starting the conceptualization of cognition.

Throughout the history of cognitive sciences, different approaches have provided different answers to the question of what cognition is (or what the minimum requirements are to speak of cognitive behaviour), depending on the class of problems being investigated and the type of tools and technologies available in a particular area of experimental research (Bianchi, 2023).

In a broader sense, cognition can be defined as *"... the mechanisms by which animals acquire, process, store, and act on information from the environment. These include perception, learning, memory, and decision-making"* (Shettleworth, 2009). As implied in this definition, there are a variety of cognitive processes, including: (i) selective attention, which allows individuals to focus on a single stimulus in their surroundings; (ii) communication, which involves the capacity to transmit information to other individuals; (iii) memory, which allows individuals to encode, store, and recall information and knowledge about previous experiences and the world; (iv) perception, which is used to take signals from the environment through the senses (e.g., vision, smell,...) to respond and interact with the world through appropriate responses; (v) higher reasoning, which allows individuals to engage in decision-making and problem-solving; and (vi) sensorimotor abilities, which allows individuals to interact according to the goals and the situations offered by the environment. Are all of these processes, which were previously referred to as human, and then non-human animals, applicable to other biological living things? Are unicellular organisms that can communicate and perceive "cognitive"? Or is a neurological system essential, which means that cognition can only be found in animals? Is it limited to the actual presence of a neocortex, or even the presence of a human neocortex (Bechtel & Bich, 2021)? To answer these questions, it is entirely dependent on how model organisms are chosen and how the key systems engaged in cognitive activities are defined.

Classical theories on cognition, define this term only in relation to the brain, and so to mental representations generated by *"nothing than a pack of neurons"* to retake the words of Francis Crick (1996), defining humans. Mental representations are how all the sensation humans perceive from the outside world are converted into signals by the brain, which are then utilized to analyse, assess, and solve daily life situations. The "mental representation" is an important term in classical cognitivism. According to cognitivists, the brain's primary job is to form cognitive processes, beliefs, and concepts by abstracting them through mental representations. According to current knowledge mental representations are formed by a variety of neurophysiological systems in the brain that are triggered by the senses. According to this viewpoint, the events that activate mental representations occur in the following order: physical signals are received through the perceptual systems and transmitted to the brain; these sensory signals are then translated into mental representations (e.g., concepts, intentions) with the mind in charge of processing them; and finally, the motor system operationalizes the mind's will. So, according to this traditional perspective, the brain is the only processor and controller of all an agent's beliefs and behaviour, while the body and the environment appear to be in the background. As a result, cognition is often connected with an information processing system that depicts how the human mind interacts in the environment by assigning cognitive abilities such as problem solving and sensorimotor abilities.

In the last decades philosophers have been re-thinking of the nature of cognition, moving their attention from the central role of the mind to the agent, the environment, and their interaction. This has brought to the development of post "classical-view" theories. These new ideas, termed "post-cognitivist", hold that cognition occurs when the organism is immersed in the ever-changing physical world and incorporates sensorimotor capacities (i.e., perception and action). In other words, the environment influences the organism, and the extent to which the environment influences the agent is determined by the organism's ability to detect and arrange external signals freely and independently (Gomila & Calvo, 2008; Cazalis et al., 2017). According to the new post-cognitivism theories (e.g., embodied cognition, extended cognition, enactivism, autopoietic cognition and basal cognition) that will be explained below, a system is defined as cognitive when it is self-sufficient, open to exploring its environment to meet its own needs and goals — rather than simply reacting to external cues — and it is capable of actively regulating its sensorimotor coupling in context-sensitive ways.

Along these lines, Lyon et al. (2020) recently advanced a basal cognition theory, an interpretation of cognition that reflects its biological basis. It refers to a set of biological abilities (e.g., perception, memory, motivation, learning, and communication) that allows organisms to keep track of environmental elements and act properly long before nervous systems evolved. These ideas bold out a novel viewpoint on cognition that may bridge the gap between brainy and brainless cognitive agents. These theories provide the “roots” for a new chapter on unravelling cognition across all biological systems.

Following a comparative approach to the study of cognition that focuses on the varied body arrangements of organisms across taxa (De Waal, 2016), below I will present an outline of these theories and how they may reconciliate cognition across living organisms.

1.2 Cognizing without a brain

There is an ongoing discussion regarding whether it might be possible to extend cognition outside the head and even beyond the nervous system. A theoretical challenge is to find an appropriate “translation” of cognitive concepts (such as “perception”, “action”, “memory”, “learning”, “communication”, “intelligence”, and “mental abilities”) for the study of cognitive processes in brainless organisms (Bianchi, 2023).

Minimal cognition can be found in the behaviour of all organisms in the tree of life, from invertebrates (Schnell & Clayton, 2021) to prokaryotes (Shapiro, 2021), not to mention the well-studied case of the unicellular protists *Physarum polycephalum*, which, despite lacking neural architecture, exhibit sensory integration, memory, and learning abilities, as evidenced by their ability to solve complex problems in a short time (Smith-Ferguson & Beekman, 2020). Adopting a comparative approach to cognition that focuses on the varied body arrangements of living things (De Waal, 2016) can provide a more integrated (complete and genuine) perspective of the mechanisms underpinning living beings' cognitive capacity.

Let's now consider the scenario of plants, which is obviously pertinent to the present thesis. Despite having diverse bodily forms and organizational systems, plants share many survival issues with other species that are indicative of "being in the world" (Bianchi, 2022). Plants use a variety of behavioural responses to detect environmental cues such as light, gravity, soil nutrients, and the presence of neighbours (Calvo & Keijzer, 2009; Trewavas, 2017). Plants may communicate and collect information on volatile chemical compounds (VOCs from now on; e.g., benzene, ethylene, jasmonate...) emitted by other plants that are attacked by insects or predators, and prepare an appropriate defence for potential attacks (Karban et al., 2011; Karban et al., 2014; Karban, 2015). Plants may detect the availability of vital nutrients and forage by changing the morphology and physiology of their roots or shoots in response to the amount of perceived resources (Hutchings & de Kroon, 1994; de Kroon & Hutchings, 1995; Grime & Mackey, 2002). Plants may also retain information in order to respond to future challenges more efficiently. For example, *P. sativum* plants were examined using two separate stimuli in an experiment: a light source (i.e., unconditioned stimulus) and an air flow (i.e., neutral, or conditioned stimulus). The presentation of the air flow, in particular, indicated to the plant when the light will come (Gagliano et al., 2016). Even when there was no light source present, the *P. sativum* seedlings grew toward the air flow. This suggests that *P. sativum* plants developed an association between the light source and the air flow, thus learning a new behaviour (Gagliano et al., 2016).

Furthermore, it has been demonstrated that plants can sense the level and variability of nutrients in the surroundings and evaluate the success and failure rates of possible occurrences based on the provided information (McNamara & Houston, 1992). Dener and colleagues (2016) separated the roots of *P. sativum* plants into two pots with varying nutrient contents, which might be constant or variable. *P. sativum* plants developed more roots in the pot with greater nutrient levels when exposed to constant nutrient concentrations. When the quantity of nutrients in the constant concentration pot was insufficient for the plant to survive, they allocated additional biomass in the variable nutrient concentration pot. These findings suggest that plants can sense and respond appropriately to changes in nutrient availability in the soil, and thus can switch between risk-prone and risk-averse behaviour as a function of resource availability, as observed in various animal species (e.g., social insects, birds, primates,...), including humans (Dener et al., 2016; Kacelnik & Bateson, 1997).

All these examples suggest that plants show a variety of behaviours and strategies to cope with different situations, which are not a simple automatic and fixed reaction to the environment. In the light of such evidence how can the behaviour of plants be defined? Can plants be described as cognitive agents?

Plants lack none of the skills that animals have if we acknowledge that every feature (including cognitive ones) arises from an evolutionary trajectory in various and dependent ecological niches. They are just different. The complexity of plant behaviour may be seen somewhere else, for example (but not entirely) in the ability to detect and produce diverse chemical compounds based on the circumstances and changing demands as a language allowing word composition (Bonato et al., 2021). This capacity underpins pathogen defence mechanisms and, more broadly, sophisticated types of plant elaborated communication. The suggestion is thus to establish an impartial and empirically oriented approach that considers the characteristics of each living organism.

In the next sections, I will unfold the idea of extending the concept of cognition to plants by embracing contemporary theories such as embodied cognition, extended cognition, enactivism, and alternative theories including autopoietic and basal cognition.

1.3 *4E* and others alternative theories on cognition

Novel “embodied” cognitive sciences have provided a few theoretical frameworks that call for a re-definition of cognition (Keijzer, 2017), expanding cognition in the extracranical world. Clark and Chalmers (1998) popularized the embodied, embedded, enactive, or extended (4E) approaches to mind and, since then, some philosophers and cognitive scientists have espoused these ideas.

1.3.1 Embodied cognition

According to the embodiment thesis, the body can be seen as a regulator of cognitive processes. As a result, an agent’s body, which is viewed as a dynamic instrument of exploration, may play a role in organizing and regulating cognitive activity throughout time and space, providing a functional linkage between cognitive processes and action. According to this viewpoint, cognitive representations of the external world (e.g., beliefs, wants, perceptions...) are “sublimations” of physical experiences rather than being produced autonomously by the mind (Merleau-Ponty, 1945; 1963). As a result, cognition is dispersed across the agent’s whole body rather than being limited to the brain, which is not the only resource employed by an organism to solve issues.

As a result, the embodied cognition thesis re-locates cognition outside the brain, with the body taking the primary role in coordinating and organizing all cognitive functions. However, sensorimotor abilities are the true overlap between the physical and cognitive worlds, allowing the agent to gain access to the structures of the environment through free-bodily goal-directed movements and modulated on the basis of the information perceived in the surrounding environment. This notion suggests that being a free moving individual with a sensorimotor structure is an essential need for cognition. The experiencing subject is always an actor of bodily and mental activities, according to embodied theories to cognition (Reed, 1996; Clark, 1997; Hurley, 1998). Sensory perceptions and higher-level cognitive states are formed by an embodied agent's active involvement with the experienced environment (Gibson, 1966). And, even before any further sensory consequences are addressed, this active involvement creates physical forces that must be assimilated across the body and regulated. Furthermore, acts in one portion of the body produce consequences in the rest of the body. To be efficient, these forces must be coordinated properly, especially under gravity, where unintended effects might disturb balance, induce postural failure, and cause harm. Thus, actions within the body must be coordinated collectively, which can only be accomplished by sensorimotor prediction of their combined effects (Delafield-Butt & Gangopadhyay, 2013).

Movements must also be monitored. The immediate future is constantly unpredictable, especially due to causes outside of the body, such as a change in wind velocity or the existence of an undetectable challenge. Movements must be perceptually led in order to stay on track even when interrupted (Delafield-Butt & Gangopadhyay, 2013). Sensorimotor intentionality's main ontogenetic manifestation is distinguished by its core prospective nature, with or without consequential sensory feedback from external or other parts of the body. All movement-based experience is based on this fundamental necessity for anticipating biomechanical forces created during movement and necessitating management (Delafield-Butt & Gangopadhyay, 2013). According to the purpose, structural sensorimotor activity is the earliest type of cognitive structure, or psychological process, which develops in parallel with fundamental sensorimotor movements led by sensorimotor intentionality. Understanding the goal-directed character of the most fundamental sensorimotor activity is thus critical for understanding the nature of cognitive processes in more complex agent-environment interactions (Hofsten, 2009). Given this premise, it would be impossible to view plants as cognitive agents because they are sessile creatures with no observable movements.

This is a mistaken idea because plants move regularly and in fashionable manner to adapt to individual and social conditions (as the research conducted in this thesis will illustrate). Some movements are observable in real time, such as the closing of the *Mimosa pudica* leaves when they are touched by an external stimulus perceived as risky (e.g., a human finger). Other forms of motions are harder to notice in reality because plants move on a different timescale than animals. However, by using specific time-lapse recording techniques, the movements of plants can be perceived and appreciated by us, as will be appreciable from the next sections in this thesis.

Plants might be considered a “free-moving organism with a sensorimotor organization” in this view. This assumption implies “motor intentions” in the context of “goal-directed” actions (Wang et al., 2021). In general, an action can be defined as deliberate or “goal-directed” when it is tailored to the task and its execution is within the agent's voluntary control. The basic purpose of the action, according to this definition, remains in the agent’s phenomenological experience throughout the action’s unfolding and completion. Could the concept of “motor intentionality” relate to plant movement? To put it another way, can plants act “intentionally”? To act intentionally, sensory inputs gained through perception have to be transmitted to a central nervous system, processed and converted into mental representation, and then implemented through appropriate motor responses (Souza et al., 2018), according to the classical view of cognition. However, the embodied cognition hypothesis does not require mental representation to behave appropriately in an environment, because actions and general cognitive capacities are dependent on the direct interaction of the body's structures with the environment rather than on mental thoughts.

The movement regarding growth toward the ideal locations for soil with abundant nutrients and sources of light might be interpreted as the intentionality of plants. When animals intend something, they enact their *directedness-toward* by moving their muscles; when plants intend something, their intentionality is expressed in modular growth and phenotypic plasticity (Marder, 2012). Each form of plant perception, according to phenomenology, exhibits an intentionality in one of three ways: directedness toward light in photosensitivity, directedness toward heat sources in thermosensitivity, and directedness toward (or away from) self and other in kin identification. In each case, it is a matter not only of receiving but also of interpreting the signals and deciding among conflicting signals in a non-automatic manner (Trewavas, 2009). Intentionality here assumes the more colloquial sense of a deliberate purposeful behaviour. Piaget (1979) described behaviour as follows: *"By behaviour, I refer to all the actions directed toward the outside world in order to change conditions therein or to change their own situation in relation to these surroundings"*. This definition is equally applicable to plant behaviour but implies intention, usually defined as goal-directed behaviour.

Plants, observed through the lens of embodied cognition, may not only detect information from their surroundings, but also make use of it to execute suitable responses, coordinating their behaviours and activities. To summarize, plant behaviour appears to be a coordinated and regulated adaptive behaviour composed of sensing, information processing, and regulation of an appropriate response such as flexible motions or morphological and phenotypic plasticity. This cognitive behaviour is not dependent on a central control unit, such as the brain, but rather embodied in the plant's whole structure with all organs. Plants might therefore be described as embodying cognitive, according to the embodied cognition theory.

1.3.2 Extended cognition

According to the extended cognition theory, brain-body-world are dynamically linked, and hence the environment is regarded as more than just a background for the cognitive system, but as an essential part of it (Clark & Chalmers, 1998). They claim that certain aspects of the natural world may be assessed as cognitive processes and that cognitive processes are not limited to the brain (Chalmers, 2019). To better explain, what distinguishes the extended cognition theory from the embodied one is that cognition may be extended outside the body in two ways: perception and action. Indeed, the dynamical interaction between the agent and the environment allows the organism to pick up different environmental information, which became available thanks to the active exploration of the surrounding. The organisms, in turn, use such information and the resources (i.e., affordance) that an environment offers to control and coordinate their behavioural responses toward the external world. Close kin to this idea is the concept of affordances theorized by Gibson (1979): *"what the environment offers the animal for good or ill".* Affordances are the most essential chances in the environment for each organism in order to interact with it and survive. Agents detect affordances as instead of practically neutral information that perceptual systems must interpret and connect to action capacities. This active, direct view of perception corresponds to a view of perceiver and environment as co-defined and co-dependent things. The environment of a perceiver is just the set of elements that can perceptually direct its ongoing operations (Souza et al., 2009; Souza & Lüttge, 2015). As a result, direct perception avoids the transmission of information through abstract mental representations, but it is directly governed by the body and the environment in which it is immerged. The primary distinction between extended and embedded cognition is that the latter originates from an organism's interaction with its environment, the cognitive process remains solidly within the body (Chalmers, 2019). In the case of extended cognition, cognition happens within and beyond the physical body and encompasses all external objects that the organism manipulates. The agent, the object, and the affordance of the object that motivates the activity of agents are all part of the same cognitive ensemble.

The spider and its web are an example of this single cognitive unit. Spiders' cognitive abilities are extended to the webs they spin. According to a recent study (Japyassu & Laland, 2018), spiders avoid compromising their cognitive capacities and overloading their tiny brains by shifting part of the information processing to their webs. In simple terms, the spider and its web would be the cognitive system. Many spider species' webs, for example, operate as a "filter" via which information reaches the spider. This information is transmitted to the spider in the form of thread vibrations induced by external factors such as wind or an attracted insect. By tying more vigorously on the strands of certain parts of the web, the spider may direct its attention to the chosen web segment, increasing its chances of success in catching a prey (Nakata, 2010; 2013). Normally, the spider's attention shifts to the most rewarding web portions. By intentionally varying the tension on the web fibres, one may influence the spider's foraging behaviour, causing it to pay attention to previously unproductive sections of the web (Japyassu & Laland, 2017). The spider's responses to stimuli and information processing are intimately conditioned to web tension, not just to its central nervous system, demonstrating that manipulating the web or the central nervous system of the spider modifies its cognitive capacities and understanding of the world.

Unlike most animals, which may move in search of food and run when threatened, plants are static organisms that are strongly linked to their surroundings. Plants, like animals, have acquired highly refined and sophisticated sensory capacities that allow them to continually observe and monitor their environment to undertake incredibly complex behaviours without the need of a brain or other centralized organs (Trewavas, 2014; Karban, 2015). What does make this possible? Could plants, like spiders, "offload" at least some of their cognitive process to the environment by extending their cognition beyond the boundaries of their bodies?

Two hypotheses for how plants could extend their cognition to the rest of the world have been offered by Parise and colleagues (2021): (i) the root exudates and (ii) the relationship between the root system and the mycorrhizal fungi. In the first place, root exudates are substances secreted by the roots in the rhizosphere (i.e., the part of the soil around the root system) that play an important role in mediating both positive (e.g., symbiotic associations with beneficial microbes such as mycorrhizae) and negative interaction (e.g., parasitic plants, herbivores, ...) between neighbouring plants and the microbes (Bais et al., 2004; Bais et al., 2006; Broeckling et al., 2008; Weir et al., 2004).

The plant's cognitive system could consist of the association between the plant and its root exudates, which may be equated to the interaction between a spider and its web. Let's take into consideration the avoidance response of plant roots to clarify this point (Falik et al., 2005). That is, the capacity of plants to change the direction of their development and the shape of their roots in response to the existence of obstacles in the soil. The capacity of the plant to move freely in the soil to obtain the nutrients required for survival is required, especially in rocky environments. Charles and Francis Darwin (1880) discovered that the tip of *Vicia Faba* roots may change their shape and development direction when they come into contact with a thin glass plate at a steep angle.

Wilson (1967) observed that the woody roots of maple trees may detect the existence of barriers into the ground and promptly adjust their development direction far away from the observed impediments. This behaviour is most likely caused by root exudates. Indeed, accumulation of root exudates between the barrier and the root cap has been shown to allow plants to sense the object in the soil and limit root development toward it (Falik et al., 2005; Semchenko et al., 2008). The removal of root exudates into the belowground area consequently impacts the plant's capacity to recognize and locate an object in the soil (Falik et al., 2005). As a result, root exudates may operate as a dynamic interface between the plant and the outside world, providing critical information that the plant uses to change its inner states and generate functional responses toward the environment.

In the second case, plants' cognitive capacities can be expanded by their interaction with mycorrhizal fungi. A link between the root system and fungus or bacteria in the soil that allows them to constantly exchange molecules, nutrients, and signals that are used by the plant to extend its perceptual system to gain information from areas outside the plant's reach (Parise et al., 2020).

Another example of extended cognition in plants is provided by the emission of VOCs which plays a crucial role in plants interactions with biotic (e.g., bacteria, animals,

…) and abiotic factors (e.g., water, sunlight, …). The emission of VOCs in the air is used by the plants to activate a variety of behaviours (Vivaldo et al., 2017). For instance, a defence mechanism towards insects or other predators (e.g., Mumm et al., 2003), pollinators attraction (e.g., Dudareva & Pichersky, 2000) and communicating with plants in the nearby (e.g., Heil & Karban, 2010; Bonato et al., 2021). For instance, when the plant is attacked by an insect or an herbivore it starts to release VOCs in the surrounding in response to the insult. Then, VOCs are intercepted by the self-plant's organs or neighbour plants leading to the activation of a variety of defence mechanisms which helps them to be prepared for a forthcoming attack (Farmer & Ryan, 1990; Karban et al., 2004; Baldwin et al., 2006). In this situation, the interaction between the plant and the external beings (e.g., insects, herbivores…) causing damage to the plant's fitness via the transmission-reception sensing technique generates information that may be used to adjust and strengthen the plant's defence measures. In conclusion, plants may incorporate physical characteristics of their environment into their cognitive system and extend their cognition outside their bodies (Parise et al., 2020) and being considered, *tout court*, extended cognitive agents.

1.3.3 Enactivism

Enactivism is based on the concept of sensorimotor contingencies, which states that perception is affected by sensory stimuli as well as the actions of the organism. The sensorimotor contingency theory proposes that action and perception interact in a bidirectional manner that impacts and alters each other (Varela, 1992; O'Regan & Noë, 2001). In a nutshell, the enactive approach points out that: cognitive structures evolve from recurring sensorimotor patterns that allow perceptually driven actions (Varela et al., 1991).

As previously outlined, the cognitive structures of interest for cognitivism are internal states that represent determined features of the world that are absent or inadequately accessible. Enactivism, on the other hand, emphasizes emergent cognitive processes that organize themselves as a result of organism-environment interactions. Consider the structure of a single-celled bacteria (Varela, 1997). A semi-permeable border separates the bacterium from the molecular broth that surrounds it, which is formed and maintained by a network of metabolic processes (i.e., absorbing nutrients, expelling waste products, ...) that weave through the organism and the environment boundaries. As a result, the bacterium is an autopoietic system, one that "*generates and defines its own organization through its activity as a system of creation of its own components*" (Maturana & Varela, 1980). In this way, a biological unity emerges from a nexus of interactions with portions of its environment. And an organism's embodiment determines structures and properties in the environment that bear on the organism's flourishing (Ward et al., 2017).

The idea of sensorimotor capacities cannot be used to split the direct relationship between action and environment in enactivism. Sensorimotor enactivists argue that sensorimotor contingencies, or patterns of dependence between perception and exploratory behaviour, can account for the content and nature of perception. Reflecting on the boundaries of our visual awareness is one method to motivate sensorimotor enactivism (Ward et al., 2017). Sensorimotor enactivists based their theory on the central role that exploratory actions have to allow an agent to grasp new features of the worlds.

And this exploratory activity is made by movement and sensorimotor activity, not only visual awareness (Ward et al., 2017).

A growing body of data suggests that plants may interact with their surroundings through active exploration depending on the affordances present in their surroundings. Using the enactivism description from above as a guide: "*cognitive structures evolve from recurring sensorimotor patterns that allow perceptually guided action*" (Varela et al., 1991). It is evident that plants meet this prerequisite. Plants perceive the structures in the environment and are able to implement guided-flexible and goal-directed actions modulated on the basis of the characteristics and the affordances offered by the environment (Guerra et al., 2019; Ceccarini et al., 2020a,b; Wang et al., 2023; Bonato et al., 2023). Further, this action is controlled and perceptually guided with an on-line control of movement that make plants accurate and flexible moving agents (Ceccarini et al., 2020b).

1.3.4 Autopoietic cognition

The autopoietic concept is closely related to enactivism. Maturana and Varela's autopoiesis theory (Varela et al. 1974; Maturana & Varela 1980, 1998; Maturana et al. 1960) captures the essence of cellular life by recognizing that life is an ongoing process that produces components that subsequently organize themselves within the process of life itself. As a result, the authors defined an autopoietic unit as a system capable of self-maintenance due to a process of component self-generation from inside. This expands the meaning of existence (Bitbol & Luisi, 2004). In particular, Maturana and Varela explicitly wrote that *"autopoiesis is necessary and sufficient to characterize the organization of living systems"* (Maturana & Varela, 1980). The most general property of an autopoietic system is the capability of generating its own components via a network process that is internal to the boundary (Luisi, 2003). The system's border must be "of its own making". Whether a given system is capable of making its own boundary or not is often the most discriminating criterion for recognizing whether a given system is autopoietic or not (allopoietic). Thus, a virus is not an autopoietic system, as it does not produce its protein coat or the nucleic acids from within its boundary (the host cell does it, and it is living; Luisi, 2003). Varela, in his latest book (Varela, 2000), has simplified these criteria to three basic ones, which can be expressed in the following way: verifying (i) whether the system has a semipermeable boundary that (ii) is produced from within the system and (iii) that encompasses reactions that re-generate the components of the system. Based on this, one is able discriminate the living from the non-living.

Further, Maturana & Varela (1980) pointed out an indissoluble link between being a living system and interacting with the environment. One facet of this connection is that all biological systems owe their existence to the selection of certain molecules from their surroundings. These substances are referred described as "nutrients" to indicate a relationship between them and the metabolic network that integrates them. This biological recognition occurs through a distinct sense. The authors coined the term "cognition" to describe this biological selective process, and they came to establish a fundamental similarity between life and cognition. They asserted that there is no life without cognition and that the co-emergence of the autopoietic unit and its cognitive activity gives rise to the life process (Maturana et al., 1960; Varela, 1979; 2000; Maturana & Varela 1980, 1998). The most extreme effort in this area is undoubtedly Maturana and Varela's theory of cognition. In this theory, the system and the environment make one another: cognition according to Maturana and Varela (1980) is a process of co-emergence. The cognitive interactions with the environment accompany the organisms during their life and during their biological evolution. Let me repeat the central point about this interaction: the environment has its own structural dynamics and, although independent of the organism, it does not prescribe or determine the changes in it (Luisi, 2003). It induces a reaction in the organism, but the accepted changes are determined by the internal structure of the organism itself. What responses the new disturbance will cause depends on the nature of the biological system and its past history of perturbations. These coupled interactions, accumulated over time, give a particular historical perspective to the autopoietic system: this becomes a historical product, the result of a long series of coupled interactions, the product of evolution (Luisi, 2003). Accordingly, evolution is seen as a result of the maintenance of the internal structure of the autopoietic organism. The interaction with the environment also includes the interaction with other autopoietic units, i.e., it encompasses the whole world of mutual interactions among living organisms. In particular, as Varela and Maturana (1998) point out, the interaction between two autopoietic units can give rise to symbiosis, or to meta-cellular systems.

When an amoeba or any other living cell selects metabolites from the environment and rejects the catabolites in it corresponds to a dynamic interaction that allows for both the live creature and the environment to act and come into existence. In other words, metabolism is always characterized by a dynamic interaction with the environment in which it occurs. As a result, metabolism is already the biological correlate of the concept of cognition. The organism chooses its material during this active interaction, and in this sense, full-fledged metabolism is equivalent to cognition. Considering the dynamic interaction of metabolism and environment as a concept of cognition, it seems evident that the photosynthesis and many other metabolic processes of plants (i.e., production and emission of VOCs, Adenosin Triphosphate biosynthesis (ATP from now on), …) are a perfect exemplification of cognitive behaviours. Therefore, can we consider plants as autopoietic, and so, cognitive systems? Barlow in his work (2010) claimed for a - *yes.*

In this thesis, I can claim for a *yes* too. Considering the three characteristics of autopoietic organisms, I can appreciate how they perfectly match with plants behaviour. (i) the semipermeable boundaries are evident in plants in their morphological structures. The boundary for the plants' range of activities is from shoot to roots, and also in the roots' surrounding soil where the chemicals exudates by the roots are presents (Barlow, 2010). The leaves are covered by stomata, tiny apertures that allow the entrance and exit of water and oxygen (Buckley, 2019). The roots are covered by a semipermeable membrane that allows the exchange of nutrients and substances from the outside (Tingey & Stockwell, 1977). Well-defined boundaries that permit the communication with the outside but at the same time, trace the edge between the plants and the outside worlds. (ii) the semipermeable boundaries are produced from within the system. All the tissues and membranes of the plants are produced by the plant itself. For example, rhizotaxy (i.e., the disposition of the lateral segments of the roots) is an example of auto-generated development of roots. In the case of shoots, another example is the phyllotaxy (e.g., the generation and disposition of the buds and leaves from the stem; Barlow & Lück, 2007). For what concern the (iii) presence of reactions that re-generate the components of the system. Not only, plants are able to generate structures of their own body, but they are also able to re-generate the components of the body multiple times. An example came from the branches and the leaves, that are re-generated after a damage, but also the ability of plants to regenerate new cells (Gutierrez, 2005). Differentiated plant cells can revert to a pluripotent state, proliferate and transdifferentiate. This unique potential is strikingly illustrated by the ability of certain cells to produce a mass of undifferentiated cells or a fully totipotent embryo, which can regenerate mature plants (Gutierrez, 2005).

Being capable of cognition is an inherent aspect of autopoiesis (Maturana & Varela, 1980), as it is the way through which the autopoietic process of life itself is perpetuated and enhanced. Cognition provides change impulses to the autopoietic process (Lyon, 2006). In general, an irregularity can be felt and registered by an internal steady-state pattern of self-maintaining metabolism. Then, if the disturbance results in a behavioural change in state that is beneficial for self-maintenance, the mechanisms causing this state-change may be chosen (Barlow, 2010). As a result, cognition may assist adaptability. Simultaneously, changes in a behavioural state may alter the surrounding environment, for example, by causing the reference organism to secrete components into its rhizosphere, which then alters the behaviour of neighbouring species. Sometimes, observations of neighbouring plant units might provide hints to the alterations, especially when neighbouring rhizospheres come into touch. Any shift might indicate cognition operating at a higher level — that of the ecology (Barlow, 2010). In this sense, as previously pointed out the autopoietic cognition span from the basic metabolism processes as photosynthesis to the interaction with other autopoietic systems (Luisi, 2003). Thus, the social interactions among living system are considered a kind of cognition too.

In this regard, plants present different modalities to interact with the environment and discriminate between themselves and other autopoietic systems through chemical, tactile and light-based stimuli, as I will point out in the next chapter.

1.3.5 Basal cognition

Basal cognition includes "*the fundamental processes and mechanisms that enabled organisms to track some environmental states and act appropriately to ensure survival (finding food, avoiding danger) and reproduction long before nervous systems, much less central nervous systems evolved"* citing Lyon (2021). Tracking existentially relevant states of affairs is inextricably linked to producing behaviour, which we define as activities that alter conditions in such a way that the results of those actions enter the stream of stimuli being tracked. Basal cognition refers to a set of biological abilities involved in becoming acquainted with, appreciating, and studying environmental aspects in order to achieve existential objectives. The cognitive toolkit is called "basal" because each of these skills, defined in the most basic terms, has been seen and characterized in prokaryotes (Lyon, 2015; Shapiro, 2020; Koshland, 1980), the lowest branch on the evolutionary tree of life, not to mention other aneural species.

