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*Comparing the effect of embodiment on
distributed information processing in
plants and ants*

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Laymen's summary

Every organism senses information and integrates it to make decisions, such as whether to run or to fight. But often groups decide together, such as when a flock of birds navigates towards its destination. Here, there is no single bird that dictates the flock's behaviour. Instead, the different parts of decision-making are divided between different birds. Each bird makes their own choice with the limited information they have, and then the flock combines those individual conclusions into an overall decision. We call this *distributed information processing*.

In distributed information processing, naturally the set of steps leading to a decision (the *algorithm*) matters. However, an equally important part is the environment or context that this algorithm operates in, such as how much 'brainpower' the group has, or whether they can calmly decide or are being chased by a predator. A key part of this context is the shape and functions of the group's 'body': here think of all cells in a tissue as the tissue's body, and all ants in a colony as the colony's body.

In this paper, we used existing scientific literature to examine the cells in a plant and the ants in a colony as groups deciding together. Specifically, we compared their decision-making processes and tried to understand the influence of their 'bodies' on these processes. Since plant cells cannot move and ants can, we expected plants and ant colonies to use different algorithms because of these bodily differences.

The first thing we found is that each group lies on a spectrum with their interaction network between members. There are more solidified networks such as plant cells, where each member can only interact with a fixed set of others. Alternatively, ants form a more liquefied network, because each ant can simply move around to interact with a new set of ants. We found that the more solidified networks structure their interactions to help with information processing, whilst movement enhances information processing in the more liquefied networks instead.

Next, we examined plant vascular networks and ant pheromone trails, which enable fast transportation of goods and information around the plant or colony. As these structures develop, they must maximise transport speed while minimising construction costs, within the limits set by their 'bodies'. Long-distance communication networks such as these are not essential to information processing, but they can make messages quicker or more reliable. They also enable plants and colonies to interact with neighbours.

Finally, the result of one information process influences the input for the next one. We suggested this output-input feedback often occurs because this result changes something within the plant or colony's 'body', which the later process then senses. This works better than changing something in the outside environment, because the plant or colony's 'body' is much more controllable.

This group-like view on plants can inspire new research questions. For example, a growing plant makes more leaves, and these are farther apart. Does this matter for integrating all the information from the different leaves to make a decision?

Abstract

Information processing is an essential part of biology, and is often distributed across multiple entities, such as cells in a tissue or ants in a colony. However, not only the computation steps themselves matter, but also the context in which they occur. An important example is embodiment: the influence of body shape and properties on information processing. Since a few years, research explicitly distinguishes between solid brains, consisting of sessile parts, and liquid brains with motile parts. Previous research separately examined plants and ant colonies as solid or liquid brains, respectively. This literature review directly compared these two systems to investigate how their solid or liquid embodiment shapes their distributed information processing. Key results were: there is a solid-liquid brain spectrum, which corresponds to computations using structure or movement, respectively. Developing networks must balance construction cost against transport speed within embodiment constraints. Local communication suffices for system-wide information integration and complex computations, but long-distance communication methods add signal robustness, quick responses due to shortcuts through 3D space, and enable interaction with neighbouring plants or colonies. Computational output typically modifies input of subsequent information processes, often through proprioception. Contrary to the dominant perspectives in the plant cognition debate, this research showed the existence and importance of whole-plant emergent processes, but started from the plant embodiment instead of forcing plants into a neural animal mould. In this way, new research questions arise, such as how communication delay and signal integration are affected when growth adds plant organs and increases inter-organ distance.

Keywords: distributed computing, information processes, embodiment, solid brains, liquid brains

Introduction

We view biological systems, from cells to ecosystems, as products of evolution by default. However, to gain new insights other views can be complementary. When we see a cell, organism, or other biological system as a **computing** unit (Box 1), we can draw on the results of fields such as computer science and information science.

When we view a tissue, organism, or ecosystem as a computing system, it can fall anywhere on a continuous sliding scale between centralised and distributed computing. Some biological systems can be viewed as fully **centralised computing** units, such as a vertebrate body with a specialised computing organ: the brain. Others may be better suited to a **distributed computing** representation, such as a flock of birds. Yet others may occupy the intermediate niche between centralised and distributed computing, such as a group of animals with dominant individuals, or the arms and brain of an octopus.