Basal cognition, like *uncaveated* cognition, importantly involves learning, including via epigenetic and genetic embedding in the course of evolutionary change, what neuroscientist Antonio Damasio elegantly calls *"holding know-how in dispositions"* (Damasio, 1999). Basal cognition thus implies a degree of tacit familiarity or acquaintance concerning correlations between environmental states. Even while the chemical itself may not be attractive or useful, a gradient of one chemical, for instance, may point to the existence of a concentrated patch of food from which it dispersed. As a result, the organism must follow the gradient. In this case, tracking is based on the organism's implicit understanding of how the environment functions and what implications it has for its own functioning. However, cues frequently co-occur or manifest separately in complex ways. In open water, for example, increasing light not only means “up”, which means less pressure and higher temperature, but also more ultraviolet light that implies damage at the level of Deoxyribonucleic acid (DNA from now on) and more predators (Lyon et al., 2021). A living thing residing in such an environment must maximize along each of these paths, which frequently necessitates making difficult choices based on the synthesis of data from several sources. Every stage of development necessitates difficult decisions. Basal cognition is used for this. This was also the purpose for which nervous systems initially arose. As it is used here, basal cognition also refers to a set of biological abilities that are employed to learn about, value, and explore, as well as to either take advantage of or avoid environmental elements in order to achieve existential objectives. The cognitive toolkit is “basal” because each of these capacities, defined in minimal terms, has been observed and described in prokaryotes (Lyon, 2015), the lowest branch on the evolutionary tree of life, to say nothing of other aneural organisms. However, the phyla covered by this toolkit range from bacteria to slime moulds and other single-celled eukaryotes to plants, aneural animals (placozoa, sponges) and simple neural animals (Hydra and other cnidaria, planaria, ctenophores) to animals with complex nervous systems capable unlimited associative learning (Lyon et al., 2021).

This toolkit presents abilities such as orienting response, learning, perception, communication, memory, decision-making, anticipation and others (Lyon et al., 2021). The challenge for the field of basal cognition is to reveal the gradualism of cellular properties underwriting this critical biological function to leverage an understanding of the clear phase transitions observed in cognitive capacities across the web of life, of which the origin and development of nervous systems is (so far) the most dramatic example (Levin, 2020).

The plausibility and utility of viewing other fundamental biological issues through a “cognitive lens”, that is, “a strategy using well-established concepts from cognitive and computer science” in a non-metaphorical sense, “to complement mechanistic investigation in biology”, is a significant implication of basal cognition (Manicka & Levin, 2019). In order to create the conceptual and theoretical tools required for responding to outstanding fundamental questions in a variety of areas of biology, not just the cognitive sciences, basal cognition has the potential to bring together in productive contact previously disparate sectors of the life sciences. If cognitive science’s tools may be used to innovative applications (such training or motivating tissues for regenerative medicine) or unorthodox expressions or extremely new application (e.g., training or motivating tissues for regenerative medicine contexts) become feasible (Pezzulo & Levin, 2015).

While there are many different instances of multicellular behaviour among unicellulars, only a few evolutionary lineages led to obligatory forms of highly differentiated and integrated multicellularity (Knoll, 2011; Niklas & Newman, 2013; Keijzer, 2021). These rare lineages are: plants, animals and fungi. In these cases, large numbers of differentiated cells, each playing a wide variety of roles within the collective, are physically and organizationally tied together into units that constitute a new kind of individual (Levin, 2020). Numerous of these multicellular organisms have developed into intricate macroscopic structures that are orders of magnitude bigger than their constituent cells. These novel people may have an enormous unicellular appearance on the outside, but they actually contain sophisticated and novel self-constructed ecosystems on the inside (Levin et al., 2020). In addition to creating and maintaining this environment, constitutive cells must also function in ways that are advantageous to the system as a whole. Major goals for basal cognition include both the global orchestration of these inner multitude's activity — involving what we might refer to as the organizing bureaucracy — and the actions of the "inbodied" individual cells (Keijzer, 2020).

For the sake of this thesis, I will primarily focus on the concept of basal cognition, applied to plants. That plants exhibit a broad range of features that fit the cognitive toolkit has been argued for quite some time and is now increasingly accepted (Levin et al., 2020). In the present chapter, I have presented evidence regarding the presence of a communication through radical and volatile compounds (Penuelas et al., 1995; Trewavas, 2016; Novoplansky, 2019; Bonato et al., 2021), regarding memory and learning processes (Gagliano et al., 2016), anticipation, motor control and orientation (Guerra et al., 2019; Ceccarini et al., 2020; Bonato et al., 2023) in the *green kingdom*.

But how can plants do these complex behaviours in terms of basal cognition? Baluška and Mancuso (2021) discussed the ways in which plants can act as individuals by the use of synaptic-like adhesion domains, as well as action potentials and other forms of long-distance signalling. When it comes to multicellular uniqueness, plants have unique difficulties, most notably having to integrate the parts that live in two very different habitats at once—above and below ground. Additionally, because they are sessile and physically extend far into their surroundings, they must cope with a variety of distinct self- and non-self difficulties and do so in a variety of ways. These examples show that plants can sense and discriminate between adaptive or maladaptive environmental elements and they are sensitive and reactive to different elements or resources that the environment offers by modulating their behaviour and actions accordingly in a flexible and *cognitive* manner.

Chapter 2

The evolution of sociality *across taxa*

> *"It appears that nutrient exchange and helping neighbours in times of need is the rule, and this leads to the conclusion that forests are superorganisms with interconnections much like ant colonies."*
>
> *Wohlleben, 2015*

2.1 Beyond the *self*: Social cognition

To reclaim the alternative theories described in the previous chapter, that are crucial for the investigation of cognition in aneural organisms, I can argue, accordingly to Krueger (2011), that extended cognition includes social cognition. Krueger (2011) posit that social cognition is fundamentally an interactive form of space management and that some of the expressive actions (gesture, touch, facial and whole-body expressions, …) drive basic processes of interpersonal understanding. Thus, do genuine social-cognitive work making use of the bodies in the interpersonal space in which the actions occur (Krueger, 2011). As a result, social interaction is a type of social cognition.

Individuals interact with conspecifics at varying frequencies depending on the ecology of the species (Miklòsi et al., 2004). Researchers in social cognition are interested in understanding behavioural processes related to interaction among conspecifics, a topic that is partly based on the assumption that the mechanisms that regulates such interactions differ from those governing interactions between individuals acting alone with their physical environment (Miklòsi et al., 2004).

As a result, Miklòsi and colleagues (2004) offered a broad definition of social cognition, with which I agree, including: (i) recognition and categorization of conspecifics (Dittrich, 1990), (ii) the development and management of social relationships (Wickler, 1976), (iii) "cooperation" or *friendship* (de Waal, 1991), (iv) the acquisition of novel skills by interacting with conspecifics ("social learning"; e.g., Whiten & Ham, 1992; Miklòsi, 1999; Byrne, 2002), (v) the manipulation of others by means of communicative signals (Hauser & Nelson, 1991; Gòmez, 1996), (vi) the competence to perform joint cooperative actions and the question of "know what the other is doing" skills (Whiten & Byrne, 1991).

Hamilton's 1964 writings on kin selection (Hamilton, 1964), followed by the 1975 release of Wilson's *"Sociobiology"* textbook, represent the beginning of what many consider to be the contemporary study of social behaviour (Dugatkin, 1997; Costa, 2006; Clutton-Brock et al., 2009). Comparative approaches to social behaviour, on the other hand, have their roots in the years after Darwin's *"On the Origin of Species"* (Darwin, 1859), in the developing sciences of sociology and ecology (Crook, 1970). Historically, scholars were primarily concerned in the evolution of human social cognition. A gradual shift in behavioural ecology that acknowledged the relevance of looking wider at different behavioural mechanisms (Dukas, 1998; Shettleworth, 1998) has given way to a rediscovery of the value of exploring social cognitive processes within a functional and evolutionary framework across species.

In a larger and evolutionary context, it is necessary to appreciate that the ability to behave socially is inextricably linked to two key cognitive abilities shared among living beings: the ability to differentiate between self and non-self (Bilas et al., 2020), and the ability to distinguish kin from strangers (Bilas et al., 2020). The *"sense of self"* (Gallup & Anderson, 2020) can be expressed visually (Ristau, 1993; Hauser et al., 1995; Nielsen et al., 2006) or through other perceptual modalities such as olfactory or auditory (Bekoff, 2001; Cazzolla Gatti, 2016; Horowitz, 2017). Furthermore, the capacity to distinguish who is who and whether they belong to the same family or not is a skill talent that is frequently applied chemically across species (Gamboa et al., 1996; Breed, 1998; Johnston, 2003).

The purpose of this chapter is to compare the traits of social behaviour and cognition across different species, stretching the frontiers of sociality beyond the mammalians' group, over the invertebrate class, farther than the microcosmos, to the extraordinary *taxon* of plants.

2.2 The evolution of sociality across taxa

Understanding social evolution is difficult since social behaviour is frequently expensive in terms of fitness and survival for individuals (Dugatkin, 1997). Furthermore, unlike many features that are passively chosen by the environment, organisms generally produce selection for themselves while interacting with one another (Szekely et al., 2010). This increased complexity necessitates a more complicated model to separate cause and effect.

Individuals do not experience their surroundings passively. Environments are chosen and adjusted based on the behavioural characteristics of an individual, such as the proclivity to take risks or to behave socially. Genes may impact such inclinations (Szekely et al., 2010). In this sense, because of the diversity with which organisms interact with their surroundings, some environmental effects may have a large impact on certain individuals but not on others (Meaney, 2001).

The term environment itself, can refer to both abiotic (temperature, humidity) and biotic (individual density, parenting, social grouping) variables. The social environment is thought to have a significant impact on an individual's gene expression and behaviour (Szekely et al., 2010). According to Darwin's *"On the Origin of Species"* (1859), for natural selection to operate, individuals must differ in qualities related to survival and reproduction. We have known since Fisher (1918) that this variation must represent genetic factors. Selection, as shown by West-Eberhard (1979; 1983; 1984), can originate via social, and particularly competitive, interactions within social contexts, and is widespread due to the ubiquity of interactions among conspecifics. West-Eberhard (1983) defined this as social selection. As a result, sexual selection is the best-characterized mode of social selection induced through social activity (Hamilton, 1964). Individual fitness is controlled in part by impacts on social partners on that individual's phenotype (Wolf et al., 1999), which varies from natural selection (Darwin, 1859). Because the change in phenotype distributions within a generation caused by selection must be translated into cross-generational changes for there to be phenotypic evolution (i.e., changes in phenotype across generations), social selection is only one half of the evolutionary equation (Szekely et al., 2010). Because social behaviour is the result of contacts, it is a composite feature that cannot be assigned to a single individual (Fuller & Hahn, 1976; Meffert, 1995).

So, could be largely accepted that individuals' fitness is significantly influenced by their social behaviour. When the benefits of living with conspecifics outweigh the drawbacks (Alexander, 1974; Couzin et al., 2002), sociality is likely to arise. The advantages of sociality are varied, but they mainly include resource acquisition, predator avoidance, offspring care and physiological equilibrium. Typical costs include resource competition and disease transmission and the exact type and amount of each obviously vary between species (Rubinstein & Abbott, 2017).

Indeed, social behaviour, with different levels of interaction and thus, different costs and benefits, are widely spread across taxa. From eusociality in insects (Michener, 1969; Wilson, 1971) through social behaviour in humans, sociality is an evolutionary phenomenon that bypasses the presence of a brain, and it seems intrinsic to the evolution of life itself.

As a matter of fact, sociality is pervasive, existing in all major primate and non-primate mammalian lineages. Many non-human primates live in large groups characterized by social behavioural patterns such as grooming, imitative and cooperative foraging, differentiated affiliative relationships, organized relationships and sexual behaviour, and also rivalry-based relationships structured by social dominance (Smuts et al., 1987; Wilson, 1975). Similar social behaviour is observed largely among marsupials such as kangaroos, wallabies and wombats (Jarman, 1991). But they were also found in the Cetacea as whales and dolphins (Connor, 2000), Hyracoidea (Hoeck et al., 1982), Proboscidea such as elephants (McComb et al., 2011) and Perissodactyla, as ungulates, (Cameron et al., 2009; Sundaresan et al., 2007) lineages.

But how did evolve these social behaviours across so many different species? Sometimes novel behaviours can develop by linking, repurposing or building on ancestral processes that previously served a different function (Katz & Harris-Warrick, 1999), and the evolution of social behaviours appears to follow this pattern across species. To clarify, the electrocommunication system of mormyrid fish is a noteworthy example of such development and reuse. These fishes have an electrosensory system positioned along the lateral line that allow them to live in conditions where the visual system is not of much use. This electric organ is a modified muscle that has lost its contractile properties. The electric organ discharge is essentially a large action potential that generates enough current to produce an electric field in the water surrounding the fish. The duration of the electric organ discharge is highly species-specific and can differ in duration by up to two orders of magnitude (Katz, 2006). This organ developed to help in orienting and motion detection (Katz, 2006). The cerebellum, which processes sensations from the lateral line system, is considerably expanded in mormyrids and plays a major role in electrocommunication, a social function that is lacking in the ancestral state (Katz, 2006). Another notable example of repurposing for social necessities is the emergence of the neuropeptide oxytocin (OT from now on). In early vertebrate, OT with effects similar to anxiolytic (Neumann et al., 2000) and approach- and tolerance-enhancing (Kemp et al., 2010; Averbeck, 2010) may have been evolved to assist parental behaviour and social bonding in mammals.

In the domain of invertebrates, insects are among the most sociable species on the planet. To elaborate, insects are great models for studying social behaviour because they participate in a wide range of both basic and sophisticated social interactions (Costa, 2006; Sokolowski, 2010). *Nicrophorus vespillo* burying beetles, for example, engage in complex direct biparental care (Eggert et al., 1998). *Polistes fuscatus*, a paper wasp, can distinguish between individuals based on facial traits (Sheehan & Tibbetts, 2011). Female *Drosophila melanogaster* participate in mate choice copying, which is a type of social learning (Mery et al., 2009). Finally, social caterpillars communicate to show protective group postures (Costa, 1997). To better explain, many social caterpillars can be likened to herding mammals, especially nomadic species that travel *en masse* from feeding site to feeding site without returning to a permanent nest or resting site. Herding behaviour involves the expression of group-cohesion signals and is thought to fill a defensive role by, for example, diluting the probability that any one individual will be taken by a predator and making it more likely that a predator will be detected in a timely fashion (Costa, 1997). Such signals effectively function as "boundary markers", defining the spatial bounds of the group to keep individuals from being separated, or simply to orient individuals to the group.

These and other instances show the presence of complex social decision-making and communication networks in insects. Insects are also great models for studying social behaviour since they often live in colony, where groups of individuals fulfil specialized activities of labour and parenting (Wilson, 1971). According to Szathmary and Smith (1995), the beginnings of eusociality in insects reflect one of the main shifts in the history of life. Importantly, this eusociality has evolved multiple times independently (once in ants, once or twice in wasps, four times in bees, and once in termites; Toth & Rehan, 2017), making it a tractable system for studying the mechanisms underlying social structure transitions and sociality in general.

The study of sociality across taxa has been expanded to include aneural creatures such as bacteria (Tarnita, 2017). For example, solitary *Dictyostelium discoideum* amoebae combine with neighbours to produce a multicellular fruiting structure composed of a stalk and spores when starved. The spores are hunger resistant and will germinate in favourable circumstances, whereas stalk cells die during stalk growth (Bonner, 1982, 2008; Strassmann & Queller, 2011). These amoebae do not perfectly discriminate against non-kin during the aggregation process; as a result, chimeras (i.e., multicellular fruiting bodies consisting of two genotypes) have been witnessed both in laboratory settings and in the natural environment (Fortunato et al., 2003; Gilbert et al., 2007; Sathe et al., 2010; Strassmann et al., 2000). These chimeras are functional: the different genotypes contribute to stalk development and spore production (Strassmann et al., 2000). *Myxococcus xanthus* is another fascinating case. These bacteria feed on a wide variety of microorganisms; when starved, they go through a development that culminates in the differentiation of rod-shaped cells into spherical spores inside a multicellular fruiting body. Not all cells, though, develop into spores; some die autolytically (though it's unclear if this is beneficial to the spores), while others continue to exist as lone, rod-shaped cells that round the perimeter of the fruiting body (Velicer & Vos, 2009). The death of a considerable proportion of the aggregated cells shows that fruiting body development is an expensive process and opens the door to cheaters. One such cheater is unable to generate viable spores in monoculture, making it an obligatory social cheater whose survival during famine is dependent on the creation of chimeric fruiting bodies with a social host (Velicer & Vos, 2009). This obligatory cheater, which led to the demise of cooperation, eventually transformed into a distinct social type in lab trials; significantly, it did so through mutations that produced fresh genetic relationships rather than a simple reversal of its flaws. Another important social competence is communication and the exchange of behaviourally valuable information (Velicer & Vos, 2009). This exquisitely complicated capacity has also been shown to characterize a variety of microorganism groupings. Cells aggregating to form fruiting bodies in certain *Myxococcus* and *Dictyostelium* have long been recognized to participate in chemical communication mediated by secreted chemicals and physical touch to coordinate their multicellular growth (Shimkets, 1990, 1999; Dworkin, 1996; Gadagkar & Bonner, 1994).

More recently, communication systems involving continuous secretion of specific chemicals into the surrounding environment, as well as detection of local levels of these compounds to assess and react to local density of cells, have been discovered and distinguished in a wide range of bacteria; this sort of communication has come to be known as “quorum sensing” or “autoinduction” (Crespi, 2001).

2.3 Competition, cooperation and communication

At the foundation of social cognition are two essential skills that allow for every other social behaviour, as previously announced at the beginning of this chapter. These talents include the ability to distinguish between self and non-self and the ability to distinguish relatives from strangers among others (Bilas et al., 2021; Bonato et al., 2021).

These are the essential criteria for social behaviour in any organisms capable of social cognition. Recognize oneself from others and a minimal ability to distinguish kin from non-kin allow individuals to live in groups, allowing collaboration (e.g., in identifying resources or hunting prey) or competition, for example, in terms of direct resource harvesting (Byrne & Bates, 2007). Foraging is one of the most primal and fundamental behavioural states, present virtually in all motile, heterotrophic species. As a result, it is not unexpected that foraging tactics are under intense selection pressure to maximize returns on investment that could implicate cooperative or competitive behaviours (Chang et al., 2013).

2.3.1 Competition

According to Miller (1967), competition is the active demand for a common resource or requirement that is actually or potentially limiting by two or more individuals of the same species (intraspecies competition) or members of two or more species (interspecies competition). This concept is compatible with the assumptions of the Lotka-Volterra equations, which remain the foundation of mathematical competition theory (Levins, 1968). It also corresponds to the intuitive view held by most current ecologists regarding the underlying behavioural processes (Miller, 1967). Competition develops only when populations grow overcrowded to the point that a scarcity of one or more resources occurs (Wilson, 1971). Competition among living organisms is considered as a fundamental aspect of the struggle for existence in Darwin's theory of the mechanism of evolution, and hence as a basis for natural selection (Darwin, 1871).

The strongest rivalry is frequently observed among individuals of the same species. Conspecific competition is a major factor of natural selection among phenotypic variations of a particular species and differs from interspecific rivalry that occurs among different species (Christiansen & Loeschcke, 1990).

Competition is nearly often related with aggression. Insofar as aggressive behaviour is adaptive, it is commonly classified as one of the types of competition (Wilson, 1971). Direct aggression is the most obvious and direct kind of competition, but as we move from species to species, we can uncover increasingly subtle and indirect forms. Ant colonies are famously antagonistic toward one another, and numerous entomologists have observed colonies both within and across species. Pontin (1961, 1963) discovered that the majority of *Lasius flavus* and *Lasius niger* queens attempting to establish new colonies in isolation are killed by workers of their own species. *Tetramorium caespitum* colonies defend their territory through pitched conflicts fought by huge groups of workers (McCook, 1909). The recent discovery that the average size of the worker and the production of winged sexual forms at the end of the season, both of which are good indicators of the nutritional status of the colony, increase with territory size demonstrating the adaptive significance of fighting (Brian et al., 1967).

Repulsion, instead of aggression, is a type of indirect assault. When workers from the ants *Pheidole megacephala* and *Solenopsis globularia* meet at a feeding place, there is some fighting, but the issue is not resolved in this manner. Instead, organizational skill determines supremacy. When workers of both species encounter a stranger, they become agitated and flee the smell trails and the food source. The *Pheidole* settle down, reroute the odor trails, and reassemble at the feeding place faster than the *Solenopsis*. As a result, they can generally dominate the feeding stations and build up their forces more swiftly during fights. *Solenopsis globularia* colonies can persist by occupying nesting and foraging grounds in more open, sandy environment not penetrated by *Pheidole megacephala* (Wilson, 1971). There are also cases where competition for resources is done through indirect kinds of repulsion.

It is now commonly known that territoriality changes progressively among species, from forceful exclusion of intruders to the gentler use of chemical signposts without threats or assaults. Territory maintenance through violent behaviour has been widely documented in a wide range of species. Dragonflies of the species *Anax imperator*, for example, monitor the ponds where their eggs are placed and use darting assaults on the wing to drive out other dragonflies of their species as well as those of the similar seeming *Aeschna juncea* (Moore, 1964). Miller (1967) observed how overt territorial violence between the red-winged blackbird *Agelaius phoeniceus* and the yellow-headed blackbird *Xanthocephalus Xanthocephalus* resulted in the former species being partially excluded. Both species' males distinguish themselves by regular exchanges of vocal and visual displays performed from perches in the marshy terrain where they nest (Miller, 1967). *Agelaius* males arrived an average of thirteen days sooner than the *Xanthochepalus* at one research site near Saskatoon, Canada, and established their territories throughout the marsh. When the *Xanthochepalus* males came, they drove the *Agelaius* off in the marsh's deep water (Miller, 1967).

Wilson (1971) defines social space as a type of floating territory in which the exclusive region is produced merely by the presence of a distance below which an individual animal will not allow another animal to approach it. It generates roosting bird and swimming school of fish spacing patterns that are sometimes amazingly regular. An overt threat can occasionally maintain social distance. A brooding hen, for example, becomes agitated when another hen approaches within twenty feet (Wilson, 1971); if the approach is less than ten feet, she lowers her wings and prepares to fight. In some situations, such as *Tribolium* flour beetles, it is maintained by chemical repulsion or another sort of indirect exclusion.

Dominance behaviour is analogous to territorial behaviour, in which a group of animals dwell within one territory (Wilson, 1971). As a result, one of them, the territorial equivalent, begins to dominate the others. Below this “alfa” individual, there may be a second “beta” animal that dominates the remainder of the underlings in the same way, and beneath it, a third-ranking creature, and so on. Dominance hierarchies based on direct interaction are common among social animals, but not universal. They have been seen in social wasps, bumblebees, thermites crabs, reptiles, birds, and mammals, among others (Wilson, 1971). They are complementary with territories in a few circumstances.

Another way to compete is steal and eavesdrop is an important behavioural information for survival. The capacity to listen on social interactions of other individuals allows to learn about the competitive abilities of others and potential allies without explicitly challenging them. Males in birds and fish utilize eavesdropping information to decide whether to challenge an intruder (Oliveira et al., 1998; Peake et al., 2002). Female chickadees (*Poecile atricapillus*) evaluate their mate's relative dominance rank by attending song competitions with surrounding males. Females coupled to dominating males in such competitions are more prone to seek extrapair copulations from presumably more dominant neighbours (Mennill et al., 2002).

2.3.2 Cooperation

Darwin (1859) went on to declare in *"On the Origin of Species"* that cooperation was *"a special difficulty, which at first appeared to me insuperable, and actually fatal to my whole theory".*

Thus, more than a hundred years before Hamilton (1964), Darwin overcame this issue by proposing an inclusive fitness theory. Darwin understood that if natural selection acted at the level of a social insect *colony*, and not a single individual, many characteristics of social insects might be explained (Dugatkin, 1997). Darwin's interest in cooperative behaviour was not restricted to social insects; he wrote extensively about grooming, sentinel cries, and cooperation in birds and mammals, and made the somewhat audacious claim that: *"most mutual common service in the higher animals is to warn one another of danger by means of the united senses of all"* (Darwin, 1871).

Many attempts have been made in the field of behavioural ecology to define words such as cooperation and altruism (Dugatkin, 1997). Grafen (1984) described these actions as "*self-interested refusal to be spiteful*", whereas Kropotkin (1908) called them "*joint stock individualism*". In this regard, I agree with Dugatkin's (1997) definition of cooperation: *"Cooperation is an outcome that, despite potential relative costs to* *individuals, is good in some appropriate sense for the members of a group, and whose achievement requires collective actions"*.

Cooperation is at the heart of sociality. Macroscopic social creatures collaborate to defend themselves against rivals, as well as to secure food, reproduce, or protect the boundaries of a new location (Crespi, 2001). Cooperation can be egalitarian, in which all individuals participate and profit more or less equally, or it can feature division of labour, in which individuals engage in various works for which they may receive different rewards, either directly or indirectly (Crespi, 2001).

In animals, individuals who are related or very likely related but are not parents will take over parental duties when the mother of a young one dies in a variety of animals, including wasps (West-Eberhard, 1975), chimps (van Lawick-Goodall, 1968), rhesus (Sade, 1965), wild dogs (Frame et al., 1979), and coatis (Kaufman, 1962).

Among cases where help is based on particular criteria, the best-studied examples are those where help is directed towards kin. Individuals preferentially help the group members that are most closely related to themselves across species, from amoebae to primates (Clutton-Brock, 2002; Mehdiabadi et al., 2006; Silk, 2009). To explain how individuals distinguish between relatives and non-relatives, a variety of theories have been put forth (Hepper, 2011). A straightforward rule like "*feed any chick in my nest*" may be sufficient in situations when relatives are continuously present in a predictable area, such as breeding birds (Komdeur & Hatchwell, 1999). In other cases, where kin are not distributed predictably in space, kin recognition may rely on the assessment of other cues and individuals may need to learn to recognize these cues (Komdeur & Hatchwell, 1999). For instance, cooperatively breeding long-tailed *Aegithalos caudatus* show kinbiased care, discriminating between kin and non-kin using vocal cues learned from adults during the nesting period (Sharp et al., 2005).

In many ways, kinship and aiding relatives is best exemplified by social insects, who show extreme levels of cooperation in conjunction with an odd genetic architecture that creates sisters that are "super relatives" (Wilson, 1971). Social insects are haplodiploid, in that males have only a single copy of each (haploid), while females have two copies of each chromosome (diploid). As a result of the genetics underlying haplodiploidy, sisters are related to one another on average by a coefficient of relatedness of 0.75, which has the effect of making females more related to sisters than to their own offspring (Dugatkin, 2002).

Outside of kinship, the path to cooperation that has received the most attention from behavioural ecologists, as well as social psychologists is reciprocal altruism. In this sense, for example, females in a nest of *Desmodus rotundus* vampire bats regurgitate blood meals to others that have failed to obtain food in the recent past (Wilkinson, 1984; 1985). This form of food sharing can be a matter of life or death, as individual bats often starve if they don't receive a blood meal every sixty hours (Dugatkin, 2002).

Alternatively, the propensity to help other individuals may be contingent on their past behaviour. For example, *Pan troglodytes* wild chimpanzees appear to reciprocate grooming over the long term (Gomes et al., 2009). Similarly, there is evidence that in long-tailed macaques *Macaca fascicularis*, individuals are more likely to groom those who have provided grooming in the recent past (Hemelrijk, 1994).

As in the "public goods" games of economists (Bowles & Gintis, 2003), cooperation sometimes results in immediate synergistic advantages shared by cooperators that outweigh the costs of offering aid (Kokko et al., 2001; Brown & Vincent, 2008).

Mechanisms of this kind probably maintain many mutualistic interactions between species, like the hunting associations found between raptors and carnivores (Paxton, 1988) that increases the chances to catch a prey, or between different predatory fish (Bshary et al., 2006) for the same hunting purpose, as well as many examples of cooperative foraging between unrelated conspecifics, like the cooperative manoeuvres of foraging pelicans (McMahon & Evans, 1992).

Research over the last thirty years shows that cooperation in animal societies most frequently involves kin and is seldom highly developed in groups consisting of unrelated individuals (Clutton-Brock, 2009). When non-kin collaborate with one another in natural populations, it's common for one or both partners to reap immediate advantages from their actions, and it's uncommon to find evidence that cooperation entails short-term fitness costs (Clutton-Brock, 2009).

2.3.3 Communication and language

When we think about language and communication, we normally think of humans talking to one another and communicating in order to establish shared goals and coordinate common behaviour. However, since Karl von Frisch was awarded the Nobel Prize for his discovery and analysis of bee languages and dialects, we have discovered that even non-human social animals may communicate to achieve complicated behavioural patterns (von Frisch, 1967). Nearly at the same time, Nobel-awarded Manfred Eigen stated that when we talk about the genetic code, we are talking about a true language, not merely a metaphor (Witzany, 1995).

Witzany established the biocommunicative theory (Witzany, 2013) in response to these basic ideas, which explores both (i) communication and (ii) language as universal necessities for existence. Communication can be chemical, visual, or physical among organisms, and it helps to coordinate activities, designate group membership, or identify individuals or their roles in a group (Choe & Crespi, 1997).

Discussions of language across species are inevitably influenced by how we define “language” and the fact that it is generally thought to be unique to humans (Christiansen & Kirby, 2003). De Saussure (2001) portrayed human language as a complicated system of signals that arbitrarily map into meanings (see also Bredin, 1984; Searle, 1976; Austin, 1975). The system has a hierarchical structure in which minimum units at one tier are joined using grammatical principles to generate bigger units at the next.

The birth of language is seen as a pivotal event in human history, an innovation that fundamentally altered the nature of human relationships (Nowak & Krakauer, 1999). If language is envisioned as a system built on abstract symbols, linguistic processing must be capable of dealing with abstract mental representations (Dennett, 1969; Fodor, 1975; Pylyshyn, 1984; Mahon & Caramazza, 2008; Indefrey & Levelt, 2004). However, taking into account the recent theories discussed in the first chapter, we can put the concepts of mental representations aside, and embrace the “embodied language” processing theory (Barsalou, 1999). This theory states that meaning is determined by the brain and body’s interactions with the social and physical environment (Clark, 1997;Barsalou, 1999; Kemmerer et al., 2010). Thibault (2011) emphasizes this concept with these words: *“the centrality of coacting agents who extend their worlds and their own agency through embodied, embedded processes of languaging behaviour rather than uses of an abstract language system”* (Cowley, 2014).

These viewpoints appear to have blurred the distinction between human and non-human language, thus embracing a scientifically grounded concept of biocommunication. According to this viewpoint, language can be defined as a natural system of arbitrary symbols generated and used according to non-reducible syntactic, semantic, and pragmatic rules (Witzany, 2010), and communication processing can be defined as sign-mediated, situation-appropriate interactions (Witzany, 2010). There are various examples of parallelisms between human language and communication in non-human animal species in the literature. For example, some birds use their vocalizing apparatus (just as humans do) to produce a wide range of sound units to form complex songs. Syllables are the minimal units used in birdcalls; organized groups of syllables are used to create song phrases, which are subsequently concatenated in different ways depending on the kind of song (Salwiczek & Wickler, 2004).

Meaning-making occurs throughout a communication encounter and is based on interaction with the environment (Thibault, 2011). In this sense the language is extended outside the individual and it is based on the environmental information, generating a perfect embodiment of the extended cognition theory. Indeed, in humans, the generation of sounds for meaning-making activity is influenced by a social context, whereas imparting meaning to these sound units is influenced by the agents' experience obtained from their contact with the environment (Thibault, 2011).

Animals may be referred to as part of the meaning-making activity, which can be viewed as a mechanism for exchanging knowledge in order to minimize uncertainty and promote survival. Communicating danger, the presence of a predator, or the amount of accessible resources are all examples of meaning-making behaviours that may be represented in a variety of ways and are at the core of social communication. For example, depending on the predator's categorization, monkeys make different alarm cries to warn one another (Seyfarth et al., 1980; Seyfarth & Cheney, 2003). Bees use their dance to exchange signals and communicate meanings about the scent, colour, shape, and size of food sources (von Frisch, 1967). Bees, like humans, appear to communicate about topics that are not immediately temporal or spatially contiguous. Because this creative feature of language can be found in an animal species so distinct from humans, the question arises: are there any "linguistic" qualities that people, animals, and even brainless organisms like plants can share?

Furthermore, there is evidence that certain animal species use regional accents or dialects (Henry et al., 2015). Some bats (Davidson and Wilkinson, 2002; Esser and Schubert, 1998), marine mammals (Schustermann, 2008), pinnipeds (Tyack and Miller, 2002) such as elephant seals (Le Boeuf & Peterson, 1969), and cetacean species (Tyack, 1986; Rendell & Whitehead, 2001) such as sperm and killer whales (Ford, 1991; Riesch et al., 2006) have vocal dialects. This signifies that in certain species, the communication is favoured among conspecific or individuals sharing the same territory, suggesting that form of cooperation are reflected in the way agents communicate through each other.

In light of these considerations, and continuing along this line of thinking, a variety of non-human systems appear to share certain characteristics of human language. Several animal investigations have revealed a sophisticated communication system that developed in the absence of big vocabularies (von Frisch, 1967; von Frisch, 1971; Hauser & Konishi, 2003). Furthermore, an increasing number of animal communication codes have been cracked (von Frisch, 1967; Evans, 2002; Pollick & De Waal, 2007). Language could be nonverbal (e.g., gestures or facial mimicry), and it is well known that animals use nonverbal forms of communication such as gestures, body language, facial expressions, as well as tactile, visual and chemical forms of communication (e.g., bacteria; Bassler 1999; Schauder & Bassler 2001; Dunn & Handelsman, 2002). Movement itself is a form of communication, indeed, as explained above, honeybees share qualitative and quantitative food-related information via their waggle dance (von Frisch, 1967). Thus I may be entitled to say that coordinated movements are an expression of intentions, and an expression of intentions is a communicative behaviour requiring social abilities.

2.4 Plants as eusocial organisms

Plants evolved from very small and relatively simple aquatic organisms to the most complex terrestrial vascular plants, with aboveground shoot lengths of hundreds of meters in the case of sequoia trees, and unparalleled longevity of several thousand years as some *Pinus longaeva* trees estimated to be older than 5000 years (Munnè-Bosch, 2018; Baluška & Mancuso, 2021).

Higher plants have several characteristics that were previously thought to be unique to animals, such as sexuality, immunity, self/non-self and kin recognition, goal-directed behaviour, language and communication, intelligence, and sociality. These unexpected animal-like characteristics of higher plants are the consequence of convergent evolution of flowering plants and animals (Baluška & Mancuso, 2009). Mammals and angiosperms, for example emerged some 180 – 130 million of years ago and since then have been co-evolving (i.e., the evolutionary process where two species adapt to each other over time) at several levels (Baluška & Mancuso, 2009).

Plants are unique multicellular organisms because they not only have autotrophic and heterotrophic organs, tissues, and cells, but they also live in two contrasting environments: an underground pedosphere and an aboveground atmosphere. This distinction implies that plant organs exist in two distinct environments: autotrophic shoots are aboveground organs exposed to the day/night cycles, and heterotrophic roots are subterranean organs subjected to darkness (Baluška & Mancuso, 2009). Furthermore, roots are far more socially active, since they participate in various intracellular symbiotic relationships with bacteria and fungus, as I shall examine in more detail below.

2.4.1 Self/non self and kin recognition in plants

Recent studies demonstrated that self and kin recognition are present in plants. Plants reject self-pollen in sexual self-incompatibility to promote outcrossing and avoid or minimize inbreeding (Takayama & Isogai, 2005). To better explain, the stigma papilla cells, which constitute the first entrance site of germinating pollen tubes into the maternal tissues of the pistil, are generally used for sporophytic self/non-self pollen grain identification (Baluška & Mancuso, 2009). Pollen self/non-self identification is performed by integrated signalling pathways including a variety of peptides, receptors, cytoskeletal systems and calcium signals (Takayama & Isogai, 2005; Wilkins et al., 2016). In addition to these early self-incompatibility processes at the stigma papilla, there are late-acting mechanisms of plant reproductive barriers that are still poorly understood. Invasion of pistil tissues through pollen tubes resembles fungal invasion, and it is possible that sexual self-incompatibility evolved from fungal invasions of ancient plants (Elleman & Dickinson, 1999). The recognition of intrusive growth, for example, of fibres as self (Levyadun, 2001), as well as the ability of plants to rapidly detect and effectively fight viral, microbial, and fungal invaders and pathogens via their plant-specific innate immunity (Dodds & Rathjen, 2010), is the best example of plant awareness of their biotic environment via self-sense. Surprisingly, plant innate immunity systems rely on receptor proteins that are comparable to those found in animal and human innate immune systems (Kwon et al., 2008). However, damaged-self detection has an ancient cellular base since animal and plant cells constantly evaluate their structural and functional integrities and mount quick reactions if faults are recognized (Heil & Land, 2014). Surprisingly, receptors implicated in plant innate immunity are similar to those involved in symbiosis (Girardin et al., 2019). This indicates the likely evolutionary genesis of symbiosis from infections at the organismal level (Lima et al., 2009), as is also true at the cellular level (Baluška, 2009).

Self/non-self recognition is also common and well defined in shoot tendrils, which relate to many vascular plants climbing tendency (Chen et al., 2012). The climbing habit evolved several times in the evolutionary history of flowering plants and is supported by a variety of organs, including tendrils that perform helical movements, which picked Charles Darwin's interest and led to the publication of *"The Movements and Habits of Climbing Plants"* in 1875 (Darwin, 1875). Tendrils of the perennial vine *Cayratia japonica*, for example, demonstrate self-recognition, allowing them to coordinate their coiling responses (Fukano & Yamawo, 2015). This self/nonself identification in tendrils was later seen in other plants (Sato et al., 2018). Shoot tendrils, like root apices, employ their chemical sense to discriminate themselves (Fukano, 2017). Tendrils of the vine *Cayratia japonica* have been shown to detect and avoid host plants infested with spider mites (Nakai & Yano, 2019).

Plants that are socially and cognitively engaged experience kin recognition in addition to self/non-self recognition (Dudley & File, 2007). Root exudation can also be used to facilitate plant-specific kin identification (Biedrzycki et al., 2010). Kin recognition regulates new root allocation within root systems, which is related to nutrient distribution and acquisition (Bhat et al., 2011; Palmer et al., 2016). Plant kin recognition has just been demonstrated in rice, with implications for crop output and grain yields. Rice plants with non-kin neighbours invest more photosynthates in their root systems and less in shoots and grains (Baluška et al., 2009). Plant kin identification is emerging as an essential phenomenon for controlling crop yield in commercial agriculture. Photoreceptors in plants may also distinguish kin plants via shoots (Bais et al., 2015; Crepy & Casal, 2016). Surprisingly, kin recognition allows plants to modulate pollinator attraction to their blooms (Torices et al., 2018). It is unknown whether this is performed by root exudates or light-sensing photoreceptors. However, there is one case in which kin recognition in roots is linked to plant sexual organs. It has been demonstrated that the identification of the sexual identity of plant neighbours is mediated by their root systems in *Populus cathayana* trees (Dong et al., 2017). Shoot-mediated and photoreceptor-based plant kin recognition, like root-mediated and exudate-based plant kin recognition, has a role in reproduction because plants that interact with their kin generate more seeds (Bais et al., 2015; Crepy & Casal, 2016).

2.4.2 Mechanisms for the detection of neighbours in plants

It was previously considered that plants could only identify their neighbours passively, by monitoring changes in resource availability (light, water, and nutrients) produced by neighbouring plants. But the mechanisms for neighbours' detection in plants are different, complex and very active (Bilas et al., 2021).

Plants mostly achieve this by using "cues", information that neighbouring plants can't resist revealing (Karlovsky, 2008; Shelef et al., 2019). For examples, plant organs absorb, reflect, and scatter solar radiation, lowering photosynthetically active radiation (PAR from now on). This produces a separate indicator of neighbour presence that differs from oscillations in ambient light levels and quality. Plants are extremely sensitive to changes in light quality, even in the absence of a decrease in PAR, since they suggest current or future light competition (Roig-Villanova & Martinez Garcia, 2016). Plants may employ light signals to recognize one other across substantial distances in the absence of shadows (Roig-Villanova & MartnezGarca, 2016). Light signals supplied by neighbours are sensed by specific phytochromes, which have a high sensitivity to far-red light. Because the tips of leaves are the principal location of light cue sensing, self-shading is less likely to activate these reactions (Pantazopoulou et al., 2017). Touch by neighbouring plants appears to play a particularly crucial role in priming plants for future interactions and has been shown to influence VOCs and root exudate emission (Elhakeem et al., 2018; Markovic et al., 2019). Touch of leaf tips increases leaf hyponasty in Arabidopsis, which shifts the leaves into a position where they may better receive dispersed light signals to "confirm" the existence of neighbouring plants (de Wit et al., 2012). Further, touch could give information of a possible presence of neighbour but it doesn't convey any information regarding the identity of that neighbour. To better identify neighbours, it is required a chemical fingerprint, a specific informative cue. For this reason, plants release a wide variety of organic substances into the environment, which are often classified as VOCs and roots exudates. Indeed, plants can "eavesdrop" the mix of chemicals exuded by other plants and respond with changes in root architecture and growth (Biedrzycki et al., 2010; Semchenko et al., 2014; Kong et al., 2018; Yang et al., 2018). Exudate gradients in the soil may thus offer information on the closeness of neighbouring plants as well as their physiological health, allowing roots to precisely avoid neighbouring roots (Fang et al., 2013). Among roots exudates, SLs are a kind of phytohormones that is secreted into the soil and has a wide signalling role in the rhizosphere, including encouraging mycorrhizal association formation (Waters et al., 2017). Because SLs substantially affect plant development, they are logical candidates for acting as plant-plant signals. Recently, Wheeldon and colleagues (2022) demonstrated the role of SLs in neighbour detection and plant communication.

2.4.3 Competition and cooperation in plants

The majority of plants live in social groupings, where neighbours compete for above- and below-ground resources (Biernaskie, 2010).

Plant-plant competition is the most common interaction in plant communities (Connell, 1983). For decades, the ecological literature has detailed patterns, mechanism ideas, and theoretical breakthroughs in this subject (Tilman, 1982; Casper & Jackson, 1997; Craine, 2006; Brooker & Kikvidze, 2008). However, advances in areas such as root foraging mechanisms and the interaction of facilitation and competition demonstrate that the processes involved in plant-plant competition are more complicated than previously imagined (Rajaniemi, 2007; Chu et al. 2008). The increasing interest in the genetic drivers of intraspecific competition (Falik et al., 2006; Boyden et al., 2008; Crutsinger et al., 2008; Hughes et al., 2008) is an example of this. In this regard, a recent study found that annual plants *Cakile edentula* can recognize kin in competitive situations and, more crucially, respond by competing less aggressively against a near relative (Dudley & File, 2007). Root biomass, a proxy of below-ground competitive capacity, was lower in individuals grown in pots with close relatives than in individuals grown in the presence of strangers (Dudley & File, 2007). The experiment’s implication is that kin identification and the accompanying reduction in root growth enhance the development of relatives living nearby.

Recognition of kin and kin selection are long-standing themes in animal evolution, with well-known behavioural and chemical processes for individual recognition (Griffin & West, 2002; Tibbetts & Dale, 2007). Individual identification systems in plants, on the other hand, are less than intuitive and have received little research (Callaway & Mahall, 2007).

Chemical processes occurring in kin recognition, are also at work during competitive interactions among plants, in which substances are emitted to *fight* chemically the neighbour (Kong et al., 2018).

Allelopathy is traditionally characterized as the release of substances that inhibit the growth, development, survival, and reproduction of rivals. I can define it an indirect aggressive behaviour, to retake the different type of competition among animals reported in the previous paragraphs. In plants, allelopathic compounds are exuded into the rhizosphere (Kato-Noguchi et al., 2010; Kong et al., 2018), emitted aboveground as VOCs (Kong et al., 2004) or deposited in pollen (Roshchina et al., 2009). Allelochemicals differ in their route of absorption and mechanism of action, and their efficacy may differ depending on spatiotemporal parameters such as activation (Rice, 2012; Weston & Duke, 2003; Gaofeng et al., 2018; He et al., 2019) and dosage (Fang et al., 2013). They may function as signals to neighbouring plants (rather than toxins) at lower concentrations, or they may detect obstacles in soil, triggering root navigation (Falik et al., 2005; Semchenko et al., 2008; Fang et al., 2013; Agathokleous & Calabrese, 2019). However, other allelochemicals produced at higher concentration have been proposed to act indirectly on rivals by inhibiting nutrient absorption or modifying soil microbiome composition (Zeng, 2014). Furthermore, allelopathy may only be produced at specific developmental periods when it is most beneficial, such as seedling establishment (Kong et al., 2018). This may provide plants with an early competitive edge over neighbours that may be sustained without the production of allelochemicals; hence, the costs of allelopathy may only be temporary (Bilas et al., 2021).

For what concerns cooperative aspects among plants, several examples can give an overview of this peculiar behaviour. In morphological terms, a plant may collaborate with its neighbours by limiting its growth to avoid competition (Semchenko et al., 2010; Wang et al., 2020).

Plants are projected to downregulate root or shoot development in the presence of related conspecifics in cooperative and altruistic social responses, which may eventually boost the reproductive success of both individuals (Dudley, 2015).

Plants may even demonstrate basic indicators of parental activities in some circumstances (Castiello, 2021). *Volvox carteri*, a multicellular green alga, for example, produces little daughter colonies that are eventually freed from the parent as they grow. Simard et al. (1997), whose study indicates that trees can exchange information, convey their requirements, and transport nutrients to one another via a network of latticed fungus buried in the soil, have considerably added to our knowledge of how plants collaborate and aid one another. The mycorrhizal network, which connects tree root systems and exchanges nutrients, carbon, and water, is primarily responsible for this. The researchers set out to investigate the relationship between *Betula papyrifera* Paper birch and *Pseudotsuga menziesii* Douglas fir in ancient forest ecosystems in Canada. They discovered that the two species of trees compete with one another, but they also collaborate by exchanging nutrients and carbon via their mycorrhizal networks (Simard et al., 1997). The researchers devised an experiment that demonstrated that the trees were aware when one of them needed assistance and gladly provided it (Simard et al., 1997; Simard, 2009). Their research found that as the Douglas fir grew shaded in the summer, its surplus carbon was passed on to the birch. Then, in the fall, when the birch was shedding its leaves and the fir had additional carbon from photosynthesizing, it reciprocated. Mycorrhizal networks appear to be the key to this interaction in evolutionary terms, as they direct carbon transfer to ensure that they and other members of the community acquire the food that they require. Molecular techniques have also been employed to investigate another curious phenomenon known as *"mother trees"* (Beiler et al., 2010). Researchers were able to identify the mycorrhizal fungal networks joining Douglas fir trees in a natural forest by analysing short sequences of DNA (Beiler et al., 2010). With a few exceptions, their examination revealed that all of the trees were related. Importantly, the network's tallest and oldest trees had the most established root systems and mycorrhizal networks. They also had more carbon going into the network, more root tips, and were more linked to the other plants in their vicinity.

Even more shockingly, they were able to recognize and favour family members (Castiello, 2021). According to recent research, mycorrhiza-mediated nitrogen transfer between trees can also aid in the survival of tree remains (Bader & Leuzinger, 2019). When Bader and Leuzinger (2019) set out to investigate how nearby trees could keep a tree stump alive, they measured the water flow in the stump and the surrounding trees of the same species and discovered that the water movement in the stump was negatively correlated with that in the other trees, implying that the stump's roots were grafted to those of the surrounding trees. Root grafts can occur across genetically dissimilar trees if they are similar enough to allow for resource exchange. Normally, trees do not act in this manner because water flow is determined by the water potential of the atmosphere. In this situation, the stump must mimic what the other trees are doing. But, whereas root grafts between living trees of the same species are typical, why would a thriving kauri tree seek to keep a neighbouring stump alive? The benefits to the stump are obvious: It would be dead without the grafts because it lacks green tissue. But why would the host trees continue to support the worthless stump? What do they stand to gain? The researchers proposed that the graftage originated before the tree lost its leaves and became a stump (Bader & Leuzinger, 2019). The larger root system improves access to resources such as water and nutrients while also increasing stability on a steep forest slope. Because one of the trees' failure to provide carbohydrates may have gone overlooked, the old stump lives on by its relationship to other surviving trees. This has far-reaching implications for our view of trees, as it appears that we are dealing with the forest as a superorganism rather than individual trees. During a drought, for example, trees with limited water availability may be linked to others with more access; sharing limited resources boosts their chances of survival (Castiello, 2021). These findings all hint to a subterranean, unseen "wood-wide web" (Sen, 2000) that supports the social life of tree and other plant groups. More than two centuries ago, explorer-naturalist von Humboldt coined the phrase *"socially organized plant life"* and we are just now becoming aware of its various ramifications (von Humboldt & Bonpland, 1807). It is now time to consider what kind of unit should be used to investigate social vegetation and how it may be classified and distinguished from other living communities (Castiello, 2021).

2.4.4 Communication and language in plants

Plants, as previously stated, may communicate both below and above ground via their root systems and mychorizzal networks (Simard et al., 1997; Heil, 2014; Gagliano & Gimnoprez, 2015; Karban, 2015; Trewavas, 2016).

Above ground, the most efficient and complex mechanism plants use to communicate is via VOCs, a chemical "language" that *"conveys multiple meanings depending on the intended recipients"* (Gagliano & Gimnoprez, 2015). As previously stated, plants can communicate using VOCs for a variety of reasons, including responding to predator attacks (Dicke & Sabelis, 1988; Turlings et al., 1990; De Moraes et al., 2001, War et al., 2012), attracting pollinators (War et al., 2012), exchanging useful information (Dudareva & Pichersky, 2000), and adapting to environmental stress (Baldwin et al., 2006). Among their various activities, VOCs appear to play a key role in mediating plant interactions with other organisms both above and below ground. Although these delicate odours are more relevant and effective among relatives (Karban et al., 2013), stranger plants appear to want to "eavesdrop" and utilize the knowledge gathered to perform tactical reactions favourable to their own survival (Pare & Tumlinson, 1999; Karban et al., 2006; Heil & Ton, 2008).

All plants emit their assimilated carbon into the atmosphere in the form of VOCs, which include alkanes, alkenes, alcohols, aldehydes, eters, esters and carboxylic acids (Penuelas & Llusià, 2004).

Terpenoids, the most diversified of these families of chemicals, have an integral number of 5-carbon units that are shared by all plants and are engaged in internal and external communication as well as plant defense (Bonato et al., 2021). Terpenoids are released in reaction to internal and external variables, and the information or effects of these terpenoids are sensed by other portions of the plant, as well as other plants, animals, and/or microbes (Penuelas et al., 1995). Some plant terpenoids are key chemical agents in plant communication because they play a function in mediating a variety of ecological interactions (Dicke & Sabelis, 1988). Importantly, in terms of ecology and biology, the concentration of terpenoids changes depending on the sort of message to be delivered. Terpenoids, for example, attract insects only when low amounts are released and become more repellent to pollinators at increasing concentrations (Harborne, 1991).

Plants may synthesize a wide range of volatile chemical compounds by combining these fundamental 5-carbon units in various combinations. The sequential combination of its fundamental 5-carbon units can result in an astounding array of structures, or terpenoid "words" (Penuelas et al., 1995). Some terpenoid "words" are found in all plants. If we analyse what terpenoids release under different environmental scenarios, such as danger associated with a sudden drought, we may be able to codify the terpenoids utilized to produce a specific message. In other words, if we understand the significance of a certain terpenoid and how it interacts with other "chemical units" we may be able to understand how a complete message works (Bonato et al., 2021).

To present, it is known that a vast variety of VOCs triggered by multiple biotic and abiotic sources allows plants to employ their chemical language to efficiently convey information. Holopainen (2004), for example, highlighted the fact that plant language has real combinatorial flexibility, which means that new meanings may be attributed to old chemical terms and employed in new settings, resulting in fresh interactions. Inducible VOCs are employed in plant-to-plant signalling, pathogen defence, and ozone quenching, in addition to attracting natural enemies of herbivores, as well as tropospheric ozone and fine-particle aerosol formation. In evolutionary terms, the inventory and the various combinations of chemical utterances were enhanced with meaning and passed down through generations exactly via usage and experience in a range of settings (Gagliano & Gimnoprez, 2015).

A crucial question arises: how do plants interpret these combinations? The symbolic units at the heart of meaning-making activity in humans are related to the social context, and the meaning attribution of phenomenal experiences is dependent on the agents' interactions with an ever-changing environment (Senghas, 1995; Thibault, 2011). Plant communication appears to be similarly context dependent (Bonato et al., 2021).

One of plants' meaning-making activities is the capacity to recognize and decode molecular combinations holding a meaning vital to their existence, while rejecting "non-meaningful" ones such as those associated with pollution, animal exhalation, and manufactured substances (Bonato et al., 2021). Orchids are a good illustration of this process: some orchid species (*Epipactis helleborine* and *Epipactis purpurata*) generate a spectrum of VOCs comparable to those emitted by other plants when pleading for help during a predatory attack by insects like caterpillars (Whitman & Eller, 1990; Brodmann et al., 2008). This chemical resemblance comprises a variety of volatiles, including six-carbon aldehydes, alcohols, acetates, and other VOCs, which are typically released by herbivore-infested green plants (Whitman & Eller, 1990). It has been shown that some orchid species produce these unique volatile substances in the absence of herbivore assaults in order to attract prey-hunting social wasps for pollination. Furthermore, another orchid species (*Dendrobium sinense*) mimics honeybee alarm pheromone to attract wasps and hornets for pollinating (Broadmann et al., 2008).

The two instances above demonstrate that plants may imitate chemical signals, employing a "chemical sign" to attract an insect of interest. Logically, this meaning-making activity is not based on representations of an idea because we are dealing with brainless systems that are incapable of creating cognitive representations; rather, it is the product of the plant's interaction with its environment. It is based on an engagement with and attunement to the organism of interest in the instance of the orchid. A process of evolution moulding the trait across species and evolving the ability to employ meanings in multiple ways appears to be at work here (Bonato et al., 2021). Language, as Tomasello (2008) pointed out, is formed by its social and cultural environment. In reality, the usage and development of signals are determined by certain environmental and social situations. To clarify, for example dialect is defined as a variant of a language spoken by a specific group of people who share the same ecological niche.

Meanwhile, botanists have been researching the number and variety of terpenoid chemicals generated and utilised by plants. It is not unexpected that there are large qualitative and quantitative changes in the chemical makeup of volatiles, just as there are in the chemical composition of plants (Takabayashi et al., 1994). Takabayashi and colleagues (1994) investigated differences in the combinations and structures of terpenoids that appear to be family specific. The ratio of different constituents in the emitted mixtures seems to have important ecological implications (Langenheim, 1994). Some terpenoid mixtures may, for example, minimize the resistance of herbivores and hence delay plant defence (Pimentel & Bellotti, 1976; Schultz, 1983; Jones & Firn, 1991) while others increase the potential for attracting pollinators (Bergstrom et al., 1991).

Terpenoids are released in response to both internal (genetic and metabolic) and exterior (ecological) variables, and their effects appear to be dosage dependent (Langenheim, 1994). They also differ qualitatively and quantitatively within the same species (Langenheim, 1994; Takabayashi et al., 1994). Orchids pollinated by euglossine bees are an example of this. More than 50 different volatile chemicals released by orchids have been found to date; each species of orchid has a unique mix, and the connections between bees and orchids are frequently quite particular (Dodson et al., 1969).

Previously allelopathy was mentioned to refer a chemical competition among plants. Here, I retake a similar concept. Synomons are allelochemicals that are adaptable to both the transmitter and the receiver (Dicke & Sabelis, 1988). Herbivore-induced plant volatiles (HIPVs from now on) are scents generated by attacked plants that serve as key indications for herbivorous insect predators to identify their prey (Vet & Dicke, 1992). Terpenoids are found in several volatile synomones (Dicke et al., 1990; Turlings et al., 1990). Each plant species and cultivar develop its own distinct mix of synomones caused by herbivores, which implies that predators encounter a variety of synomones depending on the host's diversity (Takabayashi et al., 1994).

Fascinating research assessing population-specific VOC emissions was recently devised and carried out (Karban et al., 2006). Based on the assumption that plants respond to volatile cues emitted by damaged neighbours in order to increase their defence against herbivores, some researchers attempted to determine whether plant communication is more effective with local versus distant neighbours (Karban et al., 2006). For example, several researchers discovered that sagebrush tissues increased their resistance to herbivory by responding to volatile signals emitted by experimentally wounded neighbouring plants (Karban et al. 2006, Shiojiri & Karban, 2008).

Branches incubated with the volatile signals of cut neighbours had less chewing damage than branches treated with ambient air. When the researchers examined the injured plants, they discovered that sagebrush branches responded more effectively to messages from nearby plants from the same population than plants growing 230 kilometres distant. This population-specific effect was evident in both of the trial sites, indicating that signals' efficiency varies locally and implying that sagebrush responds more strongly to local dialects than to foreign languages. Following leaf damage, individuals of the same chemotype communicated more effectively than individuals of different chemotypes (Karban et al., 2014; Moreira et al., 2016). These findings appear to show that chemotypes might be regarded examples of relatedness-based language distinctions, implying that language is influenced by the environment in which it is used and evolves (Tomasello, 2008).

Overall, these findings indicate that plants indeed communicate using population-specific "dialects" and that certain variances in language are connected to their relatedness. Plant communication is a difficult scientific issue being studied by armies of scientists from biology and neurobiology, botany and cognitive sciences, agricultural science, plant physiology, evolutionary biology, chemistry, and even psychology. These researchers are submitting findings on the informative value of volatile signals used by plants to communicate. In this thesis, I will offer the first attempt to link a communicative "word", commonly exudated by the roots, as a behavioural information to implement an adaptive movement in climbing plants acting in social situations.

Chapter 3

The movement of plants: A window to their cognition

> *"It has often been vaguely asserted that plants are distinguished from animals by not having the power of movement. It should rather be said that plants acquire and display this power only when it is of some advantage to them…"*
>
> *Darwin,1875*

3.1 Characterizing plants movement

Although plants cannot move from one location to another, they are extremely in tune with their surroundings and are capable of a wide range of movements. Some plant reactions include physical movement and are remarkably animal-like in effect, albeit on a smaller scale (Castiello, 2023). Plants may not move as far or as rapidly as animals, yet they are not immobile. The crucial point here is that certain plant movements serve many of the same functional purposes as animal movements (Huey, 2002).

Many plants and animals, for example, require movement to a new area as part of their life cycle (Croteau, 2010). Dispersal, an ecological process that includes the transfer of an individual (or multiple individuals) away from the population in which they were born to another place or population where they will settle and reproduce, is a common type of such relocation. Active or passive dispersal is possible. The former is found in both adult and juvenile animals and involves the complete organism moving on its own. Passive dispersion is seen in plants and animals that are unable to move and rely on dispersal units known as disseminules to help in reproduction or the exploitation of new surroundings. Many disseminules are designed to move in response to certain dispersion agents such as wind, water, or another animal capable of active dispersal. Invertebrates such as sponges, and corals are examples of sessile adult creatures that use passive dispersion. Their disseminules are often specialized reproductive buds or cells (Croteau, 2010). The most frequent disseminules in plants are seeds, spores, and fruits. They have all been modified to travel away from the parent plant using available ambient kinetic energy. Some disseminules are expelled explosively across short distances, while others fall to the ground near the parent plant's root. Invertebrates, mammals, and birds spread seeds and fruits while feeding and disseminate them in feces following consumption (Croteau, 2010).

Furthermore, certain plants produce sticky seeds or fruits that cling to the feathers or hair of mobile animals. Some plants have reactions that serve the same purpose as animal locomotor adaptations. Plants can successfully select where to dwell by growing toward or away from environmental stresses (Bazzaz, 1991). Neotropical stilt palms (*Socratea exorrhiza*) travel toward light gaps on their stilts (Leopold et al., 2000).

Climbing and clonal plants, for example, can crawl over the environment in search of suitable homes, just like animals do. Indeed, such movements are frequently referred to as “foraging” (Harper, 1977).

Plants may position their leaves and flourishes toward or away from the light, similar to animal orientation movements (Stanton & Galen, 1989). Many plants’ leaves rotate during the day to maintain a perpendicular orientation to the sun’s rays, enhancing photosynthesis (rather than modulating body temperature as lizards do; Ehleringer & Forseth, 1980). Other movements, such as sun tracking by alpine buttercup (*Ranunculus* *adoneus*) flowers, give a heat reward to insect pollinators while also increasing seed set (Stanton & Galen, 1989).