BOX 1: COMPUTING

Biological systems compute by using the information in an input to come to a conclusion or decision. This conclusion or decision is then the output.

All information processing steps can occur in a single organ, organelle, or other place. These are centralised computations. On the other hand, a group of cells, tissues, or organisms can also come to a conclusion together, without any centralised decision process. Instead, the conclusions of each computing unit are aggregated into a final result. We call this distributed computing.

A centralised computation has the clear advantage that all information is always available, whereas in distributed information processing messages must be passed between participants [1]. Moreover, some messages may contain misinformation, because of either random errors or deliberate maliciousness, which makes the computation more difficult [1].

However, distributed information processing has its own merits. Firstly, the system is robust against computational errors or failure to respond by individual participants [2], [3]. Secondly, creating more computational power can be done by adding more units instead of designing a more powerful (but also more complex) system [2], [3]. Thirdly, the connections between units can be adapted to run different algorithms, which adds flexibility and evolvability to the system [2], [3].

Randomness and feedback loops are important components of distributed systems [4]. Stochasticity can allow systems to decide between equally good options (symmetry breaking), and it can make information processing robust to noise [4]. Positive feedback can speed up decisions and enable distinction between small quality differences by amplifying initial subtle differences in initial assessments. However, it may also prevent slime moulds and ant colonies from switching to a better food source when it appears, because their reaction to the initial food source has been amplified beyond any reaction that the new, better option can elicit [5], [6]. Negative feedback, on the other hand, confers robustness against environmental changes (e.g. in homeostatic processes) and can be used to shut down a positive feedback loop when it is no longer necessary [4], [7].

A set of computations or information processing steps, be it in a computer or biology, can be considered as an **algorithm**. If we want to understand how a cell, organism, or eusocial colony makes a decision, we need to know the underlying algorithm. At first glance, this algorithm tells us all we need to know about the information processing. But in biology we cannot understand the computation without the algorithm's **context**, often called the model in computer science [8]. The context sets limits in which the algorithm has to operate, such as network topology or available memory, but also ecological and evolutionary constraints [7], [8]. For example, ant colonies in humid areas will forage continuously unless actively inhibited, because they will gather more energy and water than they spend [7]. Their counterparts in drier areas will only send more than a skeleton crew of foragers if the colony knows food is present, because foraging in the dry air has a net energy cost [7].

One of the most important parts of the context of any biological algorithm are its body shape and properties (here taken in the liberal way, thus everything contained in the cell membrane can be seen as a cell's body, and all ants in a colony as the colony's body), and the environment it can sense and act upon [9]. In analogy with embodied cognition, we will refer to this as embodied computing or **embodiment** for short.

Embodiment is an important part of information processing in any form, silicon-based or carbon-based. Traditional silicon computers use binary memory and logic in their architecture, and therefore the standard algorithms for almost any human-designed computation assume this binary architecture. However, synthetic biologists have found that analogue computing algorithms allow cells to process information more efficiently, since the cells can sense and encode more information in the same signalling molecules: not just their presence or absence, but also their concentration [1]. Likewise, the topology of an artificial neural network layer may greatly enhance its suitability for a certain task: for a classification task, we would choose a fully connected output layer, whilst fully convolutional output layers are good at categorising pixels in an image [10].

Biological systems show embodiment in a myriad of ways. In a striking example, ants memorise views along a foraging route [9]. On their way back to the nest, they rotate their body to match their current view with their memories, and go forward whenever the image is familiar [9]. Since they can barely rotate their head, the view is familiar precisely when they have headed this way before [9]. This allows these ants to use an extremely simple algorithm and low-resolution images to find their way, where man-made robots need complicated calculations on high-resolution visual data [9]. As another example, the escape rate of prey from a predator can only be understood by including not just biomechanical constraints, but also information processing delays [11]. In plant cells, organelles are actively transported along actin filaments in the cytoskeleton [12], [13]. It has been shown that we only need to know the topology of these actin filaments to predict cell-level properties, such as how the Golgi system moves across the cell [12], [13].

Here, we are interested in the effect of embodiment on distributed computing algorithms in plants. We may expect the primarily sessile nature of plants to play a key role in their embodiment and thus their computations: the cell wall of plant cells is rigid and prevents movement of individual cells, leaves and roots do not slide around on the stem, and once a plant has germinated, it will remain at the same position in the soil until it dies. However, at the genet (all the tissue arising from a zygote) level of clonal plants we find movement: as a genet creates new ramets (individual plant bodies) connected to the older ones, the genet can adopt a 'stay-and-move' strategy to explore the surrounding space and mine nutrients in a wider area, which may then be shared between ramets [14]. We see a similar stay-and-move pattern when a plant grows: organ growth displaces the meristems and grants the plant access to new locations in 3D space. The most extreme cases of

movement in plants are pollen and seed dispersal, but these tend to be confined to a shorter time window than growth and clonal reproduction.

To discover the effects of embodiment on plant algorithms, here we will compare plant computational processes with corresponding processes in an ant colony, which has moving parts. We will consider different aspects of embodiment and how these interact with the distributed information processing in these organisms (summarised in Table 1). We will start with the influence of movement on network structure, function, and development, then discuss local and long-distance communication, and finish with the role output may play in shaping input for the next computation.

Facets of embodiment

Solid versus liquid brains

By definition, distributed computations happen in a network of agents, such as plant cells or individual ants. A prime facet of embodiment is whether the units in this network can move. Since ants can move, but plant cells cannot, this influences which cells or ants can have direct connections with each other. What consequences does movement have for this set of connections, and what consequences does this have for how the network operates? And does only the binary motile/sessile distinction dictate these consequences or does each network fall somewhere on a continuous spectrum?

Solid brains consist of computing units which are sessile. Hence, their potential set of connections with each other is fixed over time [15]. However, which connections are actually made, and how strong these connections are, can still vary [15]. Examples of solid brains are human brains [16], artificial neural networks [17], and plants [15]. The network can tune computations by changing the actual connections between its parts, as well as the strength of these connections.

On the other hand, computing networks with moving units, such as ants [16] or termites [18], are **liquid brains** [15]. Because their units can move relative to each other, the network of potential connections can change over time, and is instead constrained by the space the ants or termites can move in [17]. This type of network is not limited to the social insects: other examples are swarm robots [17] and the immune system [16].

Some brains are more solidified than others (Figure 1). In a fully trained artificial neural network, no connection changes its strength (its weight) anymore. On the other hand, plant cells in a tissue can change their connection strength with each other in several ways. The two main methods are changing the position, number and diameter of plasmodesmata for bulk connection, and changing the position and number of membrane transport proteins for molecule-specific connections. The spectrum continues in liquid brains: an ant colony has more spatial structure and is thus more viscous than the immune system, which is much less constrained [16].

The stability of potential connections in solid brains allows for stable network structures such as hierarchies (e.g. cells-tissues-organs) in the system, so that each input can be abstracted at multiple levels [17]. This allows for complex computations such as pattern recognition [17]. Moreover, information is usually conducted more quickly in a solid brain compared to a liquid one, for example your neurons firing to move a leg versus your immune cells fighting off a cold. A drawback of such solid networks is that they need to create hub units which connect distant parts of the network (e.g. vascular cells, neurons) to allow efficient information transfer in an upscaled network. However, the reliance on such hub units decreases network robustness [17].

Table 1. Comparative overview of embodiment aspects for plants and ant colonies discussed in this work.

	Plant	Ant colony
<i>Solid or liquid brain</i>	Solid, mutable connection strengths	Viscous liquid
<i>Network structures</i>	Vascular system	Pheromone trails
<i>Network development embodiment constraints</i>	Tissue structure	Number of nest entrances
<i>Connection cost</i>	High	Low
<i>Communication methods</i>	Local signals, vascular network, volatiles	Ant-ant contact, pheromone trails, chemical footprints
<i>Information integration</i>	Moving patterns, hub cells	Walking ants
<i>Nutrient transport</i>	Vascular network	Pheromone trails
<i>Shortcuts</i>	Volatiles	Ants leaving trail
<i>Interaction with neighbours</i>	Volatiles	Chemical footprints
<i>Output-input feedback found in</i>	Tropisms, development	Nest construction