Throughout his eclectic career, Charles Darwin showed a keen interest in plant mobility. Charles Darwin and his son Francis published *"The Power of Movement in Plants"* in 1880, in which they explained how they explored all forms of plant movements in detail by tracing the trajectories of the tips of shoots over time and space. Darwin's studies helped to throw light on plants' ability to see, sense, and respond to their surroundings correctly and adaptively. Darwin distinguished two types of movements: tropism, which is a movement in response to an external factor (e.g., light), and nastic movement, which is dependent on external elements but has independent direction with respect to the stimulus position (e.g., leaf closure during the dark period; Migliaccio et al., 2013). Furthermore, he discovered that all elements of the plant (e.g., stem, tendrils, ...) are in continual motion and tend to spin about their central axis during the growth period. This movement pattern, initially dubbed "rotating nutation" by Julius von Sachs and later renamed circumnutation by Charles Darwin, was characterized as widespread and universal among all plants (Darwin, 1875; Darwin & Darwin, 1880). In the next part, I will go through the tropic movements, the nastic motions, and lastly the universal among plants: the circumnutative movement.

3.2 Type of movements

Commonly, movement refers to locomotion, that is the moving from one place to another, and it is attributed only to animal species, including human beings. However, controlled locomotion is also observed in some organisms such as flagellates and algae. But in most cases plant's movements occur as slow and tiny changes in orientation and size in various organs of plants. Movements is used by plants to deal with a wide range of problems such as finding and reaching an environment that provides adequate level of nutrients or protecting themselves against severe climate changes. In general, plant movement involves the extension or shortening of organs. This mechanism is supported by four independent processes: turgor, growth, hygroscopy, and drying. Turgor refers to variations in cell size that govern the movement of a leaf blade or a reproductive component. Growth refers to changes in the size, shape, and orientation of the entire plant's structure throughout the course of its life. Auxin, a plant hormone that may promote or prevent asymmetrical cell elongation, regulates it in plants. The orientation of the response to external stimulus is determined by the redistribution of auxin (van Overbeek, 1939; Girloy, 2008). Hygroscopy and drying are concerned with a tissue's capacity to absorb or expel water molecules from its surroundings, resulting in a change in cell membrane volume that is dependent on the degree of moisture in the surrounding environment.

Movement in plants is affected by both endogenous and exogenous factors. An endogenous movement is a biological process, such as the circadian rhythms, which lead changes within the plant structure although external conditions remain constant. Exogenous movements are responses which are elicited by external elements such as the light. In general, movements are classified in two main classes namely nastic and tropic movements which refer to the directionality of the response to both endogenous and exogenous cues. In the next section, these movements will be described in detail.

3.2.1 Tropic movements

Plants are sessile creatures that have evolved outstanding adaptation techniques to meet the difficulties of their environment. Plants, for example, must explore their surroundings in search of nutrients and water, as well as adapt well to herbivory and disease assaults. To deal with these difficult demands, plants must be able to code and interpret external information, as well as direct and manage their development toward an external stimulus in order to increase their chances of survival (Mancuso & Viola, 2013). Tropism refers to how plants respond to environmental stimuli. The tropism might be named phototropism (i.e., light), heliotropism (i.e., sun), gravitropism (i.e., gravity), tigmotropism (i.e., touch and contacts), or hydrotropism (i.e., water) depending on the environmental factor to which the response is directed.

Phototropism is defined as the tendency of plants to grow toward the light source, which can be classified as positively (bending of the plant's organ towards the light source) or negatively (bending of the plant's organ away from the light source) phototropic responses (van Overbeek, 1939). The tropic response is evoked by blue light and is mediated by specialized photoreceptor proteins (i.e., phototropins), which allow plants to distinguish between different wavelengths of light (Girloy, 2008).

To test this, Darwin and his son Francis (1880) observed the behaviour of the canary grass (*Phalaris Canariensis*) in five different experimental conditions: (a) a plant exposed to a light source; (b) a plant exposed to a light source, but the below part of the stem was covered by a tube; (c) the shoot apex of a plant was removed; (d) the shoot apex of a plant was covered by a clear cap; (e) the shoot apex of a plant was covered by a cap preventing the access to light. Darwin observed that all plants with the apex accessing light showed phototropism (i.e., ‘a’, ‘b’, and ‘d’ conditions), while when the apex was removed (i.e., ‘c’ condition) or covered (i.e., ‘e’ condition) the plant remained still. Results suggested that the sensory apparatus, that drives the tropic growth, may be located within the apex of a plant.

Heliotropism is a sort of tropism that regulates the coordination of the optimum strategy for growing towards the light (in natural surroundings, the sun). The complicated interplay between light, temperature, and the circadian clock governs the elongation and development of plant organs (Nozue et al., 2007; Muller et al., 2014). The ideal technique for capturing a large amount of light is to coordinate both the circadian clock and directional growth. In general, both phototropism and heliotropism, or solar tracking, govern this process. The sunflower (*Helianthus annuus*) is the most well-known example of heliotropic movement. The shoot apices shift from east to west during the day and then reorient at night to east in anticipation of the dawn (Atamian et al., 2016).

Gravity is another environmental component that plants employ to regulate their growth (Knight, 1806). Gravitropism is a gravity-directed growth process that directs the growth of the root system in the soil to achieve nutrients and water (Morita & Tasaka, 2004; Morita, 2010; Hashiguchi et al., 2013; Toyota & Gilroy, 2013; Su et al., 2017). Moving a plant from the vertical to the horizontal plane, for example, will result in a reorientation of the leaves upward toward the light source within a few hours (Knight, 1806).

Light and water are the two most crucial components for plant life. Indeed, one of the root system's most critical roles is to detect water gradients and utilize this information to direct root development toward the richest regions. This movement toward the water source is known as hydrotropism, and the hormone auxin may be a possibility underpinning this tropic response. Studies on the mechanism behind hydrotropic sensing yielded contradictory results from the ongoing impacts of gravity on plant development (Takahashi et al., 2002; Dietrich, 2018). To deal with this problem, mutant plants (e.g., *Arabidopsis thaliana* or *P. sativum* mutants), which are neither gravitropic nor phototropic, but do respond to a humidity gradient, have been used (Jaffe et al., 1985; Mizuno et al., 2002; Takahashi et al., 2002; Takahashi et al., 2003). Research on the root of mutant *P. sativum "Ageotropum"* revealed that when the root cap was removed, the hydrotropism response was impaired but not the root elongation. These findings confirmed the root cap's function in sensing and coding moisture gradients (Hooker, 1915; Dietrich, 2018). However, more research is needed to better understand hydrotropism, the mechanism behind it, and how it affects water intake and drought responses in plants.

Finally, thigmotropism refers to the stimulation of roots, stems, or leaves when touched (Darwin, 1875). Morphological changes induced by touch stimulation involve a plethora of inter and intracellular signalling components, including hormones and potential additional messengers (e.g., intracellular calcium – Ca^{2+}; Batiza et al., 1996; Calaghan & White, 1999), and play a variety of important roles in survival. Climbing plants, for example, use the thigmotropic response of tendrils (i.e., modified leaves) or the stem to secure their hold on a possible support and climb it to acquire a vertical height and enhance the greatest light exposure (Braam, 2005). To avoid self-pollination, many flowers have evolved touch-sensitive parts (e.g., petals and pistils). In this sense, some flowers, for example, include spring-loaded systems that cause explosive reactions to disseminate seeds far away from the *"mother"* (Simons, 1992).

3.2.2 Nastic movements

Nastic motions are characterized as responses to environmental stimuli whose direction is independent of the stimulus position. External stimuli that cause the nastic reaction include (i) temperature (thermonasty); (ii) light (photonasty); and (iii) mechanical stimulation (seismonasty). The thermonasty develops in plant organs as the temperature changes. An example may be the early blossoming of flowers in a hot climate. Photonasty is dependent on light fluctuation, which causes the leaves to open or close during the day/night cycle. Seismonasty is caused by mechanical stimulation, and some of the most fascinating nastic motions in plants involve the closure of the leaf of the *Dionea Muscipula* plant, which Charles and Francis Darwin (1888) described as *"one of the most wonderful plants in the world." Dionea muscipula* is a carnivorous plant with two leaves and needle-like tines on the leaf edges. When an insect bumps into the bi-lobed leaves and repeatedly touches the small hairs within the leaves, intercellular electrical signals are generated, causing the leaves to close and trap the prey (Fig. 3.1.; Burdon-Sanderson, 1873; Jacobs, 1954; Jacobson, 1965; Simons, 1981). Another intriguing nastic action is the quick closure of *Mimosa pudica* leaves when they are touched by an external element deemed hazardous by the plant. Mechanical stimulation causes an electric signal to be generated in the touched leaf, which spreads to the cells of pulvini, which are specialized motor organs located at the bases of the leaflets and petioles, causing a variation in turgor pressure and causing the leaves to close (Simons, 1981; Malone, 1994).

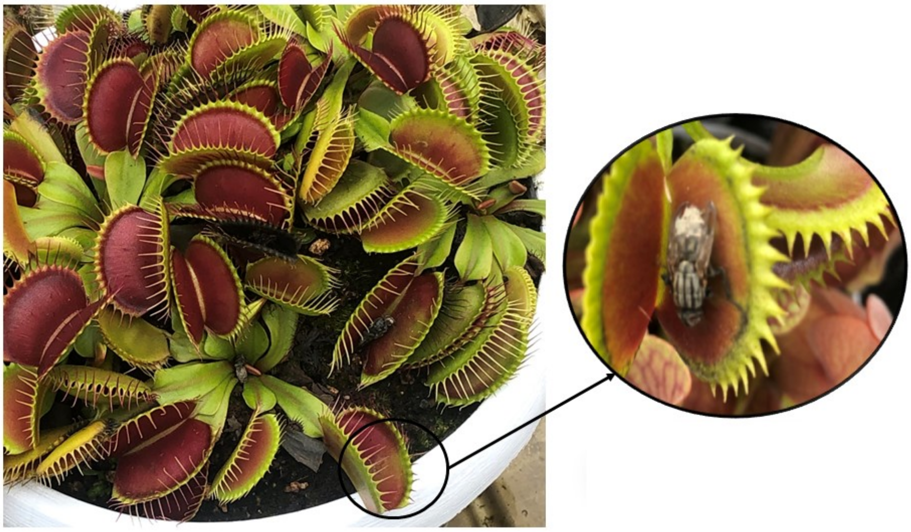

Figure 3.1. Photograph showing the *Dionea muscipula* plant which can catch insects by closing its bi-lobed leaves once the prey touches the small hairs into the leaves several times.

3.2.3 Circumnutative movements

The most widely prevalent movement among plants is the rotatory movement performed by many parts of the plants *"which bends successively to all points of the compass, so that the tip revolves"* (Darwin, 1875). This movement is called circumnutation and Darwin (1875) described its shape with these words: *"If the movement had been quite regular, the apex would have described a circle, or rather, as the stem is always growing upwards, a circular spiral. But it generally describes irregular elliptical or oval figures".*

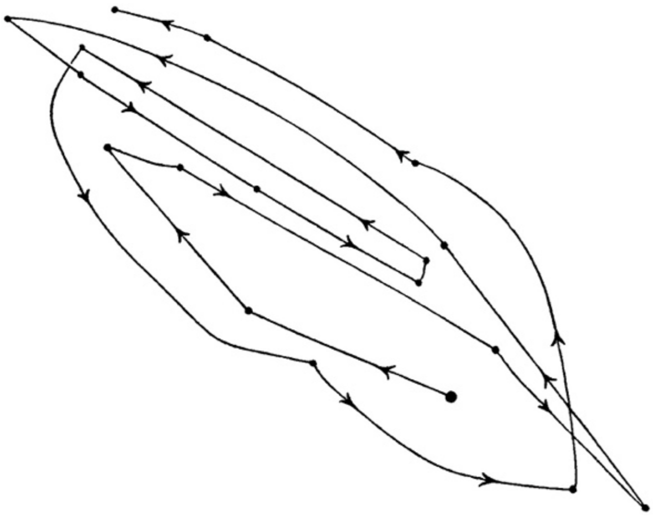

Figure 3.2. Graphical representation of the trajectory of the circumnutation movement of the shoot of the *Brasicca Oleracea* along 10 hours and 45 minutes. (From Darwin & Darwin, 1880).

Darwin demonstrated circumnutations in a variety of plant species and asserted that all other movements, such as geotropism or sleep motions, are variations on the basic circumnutation movement. The research of French physiologists such as Baillaud (1952), who showed circumnutations in various plant species and defined their trajectories (shapes and direction) and temporal features, contained descriptions of several species. There are well-known circumnutations of tendrils and roots in *P. Sativum*, tendrils in *Passiflora* and *Sicyos*, coleoptiles of rye (*Triticum*) and oats (*Avena*; Johnsson, 1973), shoots of beans (*Phaseolus*) and Cuscuta, Ipomoea, Carthamus (Johnsson, 1979), hypocotyls in *Helianthus annuus*, tulip (*Tulipa*) petiole (Hejnowicz & Sievers, 1995) and circumnutations in *Arabidopsis thaliana* (Schuster & Engelmann, 1997). Circumnutations are notable for being typical of young, developing regions of plant organs, in addition to their prevalence (Stolarz, 2009). The ubiquitous presence of circumnutations and their distinct differentiation imply a wide range of plant activity under a variety of environmental situations.

The Darwins initially noticed that circumnutation features (such as movement direction, amplitude, and so on) differed between ages and species. Indeed, as circumnutation may be halted for several hours, the plant's development may be characterized by vigorous or no oscillations. The circular movement might be clockwise or counterclockwise, and it could occur on the same or separate days.

For example, the circumunutation of *Arabidopsis thaliana* shoots is frequently clockwise (Schuster & Engelmann, 1997), but *Phasoleus vulgaris* shoots are counterclockwise (Millet et al., 1988). Then, touch and geotropic stimulation can cause a change in rotation direction (Okada & Shimura, 1990; Stolarz et al., 2003). The number of rotations around the plant's central axis varies across species. For example, the *Brassica oleracea* plant (Fig. 3.2.) is employed to execute four rotations in twelve hours, but the *Opuntia basilaris* plant accomplishes one cycle in the same time period. Furthermore, Darwin noticed differences also within the same plants during the growth phase. Indeed, in most seedling the circular movement was smaller and faster since the complete development of the first leaves. Furthermore, the amplitude of circumnutation varies between plant species and is unrelated to the length of the circumnutating plants' organs, but rather to the presence of various external stimuli (e.g., gravity; Brown et al., 1990; Millet et al., 1996).

Furthermore, the duration of circumnutation can range from a few minutes to several hours, depending on morphological characteristics, ambient circumstances (e.g., temperatures, light/dark period, ...), and components (e.g., gravity, chemical elements, ...; Johnsson et al., 1979). The nature of the process behind circumnutation has been discussed since Darwin's discovery (Darwin & Darwin, 1880). So far, three major theories have been proposed: endogenous origin, earth gravity, and combined endogenous and exogenous processes (Kiss, 2006; Mugnai et al., 2007; Stolarz, 2009). According to the first model, the driving and regulating mechanism of circumnutation movement is internal to the plant, which can adjust this process to its benefit (Darwin & Darwin, 1880).

Different hypotheses have been advanced to explain the endogenous nature of circumnutation: (i) a periodic variation in auxin fluxes from the tip (Arnal, 1953); (ii) changing in sensitiveness of elongating cell to auxin (Joerrens, 1959); (iii) each plant cell has an internal "*cellular nutational oscillator*" (Heathcote & Aston, 1970); (iv) the existence of an intrinsic oscillator given the great correlation founded between circumnutation movement and the rhythmical patterns of ion fluxen in corn's roots (*Zea mays* L.; Shabala & Newman, 1997; Shabala, 2003). In the second model, circumnutation movement is generated by the presence of an external stimulus as the gravity of the earth (Kiss, 2006; Kitazawa et al., 2005). In keeping with this viewpoint, Israelsson and Johnsson (1967) proposed a gravity-dependent model to explain the nature of plant circular nutation. They thought of circumnutation as gravity-driven, with oscillations understood as ongoing over-compensatory reactions to the changing orientation of plant organs with regard to the location of the Earth's gravity vector. According to this viewpoint, circumnutation is a type of tropic behaviour. Experiments in microgravity conditions, on the other hand, proved that gravitropism and circular nutation are distinct processes. Indeed, gravity does not appear to be a crucial component of the process driving the circumnutation of developing roots (Paul et al., 2012).

According to the third hypothesis, circumnutation is caused by both endogenous and external influences (Johnson, 1979; Johnsson, et al., 1979; Johnsson et al., 1999). The circular oscillations are produced internally by the plants; however, they may be influenced by gravity (Britz & Galston, 1982; Orbovic & Poff, 1997). Yoshihara and Iino

(2005; 2006) proposed a probable link between gravitropism and circular nutation movement. They proved that the gravitropic response altered the circular oscillations of rice (*Oryza sativa*) coleoptiles even when gravitropism was not engaged in the circumnutation process.

But what role does circumnutation play in the life of a plant? It has been proposed that circumnutation is employed by plants to investigate their environment in order to locate items needed for survival, such as a support, as in the case of climbing plants. Otherwise, the plant may employ circular motions of the main root (or radicle) to enter the earth during the elongation phase (Darwin & Darwin, 1880; Inoue et al., 1999; Minorsky, 2003; Schuster & Engelmann, 1997).

3.3 Kinematics to study plants movement

Charles Darwin (1880) was the first to explain in full the movement of plants by tracing the variations in location of the shoot apex across time and space in a variety of plants. This represents the first instance of kinematical research on plant nutation. Since then, several studies on different kinematical aspect (e.g., oscillatory shapes and directions, amplitude, period, …) of nutation's movements in different plant's organs (e.g., the root system, shoot, apex, …) have been conducted by means of time-lapse images and video processing to extract nutation-related features (Brown, 1993; Calvo et al., 2017; Guerra et al., 2019; Migliaccio et al., 2013; Millet et al., 1988; Mugnai et al., 2015; Raja et al., 2020; Stolarz, 2009). The fundamental aspect of this approach is that it tracks the movement of each recorded point of interest. The extraction and analysis of nutation-related features of various plant organs leads to research into the underlying mechanisms of such movements, such as internal oscillators, gravitation-driven mechanisms, or a combination of the two (Brown, 1993; Johnsson & Israelsson, 1968; Stolarz, 2009). In this regard, the development of innovative approaches targeted at analysing the movement of both above and belowground plant organs would be beneficial for researching and comprehending the range of behaviours displayed by plants. For example, kinematical examination of movement of belowground organs such as the root system allows for the study of spatiotemporal patterns of root development and curvature. A variety of tools have been developed to this task such as the KineRoot (i.e., Basu et al., 2007), the SimRoot (i.e., Lynch et al., 1996), the RootTrace (i.e., French et al., 2008; French et al., 2009) and the analyser for root tip tracks (i.e., ARTT; Russino et al., 2013). For instance, ARTT, which allows for the extraction of kinematical aspects of root tip movement from sampling tip locations via the capture of a sequence of photos during plant growth. The software then generates a graphical output of tracks as well as a textual output of kinematical properties that may be utilized for statistical analysis. This program enables the investigation of plant-root behaviour and kinematics within and between plant species such as *Zea mays* and *Oryza sativa* (Russino et al., 2013).

New studies on the three-dimensional (3D) reconstruction of plant-root architecture have recently proposed new methods for quantifying the growth process (e.g., Clark et al., 2011; Fang et al., 2012). However, these investigations are primarily concerned with the architectural and phenotypical assessments of the root system, leaving out the kinematical element entirely.

For what concern the analysis of the movement of the aboveground plant's organs such as the apex and the stem, Stolarz and colleagues (2014) implemented a software for plant circumnutation two-dimensional (2D) analysis (i.e., Circumnutation Tracker) which allows for the manual extraction of the kinematical parameters of the circumnutation movement by means of the analysis of time-lapse videos of the plant from a top view (Stolarz et al., 2014). The Circumnutation Tracker software has some limitations, including (i) manually extraction of the point's coordinates by users, which can be susceptible to mistakes and tedious; (ii) the top view position of the cameras, which determines constraints on camera standpoint; and (iii) a 2D trajectory analysis, which precludes keeping track of movements in additional directions. Along these lines, other research attempted to address the aforementioned limits by including side view contextual acquisition (e.g., Hatakeda et al., 2003; Kosuge et al., 2013; Schuster & Engelmann, 1997). They examined automating the circumnutation analysis procedure (Stolarz et al., 2014) or implementing a potential approach for 3D reconstruction of plant movement (Johnson et al., 2009). Indeed, the development of software that takes into account the geometrical and local effect in 3D space of the dynamic growth of all plant organs, as well as allowing for the extraction of 3D kinematical features of plant movement, would be beneficial to better understanding the variety of plant behaviour and providing a full reconstruction of them (Bastien & Meroz, 2016; Gallentine et al., 2020; Porat et al., 2020).

Raja and colleagues (2021) created a one-dimensional (1D) program based on nonlinear approaches for analysing plant nutation dynamics. This technique, which is primarily focused on the temporal dependencies that characterize the circumnutation pattern, may give additional information for the description and analysis of plant nutation in addition to the kinematical ones. For example, it provides assessments of biological and behavioural dynamics such harmonicity, predictability, and complexity (e.g., Costa et al., 2005; Mottet & Bootsma, 1999).

Recently, a program for the study of plant movement has been built, enabling for the harvest and exaction of circumnutation parameters in 3D (Fig. 3.3.; Simonetti et al., 2021). This program enables the study of plant movement and behaviour using methods similar to those used to research the kinematic aspects of movement in several animal species (Castiello, 2005; Sartori et al., 2013; 2014). A stereovision system enables the capture of images of plant movement using a pair of fixed calibrated infrared cameras, as well as the creation of time-lapse recordings of such motions. Then, a semi-automatic tracking algorithm analyses plant motions and reconstructs the 3D model of the movement. This system has been developed in our laboratory and it has been utilized for the studies described in the present thesis to investigate the flexible adaptivity of approach-to-grasp movement in *P. sativum* (Chapters 4, 5, 6, 7 and 8) in different social contexts.

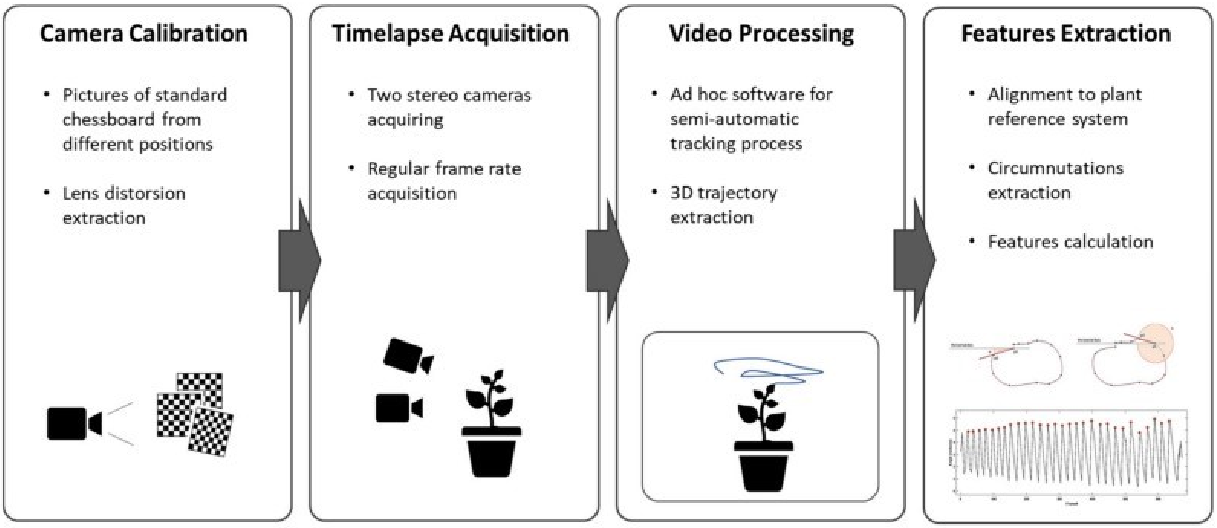

Figure 3.3. Sequence of the step for the 3D reconstruction and processing of the movement of the plant developed by Simonetti and colleagues (2021). (From Simonetti et al., 2021)

3.4 The flexible and goal-directed actions in climbing plants: kinematical studies

Darwin was enthralled by climbing plants’ capacity to develop and adapt their behaviour to an ever-changing environment in order to enhance their chances of survival. Climbing plants are not self-sustaining, thus they must locate a potential element in their surroundings to grow vertically in order to reach the light (Fig. 3.4.).

Figure 3.4. Photograph showing *Phaseolus vulgaris* plant climbing and twining around a support to grow vertically towards the light.

Climbing plants were treated by Charles Darwin in the book entitled *“The movements and habits of climbing plants”* (1875). Darwin was struck by the circular movement of the climbers’ stem, which bends from one side to the other in search of a suitable support to climb and, once found, begins to coil and develop spirally around the support (Darwin, 1875; Palm, 1827). When Darwin (1875) conducted climbing plant studies, he observed that vines could detect supports and lean towards them; yet, when the support was seen to be extremely thick or smooth, the vines leaned away from it. His reports, albeit anecdotal, support the hypothesis that climbing plants can adjust their circumnutation patterns to “anticipate” some properties of the desired support.

Recent, advances in the methods and approaches for studying plants movements have led to new discoveries shedding further light on what Charles Darwin initially noticed intuitively.

As stated in the preceding section, kinematic analysis is used in psychological research to better analyse the components of motion. Indeed, investigating movement in humans and other animal species enables researchers to shed insight on the planning and on-line control processes underlying the unfolding of an action. It is well known that the processes transforming the perceptual features of objects into suitable motor patterns for grasping is a hallmark of intelligence (Wilson, 1999). When a hand meets an object, the overlapping worlds of sensorimotor and cognitive functions connect (Castiello, 2005).

Plants, of course, do not have hands. Nonetheless, the fluid movements of tendrils when searching for a potential support are intriguing. Something about that movement reminds to of the coordinated hand-reaching movements used to prepare to grasp an object (Fig. 3.5). Plant tips or tendrils naturally travel slowly in a helical fashion to reach a support (i.e., circumnutation; Darwin, 1875), whereas hands/arms move fast in a more linear form. Nonetheless, some motor control principles appear to be relatively similar (Castiello, 2023).

Figure 3.5. Photograph of *P. sativum* plant grasping a potential support by means of the tendrils (i.e., modified leaves that allow pea plant to grasp a support), and resembling the coordinated hand-arm movements preparing to grasp an object.

Approaching the study of climbing plant movements from a psychological and cognitive standpoint, studying the kinematic characteristics of the movement to better understand the adaptability and active transformation of these movements in an ever-changing environment is promising of new discoveries.

Classic paradigms were recently applied to explore motor cognition in pea plants. First, it was investigated whether plants changed their circumnutation pattern and tendril aperture based on the thickness of potential supports (Guerra et al., 2019; 2021; 2022; Wang et al., 2023). The plants' kinematic scaling, which was dependent on the thickness of the supports, resembling to what found in humans, non-human primates, rats, and, in birds seeking to grip with its beak (Klein et al., 1985; Whishaw, 1996; Sustaita et al., 2013; Castiello & Dadda, 2019). The plants were also able to process some of the features of the support before coming into touch with it. Indeed, particular sensory mechanism are involved in objects' features sensing during circumnutation (Guerra et al., 2019). To better explain, plants have at their disposal an array of sensory modalities (Chamovitz, 2013; Karban, 2015) including vision (Crepy & Casal, 2015), acoustic perception (Gagliano et al., 2012; Hussain et al., 2023), chemosensory perception (Runyon et al., 2006), all of which might be useful to this endeavour. Furthermore, plant apexes are provided with a variety of chemical, vibrational, gravitational, and optic sensory transducers which enable the apex to perceive the surroundings and supply the information required for the plan a movement (Guerra et al., 2019).

Finally, like animals, they act in a strategic and anticipatory manner, in accordance to, for instance, a well-known principle (Fitt's Law; Fitts & Peterson, 1964) regulating their movement velocity depending on task complexity (Ceccarini et al., 2020a,b). The amount of time necessary to perform an action is a function of the distance to the target divided by the size of the target. As a result, the greater the distance and the smaller the size of the target, the longer is movement duration (Fitts & Peterson, 1964). Furthermore, the plants adjusted their movement in flight, using the same method that mammals utilize for more precise tasks (Ceccarini et al., 2020a). When reaching to grasp a smaller object, slower motions provide more time to process the information about the target and any spatial disparity between the effector and the target, leading to appropriate corrections (Meyer et al., 1988). The movement of pea plants appears to be a well-controlled and accomplished activity, rather than a simple cause-effect mechanism.

However, the "how" of an action is influenced not just by biomechanical limitation, but also by the environment in which the action is executed. The experiments reported in my thesis are specifically tailored to explore this issue. In particular, I investigated whether the kinematics of plants approach-to-grasp movements are modulated by acting either in an individual or social context (Bonato et al., 2023).

PART II

THE EXPERIMENTS

Chapter 4

General Methods

In the present chapter I will describe the methods and the procedures common to all the experiments included in my thesis. Exceptions will be reported within the "Materials and methods" section for each specific experiment.

4.1 Sample description

P. sativum plants were chosen as plants' model. They are annual climbing plants with tendrils, modified leaves used by plants to approach and grasp a suitable support in the environment. Healthy-looking *P. sativum* seeds were selected, potted, and kept at the conditions outlined below. For each experiment plants were randomly assigned to the experimental conditions.

4.2 Experimental stimulus

The stimulus was a wooden pole of 60 cm in height and 1.3 cm in diameter, positioned at 12 cm in front of the first unifoliate leaf for each plant.

4.3 Germination and growth conditions

The seeds were made to germinate in absorbent paper for six days and then the healthy and same-rate height plants were potted. The pot used was 30 cm in diameter and 14 cm in height for the social conditions and 20 cm in diameter and 20 cm in height for the individual conditions. All pots were filled with silica sand (type 16SS, dimension 0.8/1.2 mm, weight 1.4). At the beginning of each treatment, the pots for the individual condition were watered and fertilized using a half-strength solution culture (Murashige and Skoog Basal Salt Micronutriment Solution; 10x, liquid, plant cell culture tested; SIGMA Life Science). The volume of the soil and the solution culture were as such to allow for adequate soil and fertilizing conditions. They have been adjusted to allow for the same quantity of soil and fertilizer for two plants when considering the social conditions. The plants were watered three times a week. Each pot was enclosed in a growth chamber (Cultibox SG combi 80 × 80 × 160 cm) so that the plants could grow in controlled environmental conditions. The chamber air temperature was set at 26 °C; the extractor fan was equipped with a thermo-regulator (TT125; 125 mm-diameter; max 280 MC/H vents) and there was an input-ventilation fan (Blauberg Tubo 100 - $102 m^3/h$). The two-fan combination allowed for a steady air flow rate into the growth chamber with a mean air residence time of 60 seconds. The fan was placed so that the air flow did not affect plants movements. Plants were grown with an 11.25- hour photoperiod (5.45 am to 5 pm) under a cool white led lamp (V-TAC innovative LED lighting, VT-911-100W, Des Moines, IA, USA or 100W Samsung UFO 145lm/W - LIFUD) that was positioned 50 cm above each seedling. Photosynthetic Photon Flux Density at 50 cm under the lamp in correspondence of the seedling was $350\ \mu mol_{ph}/\ m^2 s$ (quantum sensor LI-190R, Lincoln, Nebraska USA). Reflective Mylar® film of chamber walls allowed for better uniformity in light distribution.