Since the parts of a liquid brain can move in space, information can be transferred easily across long distances, which allows these brains to scale to large sizes without any fragile hub units [17]. They can then cover a large and varied area, which allows for timely responses in any part of the area of

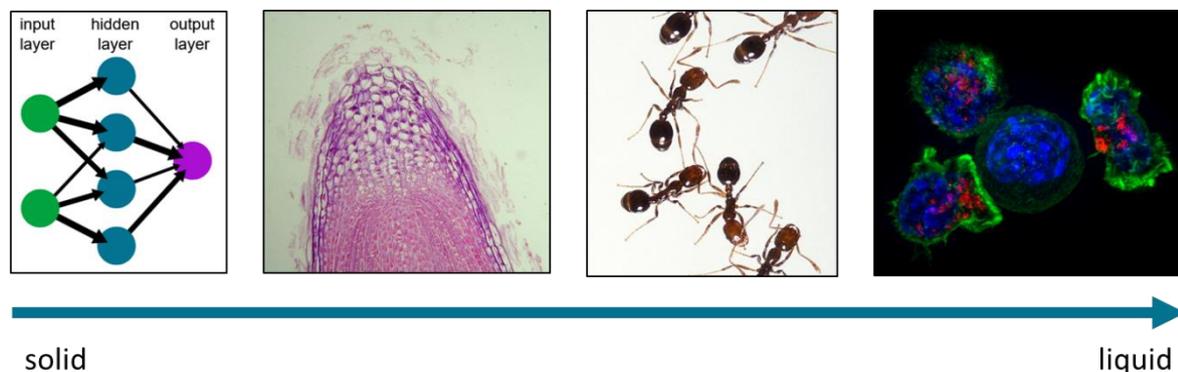


Figure 1. Solid and liquid brains fall on a continuous scale. From left to right: a neural network, plant root tip tissue, walking ants, and immune cells attacking a cancer cell.

Attributions from left to right, each modified from:

https://en.wikipedia.org/wiki/Neural_network#/media/File:Neural_network_example.svg By User:Wiso - from en:Image:Neural network example.svg, vectorialization of en:Image:Neural network example.png, Public Domain, <https://commons.wikimedia.org/w/index.php?curid=5084582>; https://commons.wikimedia.org/wiki/File:Root_tip.JPG Clematis, CC BY-SA 2.5 <<https://creativecommons.org/licenses/by-sa/2.5/>>, via Wikimedia Commons; https://en.wikipedia.org/wiki/Ant#/media/File:Fire_ants_01.jpg By Stephen Ausmus - <http://www.ars.usda.gov/is/graphics/photos/dec04/k11622-1.htm>, Public Domain, <https://commons.wikimedia.org/w/index.php?curid=10112924>; https://en.wikipedia.org/wiki/Cytotoxic_T_cell#/media/File:Killer_T_cells_surround_a_cancer_cell.png By The National Institutes of Health - <https://www.flickr.com/photos/nihgov/20673870162/in/album-72157656657569008/>, Public Domain, <https://commons.wikimedia.org/w/index.php?curid=49182097>

interest, such as territory defence for ants or an immune reaction in humans [17]. The environment can even become part of information processing, such as how termites preferentially work on their mounds in areas of positive surface curvature, which results in either smoothing out or amplifying of initial irregularities in tunnels [18].

On the other hand, whilst solid brains can use spatial structure to represent the outcomes of partial calculations, the mixing of moving ants or immune cells in a liquid brain destroys such helpful spatial distributions [17]. An example of a solid-brain advantage can be seen in plant respiration. When the air becomes dryer, stomata in plant leaves must find a balance between water loss and gas uptake, by adjusting their aperture [2], [19]. Whilst most stomata will close as expected, some patches of stomata will instead open further [19]. These patches will move over the leaf as time progresses, suggesting cellular automation-like computation processes are at work to find the correct degree of stomatal opening [19].

In conclusion, we can place networks on a solid-liquid scale. Those at the solid end of the scale, such as neural networks and plant tissues, can structure their connections to rapidly transfer information and do complex computations. However, the hub units or moving patches they need to accomplish this are fragile. On the other hand, the more liquid networks can use movement instead to scale up information processing. This allows them to respond timely anywhere in a large area, and use environmental variation to structure their information processing. However, the spatial distribution of individual units is variable and thus less suited to carry information.