4.4 Data recording and processing

For each growth chamber, a pair of RGB-infrared cameras (i.e., IP 2.1 Mpx outdoor varifocal IR 1080P) were placed 110 cm above the ground, spaced at 45 cm to record stereo images of the plant. The cameras were connected via Ethernet cables to a 10-port wireless router (i.e., D-link Dsr-250n) connected via Wi-Fi to a PC and the frame acquisition and saving process were controlled by CamRecorder software (Ab.Acus s.r.l., Milan, Italy). To maximize the contrast between the peas' anatomical landmark (e.g., the tendril) and the background, black felt velvet was fixed on some sectors of the walls of the boxes. The lens distortion and the intrinsic and extrinsic parameters of each camera were estimated using the Camera Calibrator App of Matlab. Depth extraction from the single images was carried out by taking 20 pictures of a chessboard (squares' side 18mm, 10 columns, 7 rows) from multiple angles and distances in natural non-direct light conditions. For stereo calibration, the same chessboard used for the single camera calibration process was placed in the middle of the growth chamber. Then, the photos were taken by the two cameras in order to extract the parameters of stereo calibration. In accordance with the experimental protocol, a frame was synchronously acquired every 3 minutes (frequency 0.0056 Hz) by the cameras. The tendrils developing from the considered node were studied. In those cases, in which the plant grasped the stimulus, the coiled leaf was analysed. The initial frame was defined as the frame in which the tendrils of the considered leaf were visible from the apex. The end of the plant movement was defined as the frame in which the tendrils of the leaf started to coil around the tendrils of the other plant. An ad hoc software (Ab.Acus s.r.l., Milan, Italy) developed in Matlab was used to insert virtual markers on anatomical landmarks to be investigated. Markers position was tracked frame-by-frame on the images acquired by the two cameras to reconstruct the 3D trajectory of each marker. The markers on the anatomical landmark of interest, namely the tip of the tendril was inserted post-hoc. At first, the tracking procedures were automatically performed throughout the course of the time of the movement sequence, by means of the Kanade-Lucas-Tomasi (KLT) algorithm on the frames taken by each camera, after the distortion removal. The experimenter verified the tracking executed manually and checked, frame by frame, the position of the markers. Then, the 3D trajectory of each tracked marker was computed triangulating the 2D trajectories gained from the two cameras.

4.5 Dependent measures

Tendrils developing from different nodes were considered for the data analysis. For those cases in which the plant grasped the stimulus, the coiled leaf was analysed. When no grasping occurred, the last node developed before the falling of the plant characterized by one, two or three tendrils was examined. The initial frame was defined as the frame at which the tendrils of the considered leaf were visible from the apex. The end of the plant movement was defined as the moment at which the tendrils of the leaf came in touch with the suitable support or the frame in which the tendrils fell down or remained still apart. The dependent measures specifically tailored to test the experimental hypotheses are outlined below.

1. The spatial trajectory designed by the tip of the tendrils. This measure describes circumnutation in both qualitative and quantitative terms.
2. The average velocity of the tendrils (mm/min): the average velocity reached by the tendrils during circumnutation.

3. The maximum velocity of the tendrils (mm/min): the amplitude of the maximum velocity reached by the tendrils during circumnutation.
4. The minimum velocity of the tendrils (mm/min): the amplitude of the minimum velocity reached by the tendrils during circumnutation.
5. The time of maximum tendrils velocity (%): the time at which the maximum velocity of the tendrils occurs as a percentage (%) of movement time.
6. The number of the total circumnutations performed by the plants.
7. The duration of the circumnutations (min): the time required by the plants to perform and complete a single circumnutation.
8. Number of switches: the number of switches in a clockwise or counterclockwise direction during the entire movement.
9. The distance between the center of gravity of the circumnutation to the origin of the plant (mm): It provides a measure of the plant tilting towards the stimulus during circumnutation.
10. The distance between the center of gravity of the circumnutation and the stimulus: It provides a measure for plant tilting towards the stimulus.
11. Movement time (min): the interval between the onset of the tendrils' movement and the time at which the tendrils touched the stimulus.

4.6 Data analysis

Statistical analyses were conducted using both bayesian and frequentist approach. The analyses were performed using JASP (JASP Team, 2022) and using the computing environment R (R Core Team, 2014). Further information on the analysis performed will be reported within the "data analysis" section for each experiment.

Chapter 5

Evidence of motor intentions in plants

5.1 Introduction

The results described in Chapter 3 are particularly important as they indicate that the plants exhibit forms of flexible goal-directed actions similar to those exhibited by a variety of animal species (Sustaita et al., 2013; Castiello & Dadda, 2019). For instance, through the perception of neighbours, plants are able to anticipate probable interactions and modify their behaviour to maximize their long-term gains (Novoplansky, 2009), including the grasping of a potential support (Gianoli et al., 2015). These findings contradict the widely held belief that plant movements are only determined by cause-and-effect mechanisms and hard-wired reflexes. This gives raise an odd question: to what extent can a plant execute a motor behaviour with intentions?

In the present study I ask whether the organization of climbing plants' kinematics is sensitive to the "intention" driving their movement towards a potential support. I will capitalize on the concept of intentionality conceived, in strikingly spatial terms, as "directedness toward..." (Marder, 2012; see Chapter 1).

Here, I put plants in a condition to perform "intentional" actions in two different contexts. For the individual context, plants acted in isolation in order to reach towards and grasp a potential support (i.e., individual condition). For the social context two plants were put in the same pot with a potential support in the middle (i.e., social context). These are both intentional actions; both involve a movement from one spatial location to another. The critical difference is in the "intentional" component: whereas grasping a support realizes a purely individual intention, acting in the presence of another plant inevitably involves a social intention, i.e. the intention to affect a conspecific's behaviour as part of one's reason to act. What I was interested in was the effect of social intention on kinematics. Are the characteristics of individual and social contexts played out in the kinematics of movement?

5.2 Material and Methods

The methods are identical to those reported in Chapter 4, except for the exceptions that follows:

5.2.1 Sample description

Twenty-four snow peas (*P. Sativum* var. saccharatum cv Carouby de Maussane) were chosen as the study plants.

5.2.2 Experimental conditions

Two experimental conditions were considered (Fig. 1.5.): (i) individual condition, in which the plant grew in isolation; and (ii) social condition in which two plants grew within the same pot. Treatments were replicated eight times by randomly assigning treatments to the eight growing chambers. Please note that for technical problems the data for one couple of plants could not be considered in the analysis for the social condition.

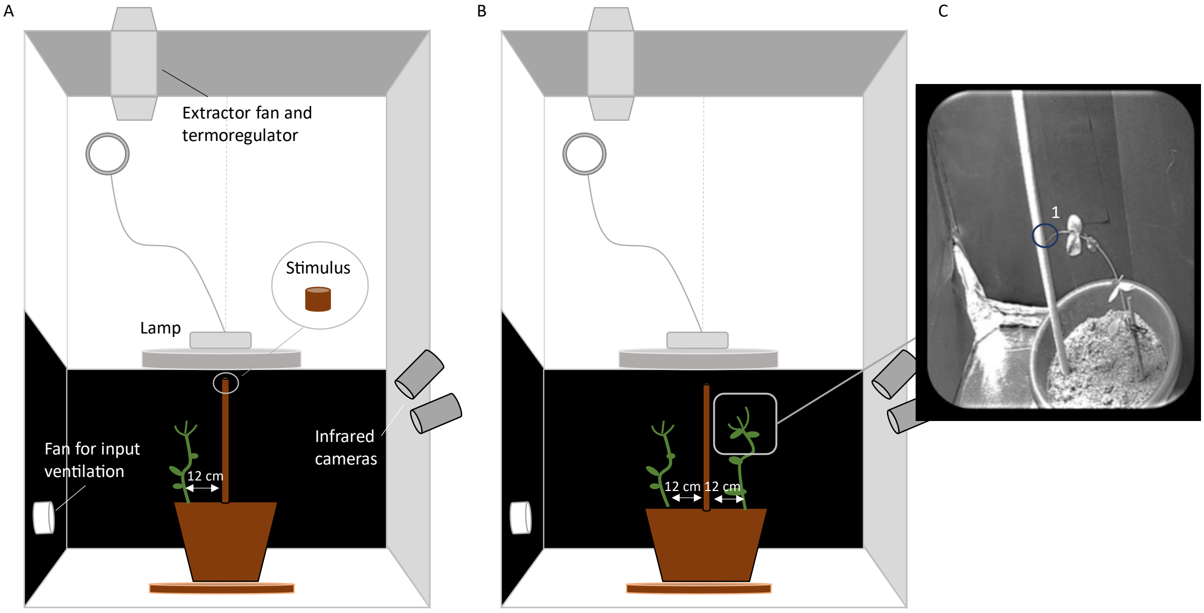

Figure 1.5. Graphical representation of the experimental set up for the individual condition (A) and for the social condition (B). The call out represents the anatomical landmark (i.e., the tendril) that will be tracked for kinematical analysis (C).

5.2.3 Dependent measures

Beyond the measures described in Chapter 4, I made a comparison between the winner and the loser plant in term of morphological measurement, namely the roots' surface area (cm^2; RSA), that was also included. That is, the surface area of the roots at the end of the movement, when the plants are removed from the soil. This measure was chosen because it provides a quantitative information regarding the portion of the soil conquered by the plants.

5.2.4 Data analysis

Statistical analyses were performed using the Bayesian approach. By producing a large number of samples using the Markov chain Monte Carlo method (MCMC), the goal of Bayesian estimation is to assign credibility to a distribution of probable parameter values (posterior distribution) that is compatible with the observed data. Next, 95% high-density intervals (95% HDI) are calculated to define which points of the distribution are most credible, and which cover most of the distribution (for a review, see Kruschke, 2013). In the present study, I performed Bayesian t-tests to compare the means of the "social" (µsocial) and the "individual" (µindividual) conditions for different variables. Moreover, within the social condition I compared the means of the "winner" (µwinner) and the "loser" (µloser) groups. For this purpose, using the BEST (Bayesian ESTimation supersedes the t test) model implemented by Kruschke (2013), I calculated the difference (β) between the mean of the social (µsocial) and the individual (µindividual) stimulus conditions, and compared the credibility of $\beta > 0$ with $\beta < 0$.

To detect the strength of the correlation between the kinematical components of the winner and the loser plants I performed Bayesian correlational analyses. All statistical analyses were performed using the computing environment R (R Core Team, 2014), and the packages BEST (Kruschke & Meredith, 2021) and BayesianFirstAid under the default settings, specifying my own priors by providing a list on the basis of our previous studies (Kruschke & Meredith, 2021).

5.3 Results

5.3.1 Qualitative results

The tendril for all plants showed a growing pattern characterized by *circumnutation* (Fig. 2.5. A-C). Once a plant detected the support, it strategically modified the tendrils so that they bent toward the stimulus as to approach and clasp it (Fig. 2.5. A-C). When considering the social condition, the "loser" plants showed a pattern of circumnutation along the vertical axis, without manifesting any orientation towards the stimulus (Fig. 2.5. C), whereas the "winner" plant exhibited a deviated pattern of circumnutation toward the stimulus (Fig. 2.5. B).

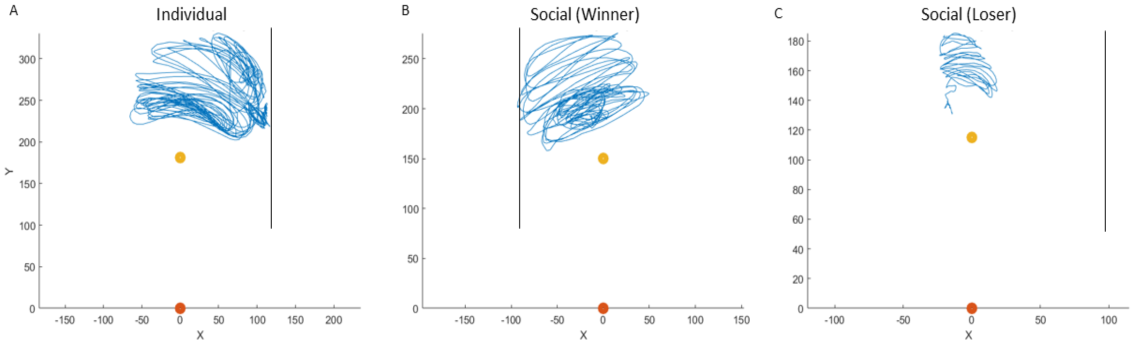

Figure 2.5. Graphical representation of a representative exemplar for a plant acting individually and for a winner and a loser plant acting socially**.** The spatial trajectory of the tendril (blue line) for the individual condition (A), for the winner plant within the social condition (B) and for the loser plant within the social condition (C). The black vertical line represents the stimulus, while the orange and yellow dots represent the origin and the last internode of the plant, respectively, in order to have a reference of the stem from which the tendril moves.

5.3.2 Kinematical results: Individual vs social condition

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

Movement time

The mean difference of movement time between the individual (μindividual = 2106 min ± 390) and the social (μsocial = 2402 min ± 305) conditions was β = 296 min, with a 95% uncertainty interval ranging from −6710 to 1270 min. The probability of β < 0 (i.e., the probability that the movement time was shorter for the social than for the individual condition) was 27.1%, whereas the probability of β > 0 (i.e., the probability that the movement time was shorter for the individual condition) was 72.9%. I can conclude that the social condition presents a longer movement time with respect to the individual condition.

Amplitude of the mean velocity of the tendrils

The amplitude of mean velocity reached by the tendrils during circumnutations between the individual (μindividual = 4.974 mm/min ± 0.82) and the social (μsocial = 4.265 mm/min ± 0.71) condition was β = -0.707 mm/min, with a 95% uncertainty interval ranging from −2.830 to 1.510 mm/min. The probability of β < 0 (i.e., the probability that the amplitude of mean velocity was higher for the individual than for the social condition) was 75.9%, whereas the probability of β > 0 (i.e., the probability that the amplitude of the mean velocity peak was lower for the Individual condition) was 24.1%. I can conclude that the social condition presents a lower average velocity than the individual condition.

Percentage of time at which maximum velocity occurs

The percentage of movement time at which the peak of maximum velocity was reached by the tendrils during circumnutation between the individual (μindividual = 63.77% ± 8.950) and the social (μsocial = 66.04% ± 9.320) condition was β = 2.21 % with a 95% uncertainty interval ranging from −23.30 to 28.00 %. The probability of β < 0 (i.e., the probability that the % time for the peak of the maximum velocity reached by tendrils was earlier for the social than for the individual condition) was 42.2%, whereas the probability of β > 0 (i.e., the probability that the % time for the peak of the maximum velocity reached by tendrils was later for the social condition) was 57.8% (Figure 3.5 A). I can conclude that the time at which the maximum velocity occur is later for the social than for the individual condition.

Duration of the circumnutations

The mean duration of circumnutation between the individual (μindividual = 72.36 min ± 3.04) and the social (μsocial = 88.10 min ± 6.10) condition was β = 15.7 min with a 95% uncertainty interval ranging from −2.52 to 29.0 min. The probability of β < 0 (i.e., mean duration of the circumnutations was longer for the individual than for the social condition) was 1.3%, whereas the probability of β > 0 (i.e., the probability that the mean duration of the circumnutations was longer for the social condition) was 98.7%. I can conclude that the social condition presents a longer duration of the circumnutations than the individual one.

Distance from the gravity center of the circumnutation to the stimulus

The center of the gravity center of the circumnutation to the stimulus between the individual (μindividual = 93.64 mm ± 10.81) and the social (μsocial = 87.04 mm ± 5.65) condition, was β = -6.61 mm with a 95% uncertainty interval ranging from −30.9 to 17.3 mm. The probability of β < 0 (i.e., gravity center of the circumnutation was more distant from the stimulus for the individual than for the social condition) was 72.1%, whereas the probability of β > 0 (i.e., the probability that the gravity center of the circumnutations was more distant from the stimulus for the social condition) was 27.9%. I can conclude that the social condition presents a closer proximity to the stimulus than the individual one.

5.3.3 Kinematical results: “winner” vs “loser”

Amplitude of the mean velocity of the tendrils

The amplitude of the mean velocity reached by the tendrils during circumnutation between the winner (μwinner = 4.431 mm/min ± 0.83) and the loser (μloser = 2.918 mm/min ± 0.95) condition, was β = 1.52 mm/min, with a 95% uncertainty interval ranging from −0.908 to 4.09 mm/min. The probability of β < 0 (i.e., the probability that the mean velocity peak was larger for the loser than for the winner condition) was 9.9%, whereas the probability of β > 0 (i.e., the probability that the mean velocity peak was highly for the winner condition) was 90.1%. I can conclude that the winner plant presents an higher average velocity with respect to the loser one.

Percentage of time at which maximum velocity occurs

The percentage of movement time at which the peak of maximum velocity reached by the tendrils during circumnutation between the winner (μwinner = 71.37% ± 7.133) and the loser (μloser = 57.41% ± 11.158) condition, was β = 13.9 % with a 95% uncertainty interval ranging from −12.2 to 39.9 %. The probability of β < 0 (i.e., the probability that the maximum velocity peak reached by tendrils was earlier for the loser than for the winner condition) was 12.5%, whereas the probability of β > 0 (i.e., the probability that the maximum velocity peak of the tendrils was later for the winner condition) was 87.5% (Fig. 3.5. B). I can conclude that the time at which the maximum velocity occurs is later for the winner than for the loser plants.

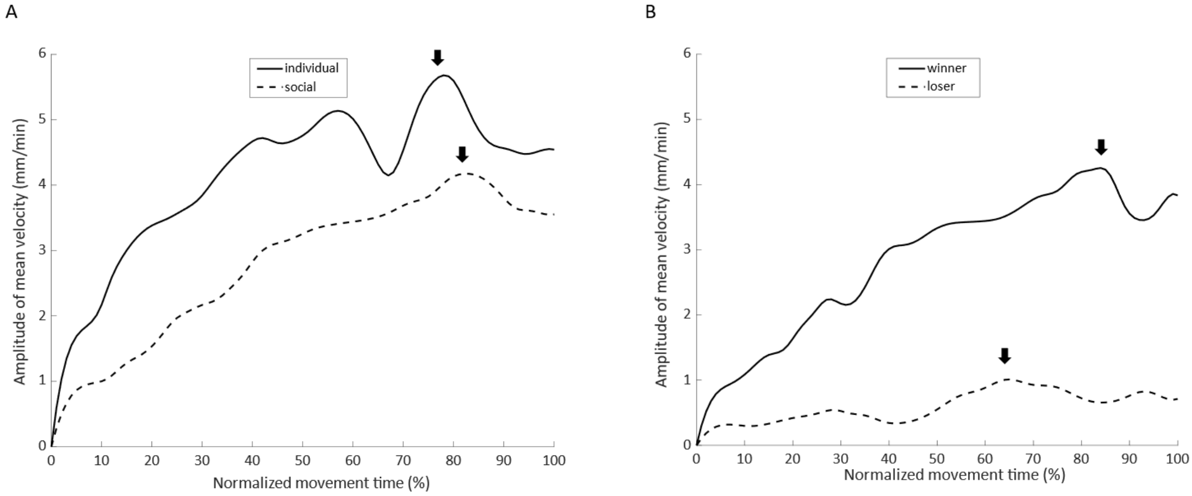

Figure 3.5. Graphical representation of the amplitude of average velocity for representative plants acting individually or socially. The amplitude and the time at which maximum velocity occurred for the individual and the social condition (A) and for the winner and the loser plants within the social condition (B). Arrows indicate the time occurrence of maximum velocity as a percentage of movement duration. Please note that the amplitude of maximum velocity during circumnutation is higher and it occurs earlier for the individual than for the social condition (A). It is higher for the winner than for the loser plant (B) and it occurs earlier for the loser than for the winner plant (B).

Duration of the circumnutations

The mean duration of the circumnutation between the winner (μwinner = 89.53 min ± 7.098) and the loser (μloser = 99.78 min ± 11.778) condition, was $\beta = -10.3$ min with a 95% uncertainty interval ranging from −37.5 to 17.5 min. The probability of $\beta < 0$ (i.e., mean duration of the circumnutations was longer for the loser than for the winner) was 79.4 %, whereas the probability of $\beta > 0$ (i.e., the probability that the mean duration of the circumnutation was longer for the winner) was 20.6%. I can conclude that the winner plant presents a shorter duration of the circumnutations with respect to the loser one.

Distance between the gravity center of the circumnutation to the stimulus

The gravity center of the circumnutations to the stimulus between the winner (µwinner= 88.36 mm ± 6.82) and the loser (µloser = 115.33 mm ± 8.33) condition, was β = -27 mm with a 95% uncertainty interval ranging from −48.2 to -5.71 mm. The probability of $\beta < 0$ (i.e., gravity center of the circumnutation was more distant from the stimulus for the loser than for the winner) was 99%, whereas the probability of $\beta > 0$ (i.e., the probability that the center of the circumnutations was more distant from the stimulus for the winner) was 1%. I can conclude that the winner plant presents a closer proximity to the stimulus with respect to the loser one.

Roots' Surface Area

The RSA comparing the winner (µwinner= 16.657 cm^2 ± 3.113) and the loser (µloser = 16.711 cm^2 ± 5.54) plants determined β = -0,0539 cm with a 95% uncertainty interval ranging from −13,5 to 12,5 cm^2. The probability of $\beta < 0$ (i.e., the RSA was larger for the loser) was 50.1%, whereas the probability of $\beta > 0$ (i.e., the RSA was larger for the winner) was 49.9%. I can conclude that there are no differences between the winner and the loser plants for what concern the roots' surface area.

5.3.4 Bayesian Correlation analysis

The Bayesian correlations between the winner-loser dyad are outlined below. For the amplitude of mean peak velocity correlation was moderately positive (r=0.33[0.43, 0.90]) with a probability of 78.2%. For the percentage of movement time at which the peak of mean velocity occurred correlation was moderately positive (r=0.46[0.27, 0.94]) with a probability of 86.2%. For the mean duration of the circumnutations correlation was moderately positive (r=0.46[0.28, 0.95]) with a probability of 86%. For the center of the circumnutations and its distance from the stimulus correlation was slightly negative (r=-

0.19[-0.84, 0.58]) with a probability of 65.9%. For the RSA correlation was moderately positive (r=0.46[-0.29, 0.93]) with a probability of 86.6%.

5.4 Discussion

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

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

Winner versus Loser

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

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

The loser plants start to orient their behaviour far from the support as soon as the defeat is perceived, so that they can invest more energy in a new search.

But is this kind of behaviour a true manifestation of a competitive attitude? An answer to this question comes from the analysis performed on the roots' surface area. Remember that plants may become territorial by proliferating roots with the intent of directly discouraging intrusions from other individuals for access to resources (Falik et al., 2005; Dudley & File, 2007). Thus, plants are expected to demonstrate a mosaic of competitive behaviours for the same or different resources. In this view I might have expected the roots' area for the winner plants to be greater than that for the loser plants. However, no differences were detected, suggesting that I am not in the presence of a competitive situation below-ground. Rather, the two individuals share available resources. I argue that plants probably perceive as a fundamental and scarce resource the single support available in the aerial part of the plant. So, the competitive attitude is expressed in the pattern of movement to reach and grasp the potential support actively using an adaptive and anticipatory "intentional" behaviour appropriate to the environment in which the plants operate (Ballaré et al., 1987; Novoplansky et al., 1990). This ability to implement anticipatory actions, is especially significant in social contexts since each part's action is intrinsically dependent on the responses of its counterparts (Smith, 1982; Maina et al., 2002).

Chapter 6

Cracking the code of social behaviour in pea plants: The role of Strigolactones

6.1 Introduction

Plants have a limited ability to choose their neighbours, but they may orchestrate a wide range of social activities that boost their chances of survival in a variety of ecological contexts. Indeed, plants may anticipate potential interactions and alter their behaviour to optimize their long-term advantages by perceiving their neighbours (Novoplansky, 2009). Put simply, they must make "informed" social decisions under a variety of ecological conditions.

In the investigation described in Chapter 5, I placed plants in a social scenario to study their behaviour while grasping a potential support in a context that appears, at first glance, competitive. The behaviour was different for each couple, with just one plant grasping the support. The activity of the winning plant was characterized by a higher velocity and a time-saving approach that minimized behavioural demands, as typical for competitive tasks in animals (Lehner et al., 2011). But what are the biological mechanisms underlying the kind of social behaviour I observed in plants?

SLs appear to be a promising candidate. SLs are a type of plant hormone that is secreted in substantial amounts into the soil by flowering plants in order to encourage the recruitment of arbuscular mycorrhizal fungus (AMF; Akiyama et al., 2005). SLs appear to be natural candidates for acting as a plant-plant signal modulator at the basis of what found in the previous study because they act as hormones in plants (Umehara et al., 2008; Gomez-Roldan et al., 2008; Xie et al., 2015) with significant impacts on shoot growth (Sorefan et al., 2003; Bennett et al., 2016) and less severe effects on root development (Villaécija-Aguilar et al., 2019). SLs are frequently produced and decoded by *P. sativum* plants (Beveridge et al., 2000) and they are often emitted at the early stages of plants development (Wheeldon et al., 2021). Furthermore, it has recently been proven that SLs play a role in neighbour recognition, acting as plant-plant signals permitting plant communication (Wheeldon et al., 2022). Also, SLs have the ability to modulate plant communication, transferring information from roots to shoots (Brewer et al., 2013). Interestingly, have been demonstrated that SLs is usually produced in large amounts in the early stages of life of the plants (i.e., the first few weeks) and in all my studies the data from the plants were collected within the first three weeks of life, up to the point they (or one of them) grasped a potential support.

In my studies, plants were potted together in an environment that allowed them to communicate at both the root and the shoot levels. With the former facilitating the exchange of root exudations. Remember that the approach to grasp movement exhibited by pea plants necessitates of a continuous cross-talk between the roots and the aerial section of the plants (Guerra et al., 2022). For these reasons, SLs appear to be an ideal candidate for playing a critical role in the modulation of plants social attitude in an alike-competitive scenario.

In the present experiment, I used pea mutant plants to evaluate the potential involvement of SLs in modifying the social behaviour of plants toward a potential support. Mutants are plants in which hereditary changes are purposefully generated.

Specifically, *rms1-1* is a pea mutant that does not synthesize SLs due to the lack of enzyme CCD8 (Sorefan et al., 2013), while *rms3-1* is a pea mutant that cannot detect SLs that is exudated by neighbours. I combined *wild-type* and mutant plants to test for the social condition described in Chapter 5.

This is the first study attempting to consider SLs as a potential candidate in the implementation of context-dependent plants movement. A preliminary step to shed light into the molecular basis of plant social behaviour. In turn this is an attempt to crack the code of social motor intentions across taxa.

6.2 Material and methods

Material and methods are different from those reported in Chapter 4 and therefore they will be described in great detail.

6.2.1 Sample description

96 pea plants (*P. sativum* L77 Wild-Type; *P. sativum rms1-1* L77 background; *P. sativum rms3-1* Torsdag background; *P. sativum* Torsdag *Wild-type*) were chosen as study plants. *Rms1-1* and *Rms3-1* were mutant plants in terms of STs. *Rms1-1* is unable to synthetize SLs (due to a lack of CCD8 enzyme; Sorefan et al., 2003) and *Rms3-1* is unable to perceive the presence of SLs from neighbouring plants. *Wild-type* with backgrounds L77 and Torsdag are different lines, and they have been matched with the respective mutants' backgrounds to reduce the influence of different genotypes during the social interaction. *Wild-type – wild-type* combination was made using the Torsdag background. I have assigned, randomly, the plants to the experimental conditions.

6.2.2 *Experimental stimulus*

The stimulus was a wooden stick of 60 cm in height and 0.5 cm in diameter, positioned in the middle of the pot, equidistant from each plant.

6.2.3 *Germination and growth conditions*

Pea seeds were made to germinate for 1 week on perlite, and equal sized plants were selected (Figure 1.6 A-B). Then the selected sprouts were potted and kept at the conditions outlined below. Plants were grown in plastic pots of 15cm of diameter and 10cm in height. All the pots were filled with agricultural sand. The plants were watered three times per week. Plants were grown under glasshouse conditions with a 16 hours day and 8 hours night regime at 22°C (Figure 1.6 C) and LED lights with an average light intensity of ~250 µmol/m^{2}s^{-1} were used.

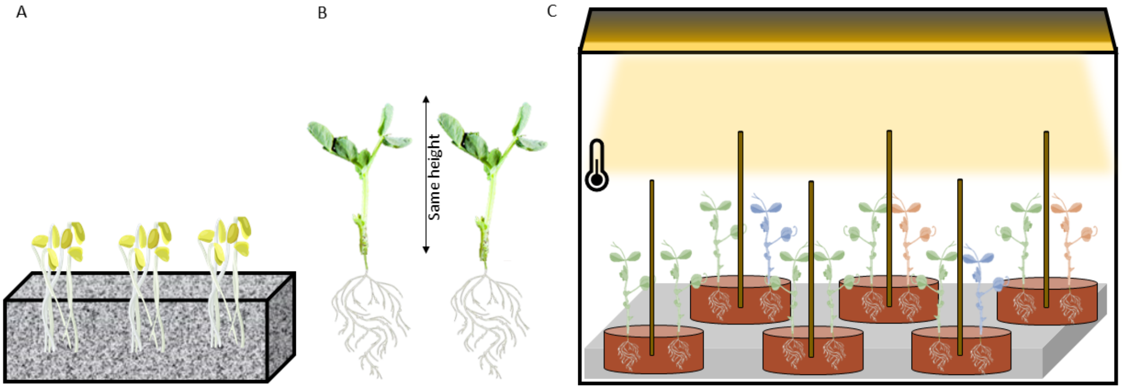

Figure 1.6. Graphical representation of the experimental procedure and set up. In panel A, plants were grown in perlite and then the healthy sprouts were chosen. In panel B, the same-height plants were combined. In panel C, the representation of the glass-house with a highly controlled environment in terms of light and temperature in which the data were collected.