Creating a network structure

Plant cell networks and ant pheromone trails perform distributed information processing, but they themselves are also a result of developmental computations, giving rise to a ‘nested distributed computation’. In the next section, we ask: what computational processes help create these networks, and which types of signals do they use? What trade-offs play a role in network creation, and do these manifest similarly or differently in plants and ants? How does embodiment constrain or facilitate network creation?

Plant vascular systems

In plant shoots, the starting material for these developmental computations is found in the apical meristems. There, cells have a shape that constrains them to a localised position: the cell wall of plant cells prevents them from forming the elongated connections we find in animal neurons, such as dendrites. As a consequence, the **degree** (direct number of connections) of even the most connected plant cells is distinctly lower than the hub cells (e.g. neurons) in animals [2], [3]. This makes the network more robust against errors in or death of individual cells, but limits information transfer speed [2], [3].

How much to invest in vasculature?

The apical meristem network is even more uniformly connected, and thus robust, than we would expect *a priori* [20]. This organ-level uniformity arises from local rules [20]. Firstly, highly connected cells are likelier to divide [20]. Moreover, the dividing cell wall is placed so that its length is minimised, which corresponds to minimising cell degree [20]. Since these meristems are relatively small organs, even the furthest cells can already communicate without much delay. Therefore, it may pay for the meristem to focus on robustness over connectivity by promoting this uniform connectedness level.

As tissue grows, vascular systems develop using local connectivity rules, which we will examine in more detail later [21]. These transport networks allow water, nutrients, and signalling molecules to

be transported efficiently within and between organs [21], [22]. However, vascular cells cannot aid in performing the primary organ function (e.g. photosynthesis in a leaf and water and nutrient uptake in a root) and thus the plant has an interest in minimising its vascular fraction [21], [22]. In their stems, plants lie along the Pareto front between total vascular branch length and nutrient transport distance [22]. This means they manage to optimize this trade-off, although different species find different optimal balances [22]. For example, sorghum plants connect each leaf separately to the central stem. This shortens nutrient travel, but requires more resources to construct vasculature. On the other hand, groups of tomato leaflets branch off the same rachis (the “stem” within a compound leaf). This lowers vascular construction and maintenance costs, but requires nutrients to take an indirect, and thus longer, route.

Minimisation of nutrient travel time in tissues depends on the fraction of vascular tissue, as well as the organ dimensionality (flat or 2D, leaf-like or 2.5D, or fully 3D) [21]. In general, in 2.5D and 3D tissues a certain fraction of vascular cells optimises the trade-off between vasculature cost and information speed, whilst for 2D tissues there is no such optimal fraction, and thus no net benefit of creating vascular tissue [21]. As such, we do not expect purely 2D tissues to invest in vasculature, whilst 2.5D and 3D tissues do benefit from creating vessels [21]. This matches what we see in nature [21].

[22] focus on the vasculature in branches, so from the base of the leaf to the base of the stem. However, this vascular cost-resource speed trade-off may also be at work in leaf venations. Sorghum and many other grasses have parallel leaf veins, which minimises travel time at the cost of extra vasculature, compared to the branching veins of a tomato leaflet. Whether these architectures indeed achieve an optimal solution to this trade-off needs to be investigated experimentally.

Where to invest in vasculature?

But which connectivity rules does vascular development use? [21] simulate this development by fusing nodes (i.e. cells), which reduces the path length of connections across the network. This corresponds to phloem cells joining together with a sieve plate, which allows for efficient transport of nutrients and signalling molecules [21]. Their algorithm decides either deterministically or stochastically which nodes to fuse, based on node centrality measures: either **closeness** or **betweenness centrality** (Box 2). This way, the algorithm aims to minimise the average path length in the tissue.

Across all dimensions and vasculature fractions tested, betweenness centrality performs better than closeness centrality, although the differences are less pronounced in lower dimensions [21]. In other words, the best candidates for vascular cells are not those in the centre of the network, but rather those which transport many molecules. We may therefore expect a plant-produced (and not external) diffusible molecule to drive the selection of vascular cells.

In leaves, vascular development starts with the main veins (midvein or main parallel veins) growing from the leaf base to its tip, after which more minor veins branch off these major veins [25]. This real-life pattern matches a betweenness centrality-based algorithm, where an established major vein allows nearby cells to transport more goods, and increasing their chances of becoming a minor vein cell. The plant hormone auxin, which is transported into the leaf from the stem, is a primary candidate for driving this selection of vascular cells [25].

In a clear example of embodiment, the cellular structure of the underlying tissue may enhance or decrease the performance of methods based on different centrality measures [21]. For example, the sepal epithelium has giant cells which act as hub cells, and their large betweenness centrality makes minimising path lengths easier for algorithms that use betweenness centrality measures [21]. In a

way, the giant cells have done part of the legwork for the vascular development algorithm already. On the other hand, the explicitly uniform topology of the shoot apical meristem requires these betweenness-based algorithms to do all their legwork themselves.

Nutrient fluxes as vascular development signals

However, not only vascular cells can be involved in optimizing transport of goods and information. [24] show that the hypocotyl atrichoblast epidermal cells in certain *Arabidopsis thaliana* ecotypes have a higher betweenness centrality than their trichoblast counterparts, and experience a higher flux of bulk diffusible molecules. If a similar patterning also occurs in the root, this epidermal 'highway' may also be adaptive by dividing labour between the hair-producing trichoblasts, which take up nutrients from the soil, and the atrichoblasts, which then transport these nutrients away and allow the trichoblasts to keep a favourable gradient [24]. A similar mechanism may be at play in vascular cells at the tip of vessels. This may resolve the apparent paradox that even though these cells score low on both betweenness and closeness centrality, the plant nonetheless invests in vasculature there.

An additional factor promoting vascular differentiation may be the flux of incoming nutrients these cells experience. Especially near the ends of veins, these cells score low on betweenness centrality (and thus not have a high enough concentration of this diffusing molecule). Yet these cells may fill an essential role in transporting gathered nutrients or produced assimilates away from their neighbours, so that these can maintain a favourable gradient. This gradient may serve double duty as another vascular differentiation cue.

In summary, the physically small apical meristems do not need to invest in connectivity, and can thus emphasise network robustness instead. Once a tissue enlarges, vasculature develops to ensure goods and information can still be transported fast enough across this tissue. However, vasculature is costly, and thus each plant faces a trade-off between transport speed and vasculature investment costs. Each species finds a different optimal balance for its branches, and possibly also its leaves.

BOX 2: CENTRALITY MEASURES

There are several ways to describe how central a protein, cell, or individual is in a network. Closeness centrality measures the average distance to all other individuals in the network, so individuals with a high closeness centrality are found near the centre. In plants, this centrality describes how embedded a cell is in its organ, and this cell can measure an oxygen gradient to know its centrality [21].

Betweenness centrality measures how many of the shortest paths between two individuals are connected through a certain individual. This centrality represents the optimal routes for information flow [21], [23]. It requires information about every individual in the network, which typically is not available in a distributed computing context. However, it can be used in computer simulations as a easier to calculate proxy for local-information-only variants such as random walk betweenness centrality. This measures the relative number of random walkers (such as diffusing molecules) that use a certain route between two predetermined individuals. Plant cells can sense this centrality by measuring the concentration of a diffusible molecule produced by other cells [21], [23], [24].

Vascular differentiation is likely induced by a plant-produced diffusible molecule, such as auxin. Nutrient fluxes or gradients may complement this signal.

Ant pheromone trails

Many species of ants create their own transport and information processing networks using pheromone trails. These transport networks are not fixed structures as plant vascular networks are, but are continuously renewed and thus remain malleable.

The basic mechanisms behind the creation and maintenance of these trails are as follows: when foragers leave the nest, they go in search of food. Ants that return with food, deposit pheromone trails on their way back to the nest, which are used to recruit new individuals to this source [26], [27]. These trails encode quality: the better the food source, the more pheromone the successful foragers deposit [26], [27]. Other ants are recruited to these trails by this pheromone and antennal contacts [26]. These new foragers may also return with food and strengthen the pheromone trail. If enough ants are recruited to the path, this creates a positive feedback loop which maintains and strengthens the path, and can recruit most foragers to this one trail [27], [28]. If not enough ants are recruited, the pheromone evaporates or disappears into the surface too fast, and the trail disappears [28].