6.2.4 Experimental conditions

A social setting, replicating the one described in Chapter 6, considering two plants potted together, was implemented (Figure 1.6 C). Couples were formed considering all possible combinations among the different populations. To test whether SLs act as a root-emitted cue that mediates social behaviour, I utilized *rms1-1* mutants, which do not synthesize SLs (Sorefan et al., 2003). Meanwhile, *rms3-1* mutants lacking a functional SLs receptor should be insensitive to the presence of neighbours early in the life cycle (Wheeldon et al., 2022). I collected data from 15 couples for each combination, with 2 replications for each couple. The data were collected for 3 weeks.

6.2.5 Dependent measures

The dependent measures specifically tailored to test the experimental hypotheses are outlined below. These measures describe the behaviour of grasping in temporal and quantitative terms from an observational perspective.

1. The total number of plants approaching and grasping the support for each population.
2. The behavioural evidence or no evidence of grasping depending on the combination examined.
3. The days required to grasp the support for each combination.

6.2.6 Data analysis

Statistical analyses were conducted using the frequentist approach. The analysis was performed using JASP (JASP Team, 2022) nested within the environment R (R Development Core Team, 2004; see used packages: https://jasp-stats.org/r-package-list/).

I performed Shapiro-Wilk test to check the normality of the dataset. Once the non-normality of the data was assessed, I performed a non-parametric Kruskal-Wallis Test to compare all the combinations. Repeated contrasts and post-hoc ρtukey test for multiple comparisons were also provided.

6.3 Results

6.3.1 Behavioural outcomes depending on the combination

To assess whether SLs play a role in social contexts characterized by competition for grasping a support, I first defined whether different SLs mutants and *wild-type* plants performed the grasping behaviour differently in quantitative terms. I found a consistent difference in terms of successful outcome (i.e., reach-to-grasp the support) depending on the populations (see Table 1.6).

Table 1.6. Total number of plants grasping the support for each population.

Population	**Outcome of grasping**
Wild-Type *(Torsdag and L77)*	44
Rms1-1	29
Rms3-1	51

Among all couples examined I found a significant difference depending on the combination considered (Kruskal-Wallis non-parametric ANOVA, statistics= 28.897, df= 5, p-value= < 0.001; see Table 2.6). This result suggests that the success to grasp the support depends on the ability to produce SLs. Indeed, the greater amount of successful outcomes derives from *wild-type* and *rms3-1* populations, able to produce SLs.

Table 2.6. Kruskal–Wallis Test for the dependent measures considered.

Dependent variables	**Statistic**	**df**	***p***
Plants grasped	28.897	5	< .001**
Days required	7.283	5	0.200

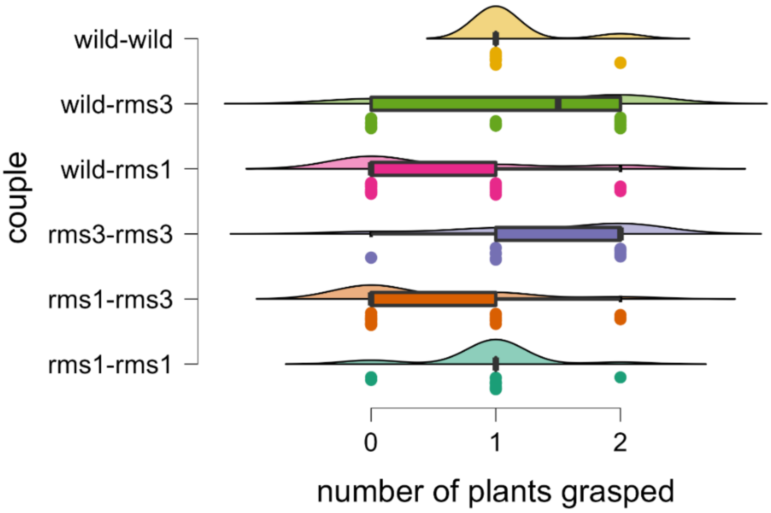

Figure 2.6. Behavioural outcomes depending on the combination. Number of plants grasping the support within each couple. The Kruskal–Wallis non-parametric ANOVA reveals a significative difference among the couples considered (see Table 2.7).

This result mirrors the behaviour of the plants studied in Chapter 5. The *wild-type* – *wild-type* combination recreates the behavioural pattern with a *winner* plant grasping the support and a *loser* one failing the attempt. This behaviour presents no differences to the one observed for the couple *rms1-1* – *rms1-1* (Table 3.6) in which the two plants not producing SLs are not able to perceive each other. Looking at the number of days required for grasping the support (Fig. 3.6.), it is evident that the couple *rms1-1* – *rms1-1* took more days than the *wild-type* (Table 4.6). Further, even if these *rms1-1* mutants are capable to move and grasp the support, they still present a lower successful outcome with respect to other populations (Table 1.6).

Table 3.6. Repeated Contrast for each couple concerning the plants grasped.

Comparison	**Estimate**	**SE**	**df**	**t**	***P***
rms1-rms1 – rms1-rms3	0.454	0.220	137	2.063	0.041*
rms1-rms3 – rms3-rms3	-0.954	0.220	137	-4.338	< .001**
rms3-rms3 – wild-rms1	0.862	0.218	137	3.961	< .001**
wild-rms1 – wild-rms3	-0.643	0.177	137	-3.629	< .001**
wild-rms3 – wild-wild	0.085	0.223	137	0.382	0.703
wild-wild – rms1-rms1	0.196	0.257	137	0.763	0.447
rms1-rms1 – rms3-rms3	0.500	0.253	137	1.980	0.050*
wild-rms1 – rms1-rms1	-0.362	0.218	137	-1.663	0.099
wild-rms3 – rms1-rms1	0.281	0.219	137	1.286	0.201

The *wild-type* produces two opposite outcomes depending when it is combined with a *rms1-1* mutant or a *rms3-1*, suggesting that the production of SLs influence the outcome of the communication within the couple (see Table 3.6). Considering the *rms3-1* mutant, when it is combined with another *rms3-1* mutant both plants grasped the support (see Table 3.6). Remember that *rms3-1* mutant is the one that produce SLs but it’s not able to perceive the SLs emitted by the neighbours. Finally, when two different mutants are combined, both plants did not exhibit the grasping behaviour. Please note, that in this case, one plant produces SLs (i.e., *rms3-1*) and the other one didn’t produce SLs (i.e., *rms1-1*).

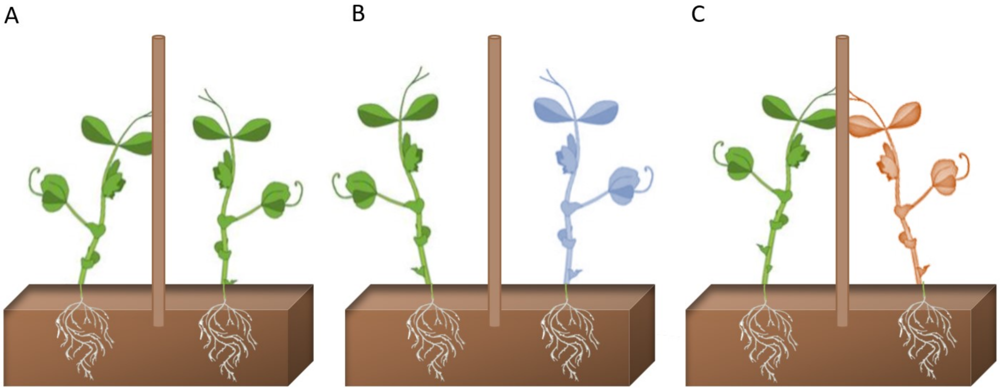

Figure 3.6. Graphical representation of different behaviours observed for the combinations considered. In Panel A it can be observed the behaviour reported for the *wild-type* plants in which a a winner and a loser patterning can be identified (see Chapter 5). In Panel B it is represented how both plants avoid grasping the support (*wild-type – rms1-1* combination). Panel C represents the grasping behaviour exhibited by both plants (*wild-type – rms3-3* combination).

6.3.2 Days required for grasping

The days take by the plant to achieve a firm grasp of the support have been calculated among all combinations (Fig. 4.6.), counting the days from the potting to the final grasp. The results suggest significant differences between specific couples as reported below in Table 4.6.

Table 4.6. Repeated contrasts among the considered combinations regarding the number of days required to achieve a firm grasp of the support.

Comparison	**Estimate**	**SE**	**df**	**t**	***p***
rms1-rms1 – rms1-rms3	1.786	1.480	85	1.207	0.231
rms1-rms3 – rms3-rms3	0.929	1.480	85	0.627	0.532
rms3-rms3 – wild-rms1	-0.582	1.449	85	-0.402	0.689
wild-rms1 – wild-rms3	-0.933	1.305	85	-0.715	0.477
wild-rms3 – wild-wild	2.087	1.248	85	1.672	0.098
wild-wild – rms1-rms1	-3.286	1.398	85	-2.350	0.021*
rms3-rms3 – rms1-rms1	-2.714	1.422	85	-1.909	0.060
rms1-rms3 – rms1-rms1	-1.786	1.480	85	-2.107	0.231
wild-rms1 – rms1-rms1	-2.132	1.449	85	-1.471	0.145

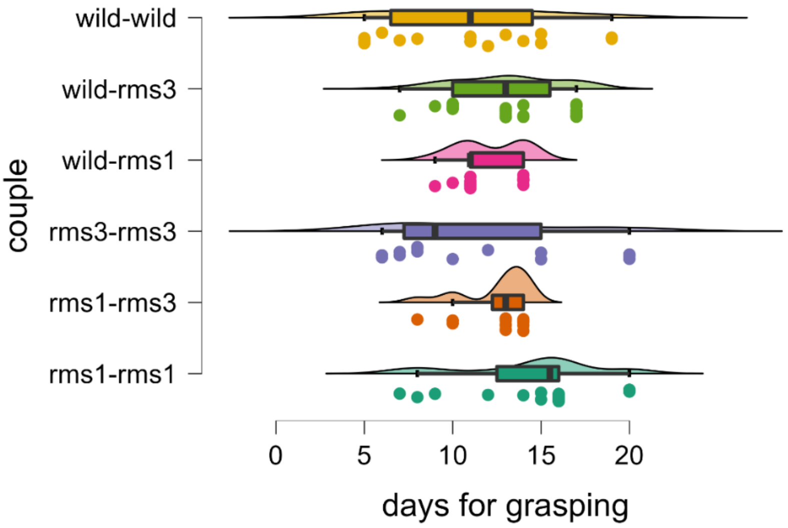

Figure 4.6. Days taken for grasping. Number of days taken for grasping by the plants for each combination considered. The Kruskal-Wallis non-parametric ANOVA reveals a non-significative difference among the couples considered (see Table 2.6).

6.4 Discussion

In the current study, I investigated for the first time the chemical process underlying the behavioural outcome of two plants competing for grasping a potential support in the environment. The findings demonstrated that the ability of plants to produce and perceive SLs affects the grasping outcomes.

By looking at the results, it can be immediately recognized how the plants behave differently for each combination. In Chapter 6, two plants exhibited a competing behaviour resulting with only one plant, designated as the winner, grasping the support. The *wild-type – wild-type* combination, with standard pea plants capable of producing and detecting SLs, replicated the results outlined in Chapter 5. This implies that SLs allow the plants to acknowledge the presence of other plants in the surroundings (Wheeldon et al., 2022) and act differently in a socially dependent manner. When the ability to produce SLs changes, so does the consequence. Combining a *wild-type* with a *rms3-1* mutant, in particular, enhanced the probability of both plants to grasp the support. In this situation, only one plant (i.e., the *wild-type*) can make and perceive SLs, whereas the mutant can produce SLs but not perceive them. This allows the *wild-type* to operate in a social fashion by perceiving the neighbour, while the mutant seems to act in isolation, being unable to perceive the neighbours in the surroundings. This suggests that an important requirement to implement the grasping behaviour is not concerned with the perception of SLs, but it's more about the emission of these compounds, probably because of their active role on the transmission of information from roots to shoots (Brewer et al., 2013).

A crucial aspect for coding the availability of a potential support in the environment. When the wild-type is coupled with a *rms1-1* mutant, the result is reversed. Since the mutant is not exuding SLs, the *wild-type* is unable to perceive a neighbour, hence the situation could be analogous to a single plant acting in isolation. The *rms1-1* mutant senses its neighbour but it is unable to produce SLs, this may impair its capacity to move appropriately and grab the support. Looking more closely at the results, I can also notice the combinations in which both plants grasp or avoid the support. Combining two *rms3-1* mutants it is evident that both plants grasped the support. In this scenario, both plants can produce SLs, but do not perceive SLs produced by the other. In other words, they both act in a likely-individual situation. This seems to suggest that the production of SLs appears to be an essential pre-requisite for the implementation of grasping behaviour, most likely due to the transmission of information regarding the qualities of the surroundings from the roots to the shoots (Brewer et al., 2013).

Meanwhile, coupling two mutants (i.e., *rms3-1* and *rms1-1*) greatly increases the possibility of both plants avoiding the support. One plant is emitting SLs, but it does not perceive the other plant not producing SLs. So, *rms1-1* is perceiving the neighbour but lacks the potential help given by SLs production in order to trigger the implementation of the movement. On the other side, the *rms3-1* is acting in an alike-individual condition, avoiding the support rather than grasping it as for the other combinations.

Overall, these findings appear to suggest the role of SLs as a potential chemical involved not only in neighbour detection and communication during a social setting, but also as an important mediator in the transmission of information from roots to shoots, which is critical for properly implementing an approach to grasp movement modulated by the social attitude. This is just a first attempt to systematize the role of SLs for the implementation of goal-directed circumnutation. But there are a number of questions still calling for an answer. So far, I may entitle to say that the behavioural outcome concerned with the grasping of a support seems affected by the SLs production and perception, but this is just a clue for explaining this complex phenomenon. It remains to be clearly understood why *rms3-1* mutant and *wild-type* decide not to grasp the support in the presence of a *rms1-1*, and how and why when two *rms1-1* mutants are combined the outcome is similar to the one reported for the two *wild-type*, even if slower.

For what concern the number of days taken by the plants to grasp, all of them require a similar number of days. One exception comes from the *rms1-1– rms1-1* couple that presents the same behavioural pattern of the *wild-type – wild-type* combination but requires more days to accomplish the grasping phase. This could suggest a general contribution of SLs for the social behaviour of pea plants, facilitating competitive movements when required. Future studies on pea mutants and social setting are in the pipeline to understand the crucial role of other compounds in the regulations of mutualistic and antagonistic behaviour between plants by investigating the kind of movement implemented by mutant plants by means of 3D kinematic analysis.

Chapter 7

“United we stand, divided we fall”: Intertwining as evidence of joint actions in pea plants

7.1 Introduction

The ability to coordinate actions with those of others in time and space is essential to improve the chances of survival as individuals and as a species. Shared actions to achieve a common goal are termed *joint actions* and involve two or more agents. To act in concert during joint actions, numerous coordination problems need to be solved. For instance, initiators of the *joint action* need to make their intentions intelligible to their partners to establish a shared intentionality. Shared intentionality is an evolutionary response to the problems encountered during the coordination of a complex *joint action*, which humans (Tomasello et al., 2005; Enfield & Levinson, 2006; Tomasello, 2014) and non-human social animals can operationalize (Trivers, 1971; Clutton-Brock, 2009; Gelblum et al., 2015; Heseen et al., 2017; 2021) via an intricate and organized cooperation. An aspect still unexplored but promising to bring new insights to the open debate on shared intentionality across taxa is the study of *joint actions* in *aneural* organisms. To test for the minimal architecture requirement allowing for shared intentionality, here I investigate whether plants can act jointly to achieve a common goal. Observations from numerous species of climbing plants reveal that climbing shoots often intertwine and provide mutual support within braided structures (Rowe & Speck, 2015). This is a behaviour that could be defined as a joint action. I examined how two pea plants coordinate their actions to grow intertwined when there is a need to climb in the absence of a potential support. A careful kinematical examination of their movement revealed a complementary pattern of movement, with a specific role that each plant of the dyad takes.

7.2 Material and Methods

The methods are identical to those reported in Chapter 5, except for the exceptions that follows:

7.2.1 Sample description

The number of subjects and the growth condition are identical to those reported in Chapter 5.

7.2.2 Experimental conditions

A condition in which two pea plants grew within the same pot without the presence of a potential support in the environment was considered (Fig. 1.7.). In such circumstances, the plants were somewhat constrained to intertwine to climb toward the light. A control condition in which a single pea plant grew in a pot without the presence of a potential support in the environment was also considered. Treatments were replicated 8 times by randomly assigning the two plants' locations within the pot.

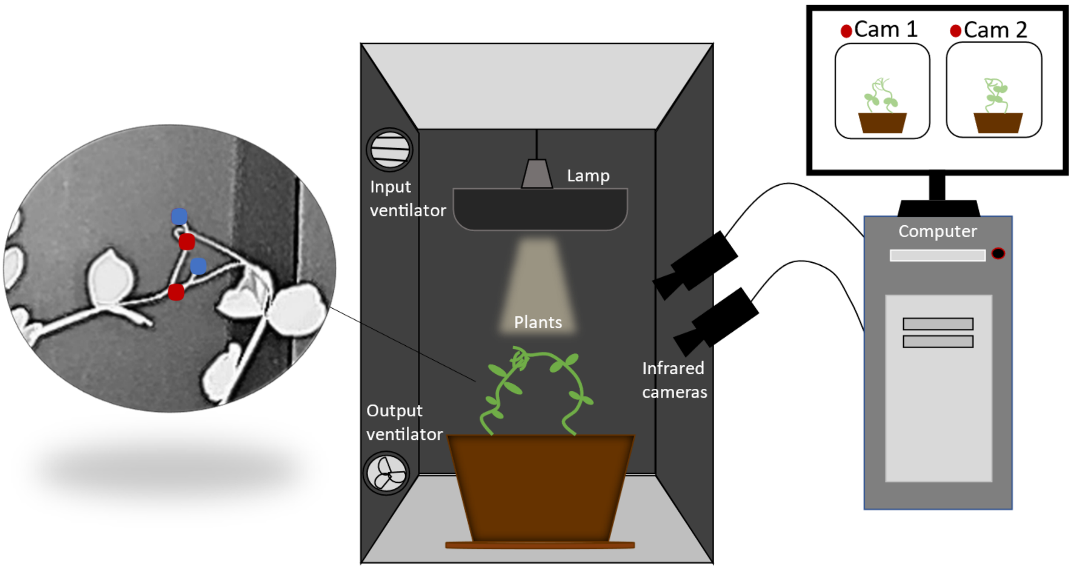

Figure 1.7. Graphical representation of the experimental set up. The red and blue circles represent the anatomical landmarks of interest (i.e., the tendrils) for the 2 plants.

7.2.3 Dependent measures

The dependent variables specifically tailored to test our experimental hypothesis were described in Chapter 4.

7.2.4 Data analysis

The descriptive statistics including median, interquartile range (IQR), range and percentiles (25th, 50th, and 75th) have been calculated. Statistical analyses were conducted using the Bayesian approach. In this study, I adopt the two-sided Bayesian Mann-Whitney U test because the dependent variables are not normally distributed. Mann-Whitney U test is a non-parametric test that does not require the assumption of normality. The analysis was performed using JASP (JASP Team, 2022) nested within the environment R (R Development Core Team, 2004; see used packages: https://jasp-stats.org/r-package-list/). I choose the default prior defined by a Cauchy distribution centered on a zero-effect size (δ) and a scale of 0.707. (Van Doorn, 2021). Data augmentation is generated with 5 chains of 1,000 iterations that allow for simpler and more feasible simulation from a posterior distribution. In the analysis, W is calculated in the Mann-Whitney U test as the smaller of the rank total between the two conditions. Bayes factor (BF) is obtained to quantify the relative predictive performance of the two hypotheses (van Doorn, 2021). In my study, BF quantifies evidence for the presence or absence of the difference between the 2 plants co-acting together. The null hypothesis here is that there is no difference in kinematics between the 2 plants. The alternative hypothesis is that there is a difference. The BF10 value is the likelihood of data given the alternative hypothesis (H1) divided by the likelihood of data given the null hypothesis (H0). The results are reported based on Jeffery's scheme that proposes a series of labels for which specific Bayes factor values can be considered either "no evidence," "anecdotal (1 – 3)," "moderate (3 –10)," "strong (10 – 30)," "very strong (30 –100)," or "decisive (> 100)" relative evidence for alternative hypothesis (Jeffreys, 1998). R-hat is also reported to check the degree of convergence of MCMC algorithms based on outcomes stability. The closer the value of R-hat is to 1, the better convergence to the underlying distribution. Credible intervals (CI) are set as 95%, which is simply the central portion of the posterior distribution that contains 95% of the values.

I also performed Bayesian correlation for non-parametric data using Kendall's τ correlation. The analyses were performed using JASP (JASP Team, 2022). Kendall's τ is one of the most widely used nonparametric tests of dependence between 2 variables (Kendall, 1938). Moreover, Kendall's τ expresses dependence regarding monotonicity instead of linearity and is therefore invariant under rank-preserving transformations of the measurement scale (Kruskal, 1958; Wasserman, 2006).

7.3 Results

7.3.1 Qualitative results

When considering each couple of plants, differences in the growth pattern emerge. At all cases, one plant, termed the *handler,* bends toward the other plant to reach it. The other plant, termed the *grasper*, deviates slightly from its central axis up to the point the *handler* was at a graspable distance (Fig. 2.7.).

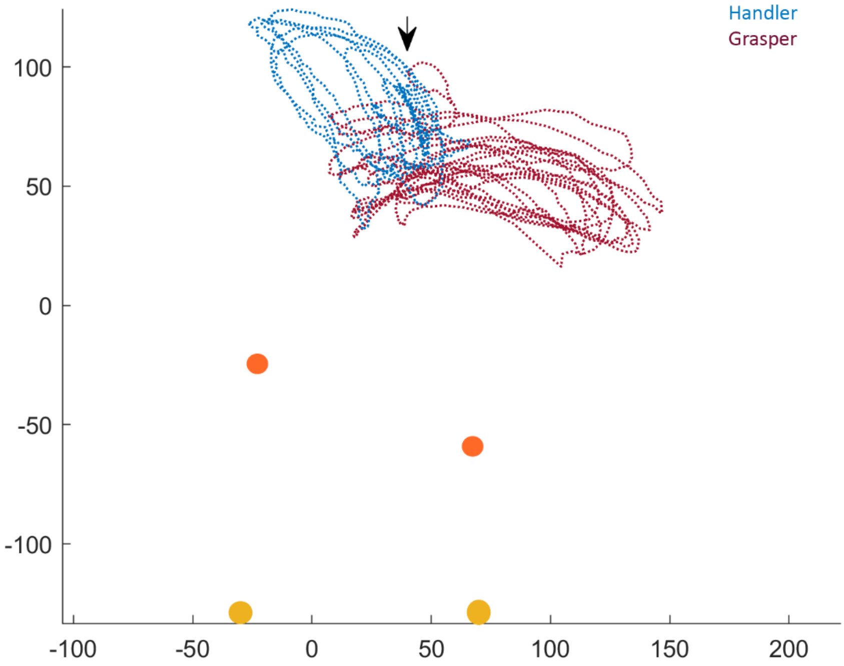

Figure 2.7. Graphical depiction of the trajectories for an exemplary couple of *handler* and *grasper* plants. The blue line represents the circumnutation trajectory for the *handler* plant. Note that it is not perpendicular to its vertical axis but is inclined toward the other plant. The red dotted line represents the circumnutation trajectory for the *grasper* plant ending with a grasping phase represented by the black arrow. Orange dots represent the origin of the plants. Orange dots represent the internode of the plants. Orange and yellow dots represent the stem of the plants.

Once the *handler*'s tendrils were nearby, the *grasper* grasped them, and the two plants intertwined and climbed toward the light. In other words, the *handler* plant initiates the joint action while the *grasper* plant strategically modifies the trajectory of its tendrils to clasp those of the *handler* (Fig. 3.7.). More specifically, the *grasper* exhibits a classic circumnutation pattern perpendicular to its axis (Stolarz et al., 2009). Instead, the *handler* exhibits circumnutations that are not perpendicular to its axis but exaggeratedly inclined toward the *grasper*. This suggests both plants exhibit a specific form of spatial navigation sub serving a common goal.

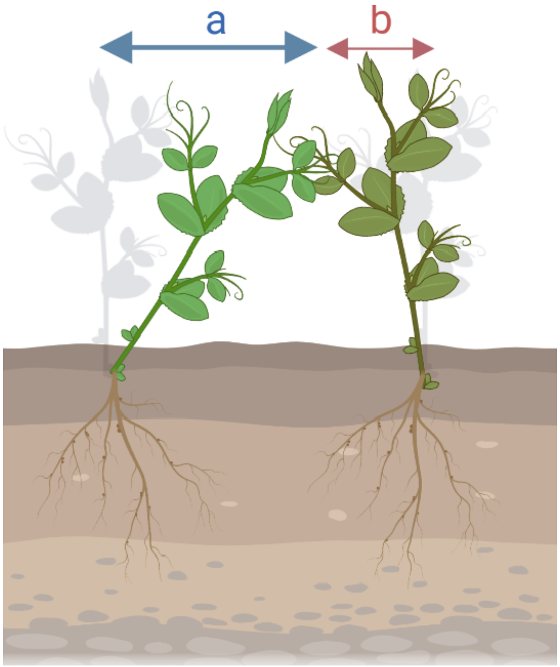

Figure 3.7. Graphical representation for the distance between the circumnutation center of gravity and the origin of the plant and the distance from the gravity center of circumnutation of one plant to the origin of the other plant. The original position of the plant before the movement started is represented by the faded grey plant. (a) The distance from the gravity center of circumnutation to the origin for the handler plant is represented in blue, which could be considered the proximity to the grasper plant' origin; (b) the distance from the gravity center of circumnutation to the origin for the grasper plant is represented in red.

7.3.2 Kinematic results

When looking at the kinematical patterning characterizing the *handler* and the *grasper*, I found no differences in the temporal occurrence of key kinematic landmarks (see Table 1.7).

Table 1.7. Bayesian Mann–Whitney U Test for the differences between the *handler* and *grasper* plants.

Dependent measures	**BF_{10}**	***W***	**Rhat**
Number of circumnutations	0.183	5,933.500	1.001
Maximum velocity during circumnutations	0.158	5,892.000	1.004
% time at which maximum velocity occurs	0.511	24.000	1.000
Mean velocity during circumnutations	0.153	5,925.000	1.002
Minimum velocity during circumnutations	0.151	5,826.000	1.004
Duration of the circumnutations	0.399	5,034.000	1.006
Total switches	0.492	37.500	1.000
Distance from the gravity center of the circumnutation to the origin of the plant	1,669.161***	8,402.000	1.065
Distance from the gravity center of the circumnutation to the origin of the other plant	1,1409.445***	3,179.000	1.018

Rather, differences emerge at spatial level. The median distance from the plant's origin to its circumnutation center of gravity is 53.578 mm (IQR = 64.799, Range = 128.057, percentiles [19.625, 53.578, 84.4425]) for the *handler* and 25.675 mm (IQR= 24.788, Range = 65.083, percentiles [13.225, 25.675, 38.043]) for the *grasper* (see Fig. 2.7.). The Bayesian Mann-Whitney U analysis revealed a Bayes factor (BF_{10}) of 1,669.161, suggesting there is an extreme difference between the two plants when considering the distance from the origin (BF_{10}=1,669.161, W = 8,402.000, R-hat = 1.065). The median distance from the circumnutations center of gravity to the origin of the other plant is 80.702 mm (IQR= 38.291, Range= 102.440, percentiles [55.946, 80.702, 94.237]) for the *handler* and 93.505 mm (IQR=22.387, Range= 105.351, percentiles [86.501, 93.505, 108.888]) for the *grasper* (see Fig. 2.7.). The Bayesian Mann-Whitney U analysis revealed a Bayes factor (BF_{10}) of 11,409.445, suggesting there is an extreme difference between the *handler* and the *grasper* (BF_{10}=11,409.445, W = 3,179.000, R-hat = 1.018) for this measure. Table 4.8 reports all the descriptive statistics.

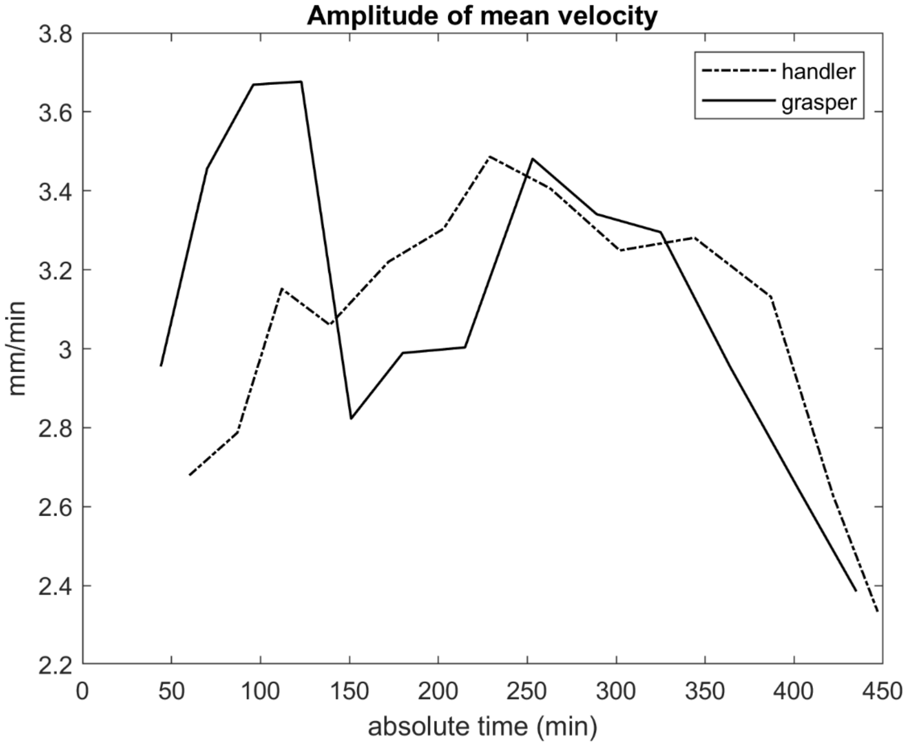

Figure 4.7. Graphical representation of the amplitude of mean velocity for representative plants. Note that the velocity profile is progressively coordinated in time and becomes increasingly more similar for the 2 plants as the joint action progresses. The movement for the 2 plants ends with a progressive deceleration to allow for the grasping phase.

7.3.3 Bayesian correlations

Kendall' τ correlation determined how two values co-vary in time. This index indicates global synchrony. Here, I use this method to test a possible crosstalk between the two plants. Table 2.7 reports all the correlations.

Table 2.7. Bayesian Kendall's Tau Correlations

Variable 1	**Variable 2**	**Kendall's tau B**	**BF$_{10}$**
Grasper mean velocity	Handler mean velocity	0.172	7.135*
Grasper duration circumnutation	Handler duration circumnutations	0.643	6.914*
Grasper total circumnutations	Handler total circumnutations	0.889	43.878**
Distance from the origin	Distance from the other plant	−0.296	1.561×10^{8}***

Note. BF$_{10}$ indicates a moderate correlation; BF$_{10}$** a strong correlation; BF$_{10}$*** a decisive correlation.*

One correlation considered is the *amplitude of the mean velocity between the two plants*. This measure indicates a kinematical harmony necessary to move in a similar and coordinated manner (Fig. 4.7.; Table 2.7). The correlation between the two plants when considering the amplitude of mean velocity is moderately positive (Table 2.7). Another correlation considered is between the circumnutation duration for the two plants. This measure is moderately positively correlated (Table 2.7). I also considered the correlation between the total *number of circumnutations* the two plants performed. The correlation was strongly positive (Table 2.7). For what concerns spatial coordination, the distance from the circumnutation center of gravity to the origin of the plant and the distance from the circumnutation center of gravity to the origin of the other plant were correlated (Fig. 5.7.). These two measures indicate the plants' spatial positions and their correlation is extremely negative. This signifies a progressive estrangement of one plant from its central axis and simultaneously a progressive approach toward the central axis of the other plant (Fig. 5.7. A-B; Table 2.7). This is an effect also evident when calculating the 3D Euclidean distance between the tendrils of the two plants for each couple.

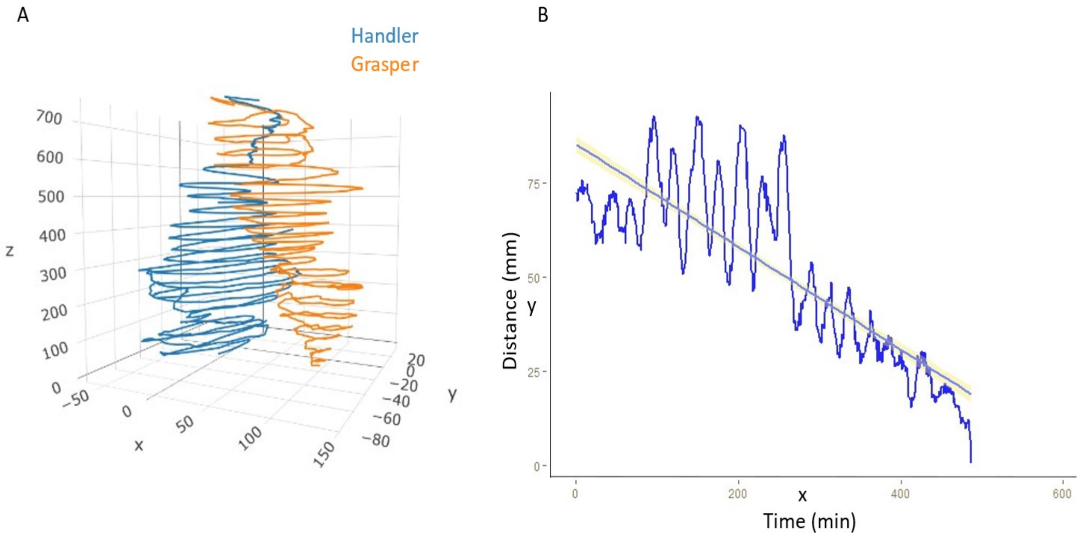

Figure 5.7. Trajectories and distance between the tendrils for the handler and the grasper during time. In panel A, a graphical representation for the 2D spatial trajectories (x,y) of the plants in time (z) is shown. From the graph, it can be appreciated the tendency of the *handler* to remain very close to the *grasper* toward the end of the movement so that the 2 plants can progress together. Panel B shows the graphical representation of the distance between the tendrils of the 2 plants for the acquired frames. The graph shows the gradual approach between the 2 plants in time, with a progressive reduction of distance between their tendrils.

7.3.4 Comparing the intertwining with an individual condition

I compared the behaviour of the *handler* and the *grasper* plants with the behaviour of plants growing in isolation in the absence of a support in the environment. Results show that the plants' behaviour for the intertwining condition differs from that the plants exhibited when acting alone (see Table 3.7).

Table 3.7. Bayesian Mann–Whitney U Test between the *individual* and *grasper* and *individual* and *handler* plants.

	Individual vs. Grasper			**Individual vs. Handler**		
	BF_{10}	W	Rhat	BF_{10}	W	Rhat
Number circumutations	$5.370\times10^{+8}$ ***	45,790.000	1.040	10,913.255***	6,644.000	1.288
Maximum velocity	2,313.206***	38,111.000	1.014	172.293***	10,724.000	1.068
Time % maximum velocity	2.727	55.000	1.000	4.072	6.000	1.002
Mean velocity	152,603.772***	39,024.000	1.009	2,106.514***	1,0247.000	1.016
Minimum velocity	12,418.432***	38,072.000	1.035	115.773***	10,668.000	1.069
Duration circumnutations	$1.699\times10^{+9}$ ***	8,758.000	1.020	66,7602.473***	23,512.000	1.058
Total switches	1.202	15.000	1.001	1.165	13.500	1.000
Distance from the gravity center of the origin of the plant	1.872	25,327.000	1.009	350.005***	19,791.000	1.027

Note. Result based on data augmentation algorithm with 5 chains of 1000 iterations.

Table 4.7. Descriptive Statistics for the *grasper*, the *handler* and the *individual* plants

	Group	**Median**	**IQR**	**Range**	**25th percentile**	**50th percentile**	**75th percentile**
Number circumnutations	Grasper	7.000	7.000	18.000	4.000	7.000	11.000
	Handler	7.000	7.000	21.000	4.000	7.000	11.000
	Individual	18.000	18.000	58.000	9.000	18.000	27.000
Maximum velocity	Grasper	2.910	3.091	18.118	1.253	2.910	4.344
	Handler	2.732	2.996	13.355	1.556	2.732	4.552
	Individual	3.964	4.156	19.656	2.262	3.964	6.418
Time % maximum velocity	Grasper	67.371	43.214	76.771	45.852	67.371	89.066
	Handler	49.886	63.288	77.275	28.106	49.886	91.394
	Individual	97.727	11.130	24.806	88.375	97.727	99.505
Mean velocity	Grasper	1.582	1.694	4.224	0.714	1.582	2.408
	Handler	1.574	1.907	0.110	0.718	1.574	2.625
	Individual	2.172	2.839	6.484	1.174	2.172	4.013
Minimum velocity	Grasper	1.582	1.694	4.224	0.714	1.582	0.890
	Handler	0.473	0.732	2.493	0.183	0.473	0.915
	Individual	0.750	1.324	4.141	0.282	0.750	1.606
Duration circumnutations	Grasper	111.000	39.000	144.000	93.000	111.000	132.000
	Handler	105.000	51.000	252.000	75.000	105.000	126.000
	Individual	63.000	18.000	159.000	57.000	63.000	75.000
Total switches	Grasper	0.500	3.000	4.000	0.000	0.500	3.000
	Handler	1.500	1.250	3.000	1.000	1.500	2.250
	Individual	3.000	2.250	9.000	2.750	3.000	5.000
Distance from the gravity center to the origin of the plant	Grasper	25.675	24.788	65.083	13.225	25.675	38.043
	Handler	53.578	64.799	128.057	19.625	53.578	84.425
	Individual	24.429	27.819	105.034	14.895	24.429	42.714
Distance from the gravity center to the origin of the other plant	Grasper	93.505	22.387	105.351	86.501	93.505	108.888
	Handler	80.702	38.291	102.440	55.946	80.702	94.237
	Individual	-	-	-	-	-	-

Note. Result based on data augmentation algorithm with 5 chains of 1000 iterations.

These findings suggest that another plant in the environment is considered a potential support from the very beginning of growth. Note that the *distance from the circumnutation center of gravity to the other plant* was not considered as a dependent measure because there is not an equivalent measure for the control condition. Table 4.7 reports all the descriptive statistics.

7.4 Discussion

In the present study, I investigated for the first time whether plants can act jointly and whether some forms of shared intentionality are at the basis of their "*intertwining*" behaviour. Results revealed specific motor patterns for the two plants in the dyad. Evidence from correlational analyses demonstrate that aneural organisms can act jointly and not simply together.

Looking at the results, it can be immediately appreciated the two plants' non-casual behaviour during the intertwining interaction. This supports the idea that pea plants move in a flexible and anticipatory manner (Guerra et al., 2019, 2021; Ceccarini et al., 2020a, Ceccarini et al., 2020b; Wang et al., 2023; Bonato et al., 2023). I explain these effects in terms of affordances (see Chapter 1; Gibson et al., 1979). Affordances are also an essential part of socialization. Social affordances, a subcategory of affordances, provide the opportunities in the environment to promote social relationships and interactions (Becchio et al., 2008; Ferri et al., 2011). In the case of our plants, the intertwining phenomena represent a perfect exemplification of the social affordance concept. The pea plants perceived each other as a potential support and then acted in concert. This is witnessed by how the two plants coordinate their action in time to meet at a precise point in space to reach kinematical consonance.

Kinematical consonance serves as an index to demonstrate that plants act jointly and not simply together. To elaborate, in humans' movement, attunement may make the interacting partners more similar and thus more predictable to one another (Vesper et al., 2010; Keller et al., 2007). Here, I show that this can also happen in plants. My findings suggest that the pattern of movement is the very same for the two plants. To reach such a level of coordination, agents need to solve numerous coordination problems. To this end, "coordination smoothers" can be implemented to simplify coordination. For an agent, one way to facilitate coordination is to modify its behaviour to make it easier for others to predict upcoming actions, for example, by exaggerating the movements or by reducing the actions' variability (Vesper et al., 2010). Another example of coordination smoother is the assignment of tasks between partners (Vesper et al., 2013; Skewes et al., 2015). From the present results, it is evident that the two plants in the dyad manifest specific but complementary behavioural patterns. The *handler* plant bends exaggeratedly toward the *grasper* to facilitate intertwining and then they travel together toward the light. Therefore, it seems that the initiator of the joint action is the *handler.* It signals the other plant on the potential common goal and it coordinates the action. The possibility that each plant plays a specific role suggests I am not in the presence of an "imitative' behaviour, but to a complementary behaviour driven by a shared goal, requiring cooperation and some forms of shared intentionality. These are two plants taking two roles, it is not simply an "action performed together." The exaggerated behaviour of the *handler* toward the neighbour could be explained as a coordination smoother to render intentions intelligible. Further, that this pattern differs hugely from that exhibited by the control group means this is a type of behaviour that is enormously exaggerated regarding the plants' usual behaviour.

Another interesting result concerns the progressive approach between the two plants, demonstrated via the calculation of the 3D Euclidean distance (Figure 5.7 B). The correlational analysis allows appreciating a non-casual correlation between the progressive distance between *the origin of the plant and the gravity center of the circumnutations* and the *distance between the gravity center of the circumnutations to the origin of the other plant*. This signifies they do not approach each other casually. When plants circumnutate, they perform an elliptical rotatory movement that allows for exploring each sector of the proximal environment. For the intertwining condition of our study, the plants' progressive distance from their original axes is functional to reach the point in space where the other plant is placed. This negative correlation occurring between the above-mentioned dependent measures witnesses this.

Altogether, these strategies seemed to be aimed at saving energy. At the basis of the processes described here is a high ATP consumption (Putz & Holbrook, 1992). Fewer circumnutations, fewer switches in direction, and a lower velocity may allow the two plants to preserve energy to reduce the risks of errors and attach firmly to each other. Remember that plants for the control group (those acting in isolation) show a higher amount of circumnutations and switches in direction than for the intertwining plants. This strategy is further supported by the "velocity" results showing that the *intertwining* plants exhibit a longer deceleration phase than the plants acting in isolation do. This suggests social actions require a more careful movement patterning for the sake of the necessary monitoring when acting jointly (Vesper et al., 2017). This signifies that acting together or acting in isolation reflects on kinematic patterning. Ascribing a specific *affordance* to the other plant, and not simply perceive it as a neighbour might be taken as the evidence of implementing the shared intention to intertwine and grow together toward the light.

A final aspect of the present findings relates to movement duration, which is longer for the intertwining than for the control group. For the intertwining plants, the extra time needed may allow to control better the tendrils' trajectories and select more accurately contact points to twine firmly around the neighbour. This interpretation is consistent with the most prominent theory of speed accuracy-trade off (Meyer et al., 1988) recently confirmed in plants (Ceccarini et al., 2020a).

To conclude, I provide the first empirical account of intertwining behaviour. I nest my findings within available theories explaining joint and complementary actions in animal species (see General Discussion). This is not to make plants resemble animals but to say that in aneural organisms, movements that a shared intentionality drives is possible. This calls for a reformulation of traditional definitions of intentionality based on concepts belonging to sometimes arbitrary and limited conceptions. Everything now must find empirical confirmation not only at the behavioural but also at the physiological level and needs to be done through species-specific tests under the banner of a pluralistic interdisciplinary approach, open to future breakthroughs and additions.

Chapter 8

Competing or cooperating? A matter of accuracy

8.1 Introduction

In the previous studies of the present thesis, I examined whether it was possible to differentiate between movements performed with an individual from those performed with an alike competitive intent. Further, via intertwining, I explored forms of cooperation driven by a sort of shared intentionality. Here I delve into the possible differences between the kinematics of cooperative or competitive action patterns. If the kinematics are sensitive to context, as I hypothesize, then a difference in kinematics should be found between an action performed in the context of a cooperative task and the same action performed as part of a competitive interaction. In order to do this, I shall capitalize on the issue of accuracy.

For climbing plants, movement accuracy is critical for adaptation and determines their long-term survival (Ceccarini et al., 2020a,b), as I mentioned in Chapter 3. In the present experimentation I ask whether climbing plants possess a motor accuracy mechanism that allows them to alter their movement online while interacting within a social context, lowering the risk of errors during shared actions. In general, a movement consists of two phases: the initial impulse, which involves driving the effector toward the target, and the on-line control, which allows for to adjust the movement and improve its accuracy (Ceccarini & Castiello, 2018; Novak et al., 2002). Zooming into the fine structure of movement it emerges that it is organized into smaller units, or primitives (Hogan & Sternad, 2012) termed submovements (Miall et al., 1993; Navas & Stark, 1968). Continuous movement is never truly smooth when examined through the appropriate lens, and its elementary units become visible as disruptions in the kinematic profile (Tomassini et al., 2022).

Correction of an aimed movement is provided by the generation of these submovements, which are envisioned as corrective adjustments that contribute to the decrease of any spatial disparity between effector and target position (Fradet et al., 2008). Indeed, in the presence of a difficult task, which requires more precision, more submovements are produced to reduce the end-point variability of an effector, and thus, the probability that the effector fails to grasp the target firmly (Eliasson et al., 2004; Meyer et al., 1988).

As a result, when the necessity for precision grows, movement velocity drops, yet the generation of secondary submovements increases in order to lower an effector's end-point variability. (e.g., arm for humans), and thus, the probability that the effector falls outside of the target bound (Meyer et al., 1988; Eliasson et al., 2004).

In available literature (including plants; see Chapter 3), it has been traditionally reported and described three types of submovements emerging in the final 10% of the movement, that means that corrective submovements usually emerge in close proximity to the target (Fradet et al., 2008; Ceccarini et al., 2020b). These submovements are: the zero crossing phenomenon occurring along the velocity profile (Type 1 submovement), the zero crossing phenomenon occurring along the acceleration profile (Type 2 submovement); the zero crossing phenomenon occurring along the jerk profile, commonly defined as rate of changes in the acceleration profile (Type 3 submovement).

Further, where the effector ends its movement gives important information regarding the accuracy of the final phase of the movement. To quantify the precision of the position of the effector on the target, a measure traditionally reported is the endpoint variability, conceived as the standard deviation of the euclidean distance between the final position of the effector and the target (Ceccarini et al., 2020b).

When an action is executed in concert with another agent, some forms of coordination are required. Coordination necessitates constant corrections based on an accurate evaluation of others' behaviour toward a joint motor outcome. Information must flow within both individual and inter-individual action-perception loops for such coordination to be successful (Tomassini et al., 2022). Several pieces of evidence suggest that the observed behaviour is the result of active co-regulation of submovements between the interacting partners (Tomassini et al., 2022).

Notably, decreasing movement time and/or speed beyond a certain limit also impedes successful online motor corrections, significantly compromising interpersonal submovement coordination. As a result, the mechanism controlling submovement creation is not blind, but rather tuneable, implying that it is most likely relevant to motor coordination. Indeed, one of the most important aspects of recent findings is that submovements switch between two agents (Tomassini et al., 2022). This indicates a continuous co-regulation in which submovements are consequential and reciprocal adjustments to the partner's behaviour (Tomassini et al., 2022).

Along these lines, here I examine whether climbing plants may have evolved a motor accuracy mechanism as to improve the precision of their movement when they act in concert with another plant (i.e., a moving organism) and how this may differ from when they compete with another plant to access a static potential support.

8.2 Material and Methods

Material and methods that differ from those described in Chapter 5 will be outlined below.

8.2.1 Experimental conditions

Two experimental conditions were considered (Fig. 1.8.). (i) a competitive condition (COMP) in which a plant grew with another pea plant within the same pot in the presence of a potential support in the environment (see Chapter 6). In such circumstance plants have to reach and grasp a fixed support in the presence of a competing plant. (ii) a cooperation condition (COOP) in which two pea plants grew within the same pot without the presence of a potential support. In such circumstances the plants were somewhat constrained to reach and grasp each other as moving targets, in order to climb towards the light. Between the two conditions two different motor behaviour can be identified. For the COMP condition, just one plant per couple (i.e., *winner,* see Chapter 5) executed the grasping. The movement for this plant will be compared with the *grasper* plant for the COOP condition, that is the plant that finalized the grasping phase coiling the tendrils of the *handler* at the end of the movement (see Chapter 8). Submovements investigation will be conducted also considering the differences between *handler* and *grasper* plants for the COOP condition. Treatments were replicated eight times by randomly assigning the location of the two plants within the pot.

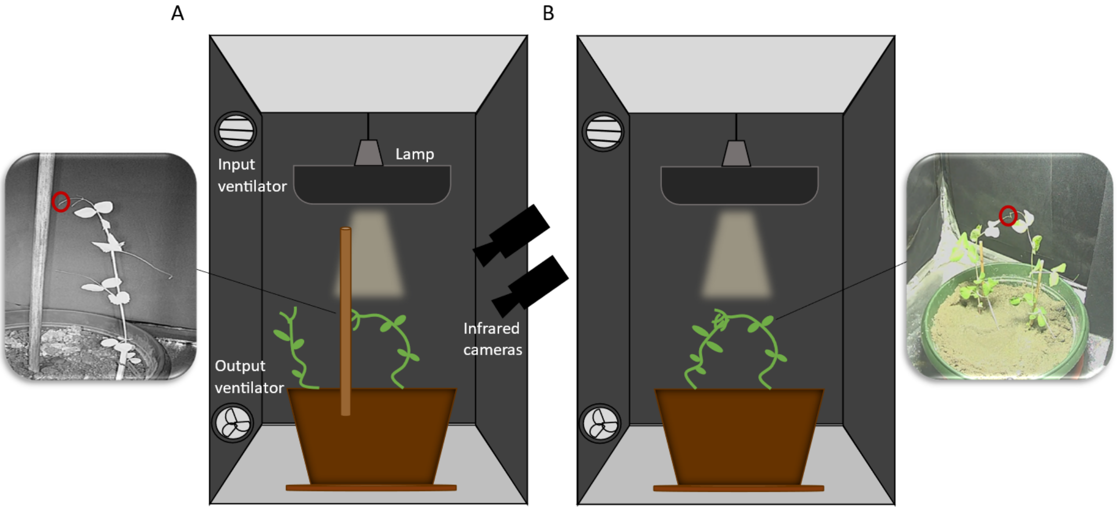

Figure 1.8. Graphical representation of the two experimental conditions (Panel A: COMP condition; Panel B: COOP condition). For the Panel A the call-out represent the picture of a plant grasping the pole in the social competitive condition. For the Panel B the call-out represent the picture of two plants intertwined together in the absence of a support in the social cooperative condition. The red circle represents the point of interest for our analysis that is the tendril towards a static target in the competitive (panel A) or towards the other tendril in the cooperative (panel B) condition.

8.2.2 Dependent measures

The dependent variables specifically tailored to test our experimental hypothesis on the basis of previous on-line control of movement accuracy in plants (Ceccarini et al., 2020b) were: (i) the number of *type 1* submovements computed as the total number of zero crossing from the velocity profile performed in the last 10% of the movement time; (ii) the number of *type 2* submovement computed as the total number of zero crossing from the acceleration profile performed in the last 10% of the movement time; (iii) the number of *type 3* submovements computed as the total number of zero crossing from the jerk profile performed in the last 10% of the movement time; (iv) the total number of submovements (acceleration, velocity and jerk) in the last 10% of movement time; (ix) the variability of the endpoint positions at the end of the movement.

8.2.3 Data analysis

In order to quantify the *type 1* submovement, I defined the following parameter concerning velocity array computation in a discrete mood:

$$v_i = \frac{s_i - s_{(i-1)}}{t_i - t_{(i-1)}}$$

Where v_i is the velocity computed at time point i, s_i is distance from the stimulus on the XZ plane at time point i and t_i is the time for point i referring to the last 10% of the movement.

To quantify the *type 2* submovement, I defined the following parameter concerning acceleration array in a discrete mood as a derivative of the velocity previously described:

$$a_i = \frac{v_i - v_{(i-1)}}{t_i - t_{(i-1)}}$$

Where a_i is the acceleration computed at time point i, v_i is the velocity computed at time point i and t_i is the time for point i referring to the last 10% of the movement.

In order to quantify the *type 3* submovement, I defined the following parameter concerning jerk array in a discrete mood as the rate of changes of the acceleration previously described:

$$j_i = \frac{a_i - a_{(i-1)}}{t_i - t_{(i-1)}}$$

Where j_i is the jerk computed at time point i, a_i the acceleration computed at time point i and t_i as the time for point i referring to the last 10% of the movement.

The analysis was performed using JASP (JASP Team, 2022) nested within the environment R (R Development Core Team, 2004; see used packages: https://jasp-stats.org/r-package-list/). I performed Shapiro-Wilk test to check the normality of the dataset. Once the normality of the data was assessed, I performed a parametric Student t-test to compare the dependent measures between the two conditions.

8.3 Results

8.3.1 *Qualitative results*

All plants exhibited a growing pattern characterized by circumnutation (Figure 2.8). Observing the trajectories, we can appreciate a different motor pattern for the two conditions. For the COOP condition the circumnutations do not present a significant slant in the final phase of the movement, considering that the other plant is moving too with a progressive approach (Fig. 2.8. B). For the COMP condition, since the very beginning of the movement, the circumnutations are oriented towards the support, and at the end of the movement the tendril approached and grasped the support (Fig. 2.8. A).

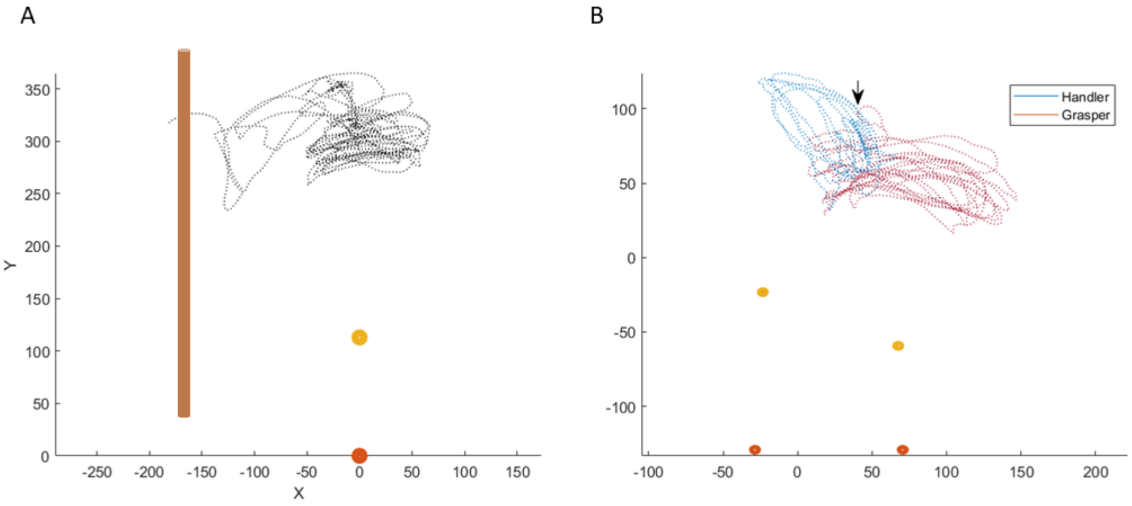

Figure 2.8. Example of the trajectories for the *winner* plant of the COMP condition (Panel A) and the COOP condition (Panel B). In Panel B, the black arrow indicates the final grasping phase of the movement.

8.3.2 *Kinematic results*

All the descriptive statistics for the kinematic results are provided in Table 1.8. As it is evident, there is a difference between the plants aiming towards a moving target (i.e., the other plant) to cooperate with respect to the plants aiming towards a static object (i.e., the wooden pole) to compete in terms of submovements. The total number of submovements and circumnutations required to accomplish the grasping phase seems greater for the COMP condition, suggesting a kind of movement that requires higher accuracy (see Table 2.8).

Table 1.8. Descriptive statistics for all the dependent measures considered

		Mean	Std. Deviation	Shapiro-Wilk	P-value Shapiro–Wilk	Min	Max
Submovement_type1	grasper	48.000	13.148	0.884	0.207	33.000	66.000
	handler	48.375	12.828	0.941	0.617	30.000	67.000
	COMP	67.125	20.490	0.991	0.997	35.000	101.000
Submovement_type2	grasper	26.250	7.025	0.961	0.817	14.000	35.000
	handler	28.250	10.389	0.912	0.369	17.000	45.000
	COMP	43.250	21.684	0.948	0.688	17.000	81.000
Submovement_type3	grasper	37.500	7.982	0.887	0.220	26.000	46.000
	handler	39.000	10.677	0.934	0.550	25.000	54.000
	COMP	59.375	26.403	0.969	0.891	24.000	100.000
Total submovements	grasper	115.500	23.513	0.951	0.722	79.000	145.000
	handler	115.625	32.040	0.950	0.709	72.000	161.000
	COMP	169.750	63.209	0.951	0.722	80.000	259.000
End point variability	grasper	18.072	11.294	0.977	0.949	0.369	34.438
	handler	18.072	11.294	0.977	0.949	0.369	34.438
	COMP	242.397	45.776	0.973	0.919	175.622	307.567

The mean of the submovements (Table 1.8) as reported in the descriptive statistics appears to be twice for the COMP with respect to the plants acting in the COOP condition (*handler* and *grasper*). This could suggest a complementary distribution of the submovements required to adjusting the movement between the two agents in the COOP condition. This become clearer looking at the statistical analysis, in which the submovements, in particular *type 1* and *type 3* showed significantly differences in the two conditions (*type 1* t(df)=-2.222, *p*-value=0.043; *type 3* t(df)=-2.243, *p*-value=0.042) as reported in Table 2.8.

Table 2.8. Independent Samples T-Test between COMP *winner* and COOP *grasper* condition for the dependent measures considered

						95% CI for Cohen's d	
	t	**df**	***p***	**Cohen's d**	**SE Cohen's d**	**Lower**	**Upper**
Submovement_type1	-2.222	14	0.043*	-1.111	0.572	-2.156	-0.033
Submovement_type2	-2.109	14	0.053	-1.055	0.565	-2.092	0.015
Submovement_type3	-2.243	14	0.042*	-1.122	0.573	-2.168	-0.042
Total submovements	-2.275	14	0.039*	-1.138	0.575	-2.186	-0.055

Note. Student's t-test.

The two plants within the COOP condition, presents the same amount of submovements and the same value of key kinematic features (see table 3.8), suggesting a coordinated and complementary pattern of movement as reported in Chapter 7. From the descriptive statistics I can also evidence how the *grasper* and the *handler* acting within the COOP condition present almost the identical amount of submovements corresponding to half as the submovements performed for the COMP condition (see Table 1.8) suggesting a kind of complementarity in the execution of corrective adjustments between the two plants.

Table 3.8. Independent Samples T-Test between *handler* and *grasper* within COOP condition for the dependent measures considered

						95% CI for Cohen’s d	
	t	**df**	***p***	**Cohen’s d**	**SE Cohen’s d**	**Lower**	**Upper**
Submovement_type1	-0.058	14	0.955	-0.029	0.500	-1.008	0.952
Submovement_type2	-0.451	14	0.659	-0.226	0.503	-1.205	0.762
Submovement_type3	-0.318	14	0.755	-0.159	0.502	-1.138	0.825
Total submovements	-0.009	14	0.993	-0.004	0.500	-0.984	0.976

Note. Student's t-test.

For what concerns the endpoint position, the variability of the endpoint is conceived as the standard deviation of the Euclidean position of the tendril on the target. As reported in the descriptive statistics (see Table 1.8) the endpoint variability for the COMP condition (DS=45.776) is greater than the endpoint variability reported for the COOP condition (DS=11.294) suggesting a greater accuracy and a more precise reaching phase towards a moving target than a static one.

8.4 Discussion

In the present study, I investigated whether plants are equipped with different forms of movement accuracy mechanisms when they act towards static or dynamic targets in the framework of cooperative and competitive social attitudes.

The findings suggest differences in terms of submovements (submovements *type 1,2,3* and endpoint variability) for the COOP and the COMP conditions. In particular, for the COMP condition more submovements with a higher endpoint variability than the COOP condition can be noticed. This pattern of movement suggests a fine structure made by numerous corrective adjustments at the end of the movement in order to grasp the support firmly. For the COOP condition, the total number of submovements required is lower and the endpoint variability is smaller than for the COMP condition, suggesting a great accuracy when liaising with another plant. Looking at the results more carefully, I can appreciate how the total amount of submovements not only seems perfectly divided between the two plants co-acting together, but also it corresponds to the exact half of submovements performed by a single plant towards the static support for the COMP condition.