Even while positive feedback is implemented, negative feedback mechanisms are at work: whilst naïve foragers prefer occupied food sources, foragers with previous experience of an unoccupied food source will leave the occupied source, and instead switch to the unoccupied one [27]. They will also deposit less pheromone to the occupied source [27]. All foragers also deposit less pheromone on pheromone-rich trails and on trails where they encounter other ants [27]. This crowding-effect allows the pheromone to evaporate and the colony to switch to other high-quality sources, restoring flexibility and minimising forager waiting times [27].

Just as plant vascular systems need to optimise the trade-off between construction cost and transport efficiency, the ant colony needs to balance the amount of unsuccessful foragers against finding the shortest paths to a given resource. The pheromone intensity also influences the probability of an ant losing the trail [29]. If ants never leave a pheromone trail, they will always find the food at the end. However, if this path is not the fastest route between the nest and the food, the colony will spend more time than necessary harvesting this resource.

When ants lose a pheromone trail, even temporarily, they may discover shortcuts. Because the density of ants on shorter paths is higher, these paths will have more pheromone deposition. Their total surface area is also lower, so pheromone will evaporate slower from these paths than from longer ones [16]. These two factors favour retention of shorter paths, enabling the colony to compute shortest paths to food using simple heuristics for individual ants. However, this comes at the risk of ants losing the trail entirely and failing to find food (although they may also explore the environment and discover novel resources instead [29]). Therefore, the colony must tune the baseline pheromone intensity to optimise between ants following the trail and ants getting lost.

As we saw previously, plant vasculature formation algorithms depend on the structure of the tissue they compute in (e.g. the uniform apical meristem versus the giant cells in the petiole). Likewise, ant pheromone paths and their adaptability depend on the structure of the physical environment they are embodied in. For example, the computations of ant colonies are usually tested in the lab with nests with one entrance, though natural nests may have up to six entrances [28]. The information sharing between returning foragers to new recruits is an independent process at each entrance [28]. Therefore, having two nest entrances instead of one interferes with path optimisation: both exploring and recruited ants are less likely to reach food, and pheromone trails are less likely to be

established if more than one food source is found in the environment. [26], [28]. Even if paths are established, these last shorter [26], [28]. Moreover, the colony is not able to focus on higher-quality food sources, resulting in a lower overall food gathering output [26], [28]. On the other hand, an increase in nest entrances facilitates the discovery of more food sites, which is useful for species harvesting many small, scattered packets of food [28]. Exploiting more resources simultaneously is also a good bet-hedging strategy against losing resources, for example to competing colonies or by depletion [26].

In summary, pheromone trails are continuously remodelled based on both positive feedback, which promotes efficacy, and negative feedback, which restores flexibility. The intensity of pheromone deposition allows the colony to tune between the competing costs of lost and thus unsuccessful foragers (construction cost) and excess path length (transport efficiency cost). A colony with more than one nest entrance may discover and exploit more resource sites, but the colony is less efficient in its exploitation, since not all information can be integrated at a single nest entrance.

Conclusion

Both plants and some ant colonies construct networks to transport goods and information: vascular systems and pheromone trails, respectively. Embodiment constraints such as plant tissue structure and number of ant nest entrances shape these networks as they develop. In addition, both plants and ants must balance construction costs against transport speed. As we have seen, each plant species strikes a different optimal balance between these two competing goals. Likewise, we may expect different ant species to each find their own optimum under this trade-off.

The severity of these two constraints likely differs between plant vascular systems and ant foraging trails, which may in turn influence the computational steps they employ to achieve an optimal network architecture. For plants, adding a cell to the vascular network is an irreversible process, especially when creating xylem. This makes creating a large number of vascular connections, and then pruning these to retain the shortest paths, an expensive and thus unfavourable method. On the other hand, the limited time investment by a single worker ant is a small cost for an ant colony. Therefore, we see exactly this dense coverage and subsequent pruning: multiple ant foragers crisscross terrain in search of food, and afterwards the shortest paths found are strengthened.