As previously reported in the introduction, decreasing speed helps to improve the accuracy of the movement, and corrective adjustments in shared actions helps the interpersonal submovements coordination. As a consequence, the mechanism controlling submovements creation is tuneable, and implemented to actively co-regulate the partner's behaviour (Tomassini et al., 2022).

In general, I can argue that the frequency of submovements tends to increase when the support is inanimate. This evidence suggests that plants can process the properties of the support and benefit of a motor accuracy mechanism for improving the precision of their movements to firmly approach the support. Further, the endpoint variability confirms this evidence: the standard deviation of the final position of the tendrils is larger for movements directed towards an inanimate support than for the moving plant. This could be explained in the fact that when moving towards a dynamic target, the point where the movement ends required a greater precision due to the smaller size of the tendrils with respect to the wooden pole.

The present results replicate somehow those reported by Ceccarini and colleagues (2020b) where plants produced more secondary submovements when they reach-to-coil a thick support suggesting that plants exhibit more difficulty to grasp a thicker than a thinner support. Here I go a step forward, suggesting that plants co-acting together to reach a shared goal are able to divide the accuracy load in order to save energy and contribute to the fine-tuning of the action. They can do this dividing, complementarily, the number of corrective adjustments.

In literature, the "minimum jerk model" (Flash & Hogan, 1985) explains how the smoothness of an action is based on the smallest amount of corrective adjustments required. In plants, the COOP condition seems the one in which the movement could be implemented in the smoothest possible way by adopting an energy-saving approach evident in the sharing of the demands imposed by the on-line control of movement in order to facilitate the achievement of a goal.

This study demonstrated, the very complex accuracy mechanism of plants when acting in a goal-directed manner, as well as their ability to attune motor adjustments to those of another agent during a joint action. As outlined within the “General Discussion” section, these findings contribute to the notion that plant movement is not simply driven by cause-effect mechanisms and hard-wired reflexes.

Chapter 9

General discussion

9.1 An overview of the present research

The main goal of my research was twofold. Firstly, to demonstrate that plants, despite lacking a nervous system, are agents equipped with a form of motor intentionality able to perform flexible movements depending on the kind of context in which they interact. Secondly, to demonstrate that plants are social organisms able to reflect their sociality in the way they move. These aims provide a link between the concept of motor intentions in an evolutionary perspective that embraces also plants.

In order to reach these goals, I conducted a series of studies in which I used 3D kinematic analysis and gene-mutant plants, to characterize motor intentions in *P. Sativum* acting in different contexts, namely individual, competitive or cooperative.

In the first experiment (Chapter 5) I ask whether the organization of climbing plants' kinematics is sensitive to the "intention" driving their movement towards a potential support. I put plants in a condition to perform "intentional" actions in two different contexts: an individual and a social one. For the individual context, plants acted in isolation to reach towards and grasp a potential support. For the social context two plants were put in the same pot with a potential support in the middle. These are both intentional actions; both involve a movement from one spatial location to another. The critical difference is in the "intentional" component: whereas grasping a support realizes a purely individual intention, acting in the presence of another plant inevitably involves a social intention (i.e., the intention to affect a conspecific's behaviour as part of one's reason to act).

Results revealed specific motor patterns for individually intended actions and actions motivated by a social intention. Pea plants plan and execute actions differently depending on the intention underlying them. When comparing individual and social actions, movement time and the mean duration of the circumnutations were longer for the social than for the individual condition. And, the maximum velocity reached by the tendril during circumnutation was lower for the social than for the individual condition. This signifies a more cautious kinematic patterning for the social situation. These results are suggestive of a more careful honing phase when the goal is nested within a social interaction and they are in line with human studies showing a more careful movement when acting within a social context (Becchio et al., 2008; Sartori et al., 2009). Of relevance, this occurs despite the shape, the size, and the location of the support for the individual condition matched the location, shape, and size of the support for the social condition.

Within the social condition, I noticed an opposite behavioural response between the two plants, showing that the examined context, at first sight, may appear competitive. The winner plant (i.e., the plant who grasped the support) exhibited a higher velocity during circumnutation and a closer proximity to the stimulus for a longer time, waiting for the right conditions to unfold a firm attachment. In contrast, the action for the loser one (i.e., the plant who doesn't grasp the support) is characterized by a submissive behaviour with a lower velocity of reaction. All in all, these results provide the first empirical demonstration that motor intentions in plants are real and context-dependent, guiding the behaviour of plants also to challenge with other organisms.

In the second experiment (Chapter 6), I decided to introduce a multi-disciplinary approach to the study of plants' social behaviour. I asked whether the different behavioural responses produced by the two plants in the dyad were affected by the exudation of specific chemical compounds that regulates their communication and interaction. As a promising candidate I recognized SLs. In the present experiment, I used pea mutant plants to evaluate the potential involvement of SLs on modifying the social behaviour of plants toward a potential support. Mutants are plants in which hereditary changes are purposefully generated. Specifically, *rms1-1* is a pea mutant that does not synthesize SLs due to the lack of enzyme CCD8 (Sorefan et al., 2013), while *rms3-1* is a pea mutant that cannot detect SLs that is exudated by neighbours. I combined *wild-type* and mutant plants to test for the social condition described in the first experiment (Chapter 5). By looking at the results, it can be immediately recognized how the plants behave differently for each combination. Combining a *wild-type* with a *rms3-1* mutant, in particular, enhanced the probability of both plants to grasp the support. When the wild-type is coupled with a *rms1-1* mutant, the result is reversed. Since the mutant is not exuding SLs, the *wild-type* is unable to perceive a neighbour, hence the situation could be analogous to a single plant acting in isolation. Combining two *rms3-1* mutants it is evident that both plants grasped the support. In this scenario, both plants can produce SLs, but do not perceive SLs produced by the other. In other words, they both act in a likely-individual situation. This seems to suggest that the production of SLs appears to be an essential pre-requisite for the implementation of grasping behaviour, most likely due to the transmission of information regarding the qualities of the surroundings from the roots to the shoots (Brewer et al., 2013).

Overall, these findings appear to suggest the role of SLs as a potential chemical involved not only in neighbour detection and communication during a social setting, but also as an important mediator in the transmission of information from roots to shoots, which is critical for properly implementing an approach-to-grasp movement modulated by the social attitude. This is just a first attempt to systematize the role of SLs for the implementation of goal-directed circumnutation.

To sum up, in these first two experiments my focus was on assessing the individual and social motor intentions in plants, both in kinematic and chemical terms, suggesting a possible chemical mechanism at the basis of the complex behaviour observed, that at first sight seemed competitive.

In the second part of my thesis concerned with the last two experiments, my methodology focusses entirely on kinematics. In particular, investigating another kind of social attitude: cooperation.

In my third study (Chapter 7), the main goal was systematizing in kinematic terms the cooperative motor behaviour of plants, focusing on a specific social behaviour: joint actions requiring a shared intentionality to reach a common goal. An aspect still unexplored but promising to bring new insights to the open debate on shared intentionality across taxa. To test for the minimal architecture requirement allowing for shared intentionality, I examined how two pea plants coordinate their actions to grow intertwined when there is a need to climb in the absence of a potential support. A careful kinematic examination of their movement revealed a complementary pattern of movement, with a specific role that each plant of the dyad takes.

Looking at the results, it can be immediately appreciated the two plants' non-casual behaviour during the intertwining interaction. It is evident that the two plants in the dyad manifest specific but complementary behavioural patterns. The *handler* plant bends exaggeratedly toward the *grasper* to facilitate intertwining and then they travel together toward the light. Therefore, it seems that the initiator of the joint action is the *handler*. It signals the other plant on the potential common goal and it coordinates the action. Further, correlational analysis allows appreciating a non-casual correlation both in temporal and spatial terms between the two plants. This signifies they do not approach each other casually. To conclude, I provide the first empirical account of intertwining behaviour. I nested my findings within available theories explaining joint and complementary actions in animal species. This is not to make plants resemble animals but to say that in aneural organisms, a flexible movement driven not only by the intentional stance to reach a goal, but by the shared intention to do it with another agent, is possible too. This is a crucial notion, that vigorously calls for a reformulation of traditional definitions of intentionality based on concepts belonging to sometimes arbitrary and limited conceptions.

Finally, in my last investigation (Chapter 8), I delve into the possible differences between the kinematics of cooperative and competitive action patterns. If the kinematics are sensitive to context, as I hypothesize, then a difference in kinematics should be found between an action performed in the context of a cooperative task and the same action performed as part of a competitive interaction. In order to do this, I capitalized on the issue of accuracy by means of analysing 3 types of submovements. Two experimental conditions were considered. (i) a competitive condition (COMP) in which a plant grew with another pea plant within the same pot in the presence of a potential support in the environment (see Chapter 5). In such circumstances plants have to reach and grasp a fixed support in the presence of a competing plant; (ii) a cooperation condition (COOP) in which two pea plants grew within the same pot without the presence of a potential support (Chapter 7). The findings suggest differences in terms of submovements (submovements *types 1,2,3* and endpoint variability) for the COOP and the COMP conditions. In particular, for the COMP condition more submovements with a higher endpoint variability than the COOP condition can be noticed. This pattern of movement suggests a fine structure made by numerous corrective adjustments at the end of the movement in order to grasp the support firmly. For the COOP condition, the total number of submovements required is lower and the endpoint variability is smaller than for the COMP condition, suggesting a great accuracy when liaising with another plant. Looking at the results more carefully, I can appreciate how the total amount of submovements for the COOP condition not only seems perfectly divided between the two plants co-acting together, but also it corresponds to the exact half of submovements performed by a single plant towards the static support for the COMP condition.

The present results replicate somehow those reported by Ceccarini and colleagues (2020b) where plants produced more secondary submovements when they reach-to-coil a thick support suggesting that plants exhibit more difficulty to grasp a thicker than a thinner support. Here I go a step forward, suggesting that plants co-acting together to reach a shared goal are able to divide the accuracy load in order to save energy and contribute to the fine-tuning of the action. They can do this dividing, complementarily, the number of corrective adjustments.

9.2 Possible mechanisms underlying the observed behaviour

In the second chapter, I described the mechanism through which plants detect and communicate with their neighbours. As previously said, plants live in two contrasting environments: an underground pedosphere and an aboveground atmosphere. This distinction implies that plant organs exist in two distinct environments, and the modalities by means plants communicate and interact are both below-ground and above-ground (Baluška & Mancuso, 2009). Indeed, in nature plants are permanently releasing different compounds to their surroundings. This process of secretion is known as exudation, and it may be carried out by various organs such as leaves, shoots, or roots, which can discharge chemicals in liquid, gaseous or solid forms to their surrounding space (Vives-Peris et al., 2020). In the next sections I will provide a description of the detection and interaction processes both below-ground and above-ground that could be of interest for the present results.

9.2.1 Under-ground interactions

Communication between plants, microbes, and soil animals below ground is driven by the exchange of substances released by one organism and detected by another (Bais et al., 2004). Barto and colleagues (2012) use the term "infochemical" to encompass all substances, generally secondary metabolites and plant hormones, used in communication. For below-ground communication to be effective, enough of the infochemical must be produced by the emitter to get through the soil matrix and reach the receiver in large enough concentrations to trigger a response (Barto et al., 2012). Root-secreted metabolites are engaged in a number of activities in the rhizosphere. Plants may affect soil qualities by modifying the composition of root exudates, allowing them to adapt and survive under harsh environments. They employ a variety of techniques, including (i) modifying soil pH to solubilize nutrients into assimilable forms, (ii) chelating harmful chemicals, (iii) attracting beneficial bacteria, and (iv) releasing poisonous molecules for pathogens, among others. These infochemicals mediate many types of communication between plants and, for example, their plant neighbours (Inderjit et al., 2005), parasitic plants (Fernandez-Aparicio et al., 2011), symbiotic rhizobia and fungi (Mathesius, 2003; Smith & Read, 2008), plant growth promoting bacteria (Compant et al., 2010), and other soil organisms (Badri et al., 2009).

Root exudates are a mix of a wide variety of compounds, including primary and secondary metabolites (Vives-Peris et al., 2020). Carbohydrates, amino acids, and organic acids, i.e., primary metabolites, are released in greater amounts than flavonoids, glucosinolates, auxins, and other secondary metabolites (Badri & Vivanco, 2009). Several studies have found and measured these compounds in several plant species, including arabidopsis, soybean, rice, and common bean (Strehmel et al. 2014; Tawaraya et al. 2014). However, most of the work focused on the identification of the metabolites present in root exudates of herbaceous plants or shrubs. Similar studies with trees are limited to a few species including apple (*Malus pumila*), peach (*Prunus persica*), and jujube (*Ziziphus jujube*; Zhang et al. 2007).

Plants have developed several mechanisms to secrete metabolites into the rhizosphere, including different types of passive and active transports. Traditionally, the secretion of root exudates has been considered a passive process, mediated through different pathways: the transport through the root membrane by diffusion, ionic channels, and vesicles transport (Baetz & Martinoia, 2004). The chemical properties of the compounds to be exuded determine the secretion process that will take place in each case.

For example, diffusion is responsible of the release of low molecular weight molecules, including sugars, amino acids, carboxylic acids, and phenolics (Vives-Peris et al., 2020). Ionic channels are responsible for the secretion of carbohydrates and specific carboxylates such as malate and oxalate (exuded in high quantities), which are transported across membranes not through diffusion, but through a transport mechanism mediated by proteins (Vives-Peris et al., 2020). The last group of passive transport mechanisms is vesicle transport, which is involved in the secretion of metabolites with high molecular weight stored in vesicles (Badri & Vivanco, 2009). This process is also known as exocytosis. The exuded metabolites proceed from the endoplasmic reticulum or Golgi apparatus and contribute to the protection against pathogens (Weston et al., 2012).

Root secretion of metabolites through an active transport mechanism is mediated by proteins located in the root plasmatic membrane (Baetz & Martinoia, 2014). In this context, there are two big families of membrane transporters, namely, ABC ("ATP-Binding Cassette") and MATE ("Multidrug and toxic compound extrusion"; Kang et al., 2011). Protein-mediated root exudation can take three forms, depending on their specificity: transporters that secrete different metabolites; metabolites that can be released to the rhizosphere via different membrane transporters; and compounds exuded by a single transporter (Vives-Peris et al., 2020). Root exudation pattern can be affected quantitatively and qualitatively by different physical, chemical, and biological factors (Vives-Peris et al., 2020). Most of the chemical and physical factors that affect root exudation process are considered abiotic stresses, such as drought, high salinity, flooding, extreme temperatures, or nutrient starvation. However, also other biological systems, such as the roots of neighbouring plants, from the same or different species, and some herbivores as insects or nematodes, fungi, or bacteria can all affect the root exudation process. Therefore, the presence of other living organisms in the rhizosphere can affect plant growth positively or negatively, and these relationships being widely modulated by plant root exudates (Schrey et al., 2014; Dessaux et al., 2018).

In my studies, the social situation in which all the social behaviour and motor responses occur, are strictly dependent on a close communication and interaction between the root systems of the two plants potted together in each experiment. This allows me to argue, that also in these studies several infochemical occurs to exchange information between the plants and act accordingly in a competitive or cooperative attitude. Further, as previously explained, root exudation pattern can be affected by different factor, as for example the roots of neighbouring plants. In this sense, in my studies the behavioural reponses that I can appreciate in a cooperative or a competitive way, are just the tip of the ice-berg, considering all the chemical interactions and communication happening above and below-ground and that are constantly modulated and affected by the presence and the exudation of compounds of the other plant in the pot. Future studies, with a more chemical approach will help to shed light on the quantification and identification of these infochemical during social responses in plants.

Root exudates mediate the interaction among plants of the same or different species, in a different manner depending on root exudate composition and the mechanisms of the relationship.

A multi-tasking exudate: Strigolactones

Almost 80 years after the discovery of the first plant hormone, auxin, a few years ago a new class of plant hormones, called strigolactones, was discovered. These molecules exhibit extraordinary biological activity in a variety of critical biological processes in plants, as well as outside the plant in the rhizosphere, the layer of soil around plant roots (Bouwmeester et al., 2019). Years of research have elucidated why plants secrete strigolactones into the soil.

In 2005 Akiyama and colleagues reported that strigolactones induce hyphal branching in arbuscular mycorrhizal (AM) fungi. Most land plants engage in a symbiotic interaction with these AM fungi that supply water and nutrients to the plant, in return for photo-assimilates from the plant (Harrison, 2005). This discovery led to the conclusion that plants secrete strigolactones to recruit AM fungi and that parasitic plants have hijacked this signalling molecule to ensure germination in the proximity of a host root. After the discovery of their shoot branching inhibiting effect, further studies showed that strigolactones also regulate other aspects of plant development including root architecture, secondary stem growth, and leaf senescence (Al-Babili & Bouwmeester, 2015; Waters et al., 2017).

To this end, in Chapter 2 I explained how sometimes novel behaviours can develop by linking, repurposing or building on ancestral processes that previously served a different function (Katz & Harris-Warrick, 1999), and the evolution of social behaviours appears to follow this pattern across species.

In this sense, the roles of SLs could have followed similar lines of evolution. Their original function was presumably in signaling between cells and in the control of growth and differentiation in early plants. For example, strigolactones are found in mosses, liverworts and in the alga *Chara coralline,* where they promote rhizoid growth (Smith, 2014). The filamentous moss *Physcomitrella patens* produces strigolactones that can regulate protonema branching and growth of filaments of a neighbouring colony (Proust et al., 2011). Thus, Smith and colleagues (2014) saw how growth and competition of neighbours can be coordinated by strigolactones – a principle that operates within higher plants to coordinate root and shoot growth. Fungal symbioses arose with the colonization of the land some hundred million years ago. Some liverworts enter into symbiotic relationships with mycorrhizal fungi, and although it is not yet know if this interaction depends on strigolactones, it is a hypothesis worthy of testing (Smith, 2014). With the evolution of vascular plants came complex patterns of shoot branching and the opportunity for long distance transport of strigolactones. It is in the flowering plants that the important functions of strigolactones are best known and best understood (Smith, 2014). The use of SLs for communicative and detection of neighbours' purposes is one of the latest role of SLs in its invention in the evolutionary history (Smith, 2014).

Recently, researchers demonstrated that plants are able to adjust their growth in response to increased competition for soil resources by measuring the levels of SLs surrounding the root (Wheeldon et al., 2022). They proved that SLs play a role in neighbour recognition, acting as plant-plant signals permitting plant communication (Wheeldon et al., 2022). Also, SLs have the ability to modulate the internal plant communication, transferring information from roots to shoots (Brewer et al., 2013).

The data included in my thesis, with two plants potted together during the social conditions calls for a kind of communication through the roots system.

All the experiments were made controlling and balancing the nutritional resources for both plants. This is also confirmed by the RSA (see Chapter 5) that showed how the two plants acting in the social conditions do not present morphological competition at a root-level (i.e., RSA). Remember that plants may become territorial by proliferating roots with the intent of directly discouraging intrusions from other individuals for access to resources (Falik et al., 2005; Dudley & File, 2007). Thus, plants are expected to demonstrate a mosaic of competitive behaviours for the same or different resources. In this view I might have expected the roots' area for the winner plants to be greater than that for the loser plants. However, no differences were detected, suggesting that I am not in the presence of a competitive situation in the under-ground sector. Rather, the two individuals share available resources via roots system and energy is saved to behave appropriately and competitively in the above-ground sector of the plants.

At the roots level, the metabolites produced by each plant could have played a role in detecting and communicating with the neighbours. In this sense, my studies cannot demonstrate quantitatively and qualitatively the amount of exudates possibly involved in the interaction and then in the unfolding of the motor response. However, the data reported in Chapter 6 using SLs mutants may say something in this respect. As outlined above SLs seems the perfect candidate to play a role in sending information from the roots to the shoots, thus allowing the plants to perceive the features of the environment and produce an adaptive response.

In light of this, I can argue that my study (Chapter 7), add another contribution to the understanding of the multifaceted roles of SLs. SLs not only seems implied in the detection of neighbours and the communication among plants positioned in close proximity. Also, SLs seems involved in the implementation of specific social responses through the motor outcomes that a situation, as the one of grasping a potential support in the environment, can offers. In this sense, the role of SLs in sending information from roots to shoots seems the crucial transfer of the result of the communication happened below-ground between the two plants, and then made it explicit in the organization of the motor response of the aerial parts of the plants, above-ground.

9.2.2 Above-ground interaction

Plants possess several mechanisms to communicate and interact with other organisms also with their aerial sector. Indeed, from stems, leaves and flowers plants are able to emit volatile organic compounds (VOCs). These chemical messages may also the control and execution of the circumnutative movements that are performed above ground. In particular, the study related to the intertwining behaviour (Chapter 7) seems a perfect exemplification of the ability of plants to communicate and distinguish self from others. The ability to get in touch and provide a mutual support with the tendrils of the other plant could claim for a chemical cue that allow plant to recognize each other and coordinate the movement properly. Touch by neighbouring plants appears to play a particularly crucial role in priming plants for future interactions and has been shown to influence VOCs and root exudate emission (Elhakeem et al., 2018; Markovic et al., 2019).

For example, as happens in the *Cayratia japonica,* tendrils demonstrate self-recognition, allowing them to coordinate their coiling responses (Fukano & Yamawo, 2015). This is possible because shoot tendrils, like root apices, employ their chemical sense to discriminate themselves (Fukano, 2017). Tendrils of the vine *Cayratia japonica* have specific chemical cue that recognized their own identity from the tendrils of other plants (Fukano & Yaamawo, 2015).

In the present thesis, the presence of a potential chemical cue on the tendrils' tips could explain the coordinated and organized pattern of movement of two plants intertwining their tendrils together and not with their owns. In this sense, the intertwining behaviour observed (Chapter 7) could be a matter of shared intentionality expressed through a coordinated action, via a possible chemical tool favouring the recognition of the other plant's tendrils. Intertwining, in this broader sense, could be also a matter of proprioception (i.e., the sensation of position and movement of a body; Tuthill & Azim, 2018).

Indeed, recent reports demonstrate that the proprioception of plants is mediated by the long actin filaments in elongating fibre cells, which, acting as a bending tensile sensor, perceive the plant's posture (Hamant & Moulia, 2016). These findings are supported by research on Arabidopsis mutants deficient in actins (particularly ACTIN-8), which show an aberrant sensitivity to gravity, tilting, or other external disturbances (Okamoto et al., 2015). Proprioception may help climbing plants to know the location of their tendrils and contribute to the generation of feedback information needed for altering movement execution when used in conjunction with other sensory modalities (Ceccarini et al., 2020b). Indeed, in addition to proprioception, plants have at their disposal a great variety of sensory modalities (Karba, 2015), including vision (Crepy & Casal, 2015), acoustic perception (Gagliano et al., 2017; Hussain et al., 2023) chemosensory perception (Weidenhamer, 2016).

Other strategies to communicate and detect the other plant in the environment came from the primitive concept of vision. In particular, as previously explained in Chapter 2, plants are able to perceive some lights, and refer them to the presence of other individuals. Plants are extremely sensitive to changes in light quality, even in the absence of a decrease in PAR, since they suggest current or future light competition (Roig-Villanova & Martinez Garcia, 2016). Further, light signals supplied by neighbours are sensed by specific phytochromes, which have a high sensitivity to far-red light. Because the tips of leaves are the principal location of light cue sensing, self-shading is less likely to activate these reactions (Pantazopoulou et al., 2017).

The ability to discriminate lights and dark area could be also at the basis of the motivation for which the plants in my experiments (Chapters 5 and 6) don't want to grasp the same support at the same time, maybe to avoid the shadow produced by the close proximity on the same support of one another. This could explain why the other plant *decide* to search for alternatives, in order to maximize the amount of light in the environment.

All in all, these possible explanations are speculative ideas on the biological mechanisms that needs to be clearly examined with an empirical approach. In this thesis, only one of the possible biological mechanisms involved to explain this behaviour has been investigated. The role of SLs has been partially evoked to explain the findings concerned with intentional actions in a social setting (Chapter 6). However, a further and more detailed investigation is needed, in particular by means of gas-cromatography and mass-spectroscopy techniques to identity quantitatively and qualitatively the volatile chemicals emitted by the plants to communicate.

Next studies await to cracking the code on sociality and motor intentions in plants, by means of a pluralistic approach in order to merge the kinematic and chemical analysis together. This will better explain the physiological mechanisms at the basis of plants behaviours.

9.3 Linking data to theory

At the outset of the present thesis, the first chapter describes recent theories broadcasting alternative perspective on cognition, and in particular, how sensorimotor abilities merging perception and action emerge also in aneural organism by means of their interaction with the environment. Merging cognition and action allow me to explain the complex social behaviour observed by pea plants referring it to the concept of motor cognition.

It is now time to re-take the concept of sensorimotor abilities in Chapter 1. There the concept of sensorimotor activity is related to the earliest type of cognitive structure, or psychological process, which develops in parallel with fundamental sensorimotor movements led by sensorimotor intentionality. In simpler terms, I can argue that understanding the goal-directed character of the most fundamental sensorimotor activity is thus critical for understanding the nature of cognitive processes in more complex agent-environment interactions (von Hofsten, 2009). Here, the intentionality of plants may be understood as the movement of growth, directed toward the optimal patches of nutrient-rich soil and sources of light. To echo Marder (2012) who sees intentionality in plants as *"directedness-towards"*. This ability to merge perception and intention in order to act is what brings plants to the domain of cognition, or better, in the domain of motor cognition. A domain where, in aneural organisms such as plants, the link between action and cognition appears to be possible if we consider the organism, the environment and their interaction as a *single-cognitive-unit*.

In my studies, *P. sativum* plants are able to perceive the characteristic of the environment, the neighbours and the objects in the surroundings. This active exploration, throughout their perceptual system (i.e., roots system and infochemicals) make them able to adapt in the environment, executing adapted and flexible motor responses.

Information that plants received from the environment, in an ecological and sensorimotor perspective, calls for the concept of "affordances" (Gibson, 1979). Affordances are the most essential chances in the environment for each organism to interact with it and survive. Agents detect affordances rather than neutral information that perceptual systems must interpret and connect to action capacities. This active, direct view of perception corresponds to a view of perceiver and environment as co-defined and co-dependent thing.

In my first experiment (Chapter 5) the affordances of the environment that are offered by the potential support and the presence of a neighbours (i.e., social affordances) inform the plant of a possible social interaction. In this sense the action is influenced by the social affordances provided by the interaction per se.

Looking at the results, the two plants acting in the dyad, presented different motor patterns, suggesting different kind of adopted behaviours to face the situation. The same environment and the same social situation provided different affordances depending whether the plant is a winner or a loser. How a social affordance could be perceived, is dependent on what the agent offers (i.e., body postures, communication, …). This calls, in speculative terms, for a possible influence of the communication happened between the two plants as a modulator for the perceived affordances, eliciting two different actions.

Indeed, other agents and their behaviours constitute extremely relevant elements of the environment because they offer a variety of action and interaction possibilities (Orban et al., 2021). To better explain, social and communicative affordances embrace not only the significance of events, objects, and so on for the perceiver, but also the significance of the environment for other agents (Reed, 1988; Zaff, 1989). For example, if an agent is sufficiently skilled, it can perceive not only what the human environment affords it, but what the environment could also affords to another agent. On this basis, an agent can tune its behaviour toward the other one (Loveland, 1991).

The intertwining study (Chapter 7), is a perfect exemplification of social affordances in this sense. The pea plants perceived each other as a potential support and then acted in concert. This is witnessed by how the two plants coordinate their action in time to meet at a precise point in space to reach kinematical consonance. Not only the plants perceived the others as potential support (i.e., the affordance of a support) but also, they seemed to be skilled enough to recognized also the significance of what they represent in terms of affordance for the other plant. This is evident from the progressive approach towards each other, characterized by a complementary behaviour with a role-taking that divide the amount of energy and work to spent in order to reach the same common goal.

Further, this is also clear from the last study (Chapter 8) considering the accuracy of the movement implemented to act jointly, that present a similar amount of corrective adjustment between the two plants in order to correct the trajectory of one another and accomplish the goal to climb. The affordances that a plant could offer to one another is to be a potential support, in the absence of inanimate ones, and the elaboration of this information drives the perceptual and the action towards the implementation of a correct and adequate motor response.

9.4 Final remarks

It is impossible not to consider entire woods, forests, fields as big superorganisms, in a pure *gestaltic* way in which the total is more than the sum of each single part (Bonato & Castiello, 2020).

This deep conviction allows me to investigate two big questions regarding the astonishing way plants live their social life. Are plants equipped with a form of social cognition? Are plants able to implement different motor patterns depending on the individual or social intention driving their actions?

My results demonstrated that *P. Sativum* plants seems able to detect the neighbours and integrate the perceptual information derived from the environment (i.e., presence or absence of neighbours, presence or absence of inanimate potential supports) in order to implement goal-directed actions and achieve their goal with different motor programs depending on the context and the kind of affordances that the environment could offer them.

The idea that plant communicate to each other, both above and below-ground, to adapt their movements to the requests of the environment, has been also partially investigated in this thesis. In these terms, my results on the role of SLs (Chapter 6) represent the first step towards an investigation that merge the physiological and behavioural aspects, demonstrating for the first time that SLs could have a partial role on the implementation of flexible actions depending on the absence or presence of neighbours.

My intertwining study (Chapter 7), regarding the ability of pea plants to act jointly, when potted together in the absence of the potential supports, shed light on how plants *decide* to cooperate and reach a common goal that is fundamental to their survival. This joint action is a clear example of shared intentionality in an organism without a theory of mind. Affordances offered them the sensorimotor abilities to act jointly.

Future studies need to merge kinematic and physiological analysis in order to embrace a pluralistic approach to the study of such a complex behaviour and integrate these results with ecological observations in open environments in order to better understand the ecology of ecosystems.

During these three years of research, I attempted to demonstrate that, despite lacking nervous systems, plants are social organisms too and they are able to put their sociality in the way they move, such as humans and other animals do, showing astonishing capacities of motor cognition. My findings open the debate on a reconsideration of the framework of sociality and motor intentions across taxa, in a new perspective that includes also plants.

We now know that plants and animals descend from a common ancestor (Theobald, 2010). Then, we also know that at a certain point of evolutive history, around 180 million of years ago, flowering plants and mammals began their co-evolution (i.e., the evolutionary process where two species adapt to each other over time) until nowadays at several levels (Baluška & Mancuso, 2009). Plants, animals, fungi are the results of different evolutive lines, that shaped the ability to survive on earth in different forms.

To live is a matter of adaptation, that is to say a matter of cognition to intentionally obtain the necessary to survive. Along the intricated and multifaceted tree of life, intentionality serves different needs which are shaped differently in form but not in purpose.

In this sense, I would like to conclude saying that plants are cognitive, social and intentional agents in a non-metaphorical way.

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