Communication between units

Plants and ant colonies can only perform distributed computations if their cells or ants can communicate. This communication is essential to transport information as well as to combine each individual outcome into an overall conclusion. As we will see, aspects of the plant and colony embodiment influence which communication and aggregation strategies are used. We may ask the following questions: What are some communication methods that plants and ants use, and are these analogous between plants and ants or unique for either system? Can we specify the influence of movement on communication?

Local communication

Both cells within a plant and ants within a colony communicate with others close to them. Plant cells use various signalling molecules to communicate with their direct neighbours, as well as mechanical forces [30]. Likewise, ants convey the task they are doing using smell and physical contact [7], [16]. This allows nestmates to estimate the percentage of ants working on this task, and decide between continuing their current task and switching to another task [7], [16]. For example, if a brood care worker meets a forager, its estimation of the percentage of foragers increases. This may indicate a rich food source has been found, such as a heap of spilled sugar in the kitchen. Hence, this brood

worker can decide to switch to foraging, so that the colony can maximise its sugar intake before the spilled sugar is cleaned up and the food is gone [7].

Local communication is enough to do complex calculations. As we have seen, the stomata in plant leaves compute the optimal fraction of open stomata together [19]. Each stoma uses only the humidity it senses itself, and the stomatal aperture of its neighbours, and decides to open or close [19]. The results of these local-information computations are waves of opened stomata travelling across the leaf [19]. These waves make relevant information available across the entire surface [19]. For this information processing, the embodiment in the leaf allows the stomata to sense input, do the calculation, and implement the result all at once [19].

To combine information across distant cells, plants have to rely on either these types of travelling patterns, or use non-local signalling through xylem and phloem vessels [17]. Vasculature is expensive to make and maintain, but these travelling patterns are very sensitive to noise: the opening or closing of a single stoma can make or break them [19]. Ants in an ant colony have a third option: they can move and mix. This allows them to communicate directly with many others, and spread relevant information simply by moving from one neighbourhood to the other. This is cheaper than vasculature and more robust than travelling patterns are. [17] show that walking around enables ant colonies and other liquid brains to solve a more diverse set of consensus problems than plants and other solid brains. They are also able to solve these faster, and their movement patterns can be an essential part of their algorithm [17].

Long-distance communication

Plants

Both plants and colonies also communicate across longer distances. In plants, there are two main chemical communication routes: the vascular system and volatile organic compounds (**volatiles**). These volatiles diffuse through the air to reach other parts of the plant [31]. These two systems complement each other, as we see when the plant primes itself for systematic defence after a local attack [31]. Vascular signalling is more reliable, but volatiles can bypass vascular topology and so create shortcuts [31].

For example, if a caterpillar damages a leaf, then nearby leaves may benefit from a quickened defensive response. These nearby leaves are close in 3D space, but may be far apart in vascular topology, especially in older and more branched plants [31]. Therefore, volatiles diffusing through the air are used to start the defence response, and later-arriving vascular signals intensify and prolong the change in gene expression [31].

Plant-plant volatiles also have a function in plant-plant interaction [32], [33]. Each plant constantly updates the mixture of volatiles it emits, and closely monitors the compounds it receives from others [33]. These bouquets depend both on species identity and stressed or unstressed condition of each plant [33]. As such, neighbouring plants are informed about both potential upcoming competition and (a)biotic stressors, such as drought stress or herbivore attacks, from volatiles and adapt in time [33]. They can react to volatiles by either strengthening or weakening their defences, and steer their growth to avoid competition [33]. Both sending and receiving these plant-plant signals is associated with increased fitness [32].

Computations done through vascular signals differ from those using volatiles in where the input is integrated. In plant growth and development, local computations are integrated into a vascular long-distance signal that carries generic information [34]. Next, this signal is received in distant organs and induces a simple response: grow at a certain rate [34]. On the other hand, the receiver plant

integrates many factors when it uses volatiles to decide whether to adjust its growth, such as the concentration of this and other volatiles at that moment, the duration, and total concentration of these emissions, and how related it is to the volatile emitter [33].

Ants

In ants, many species use pheromone trails for indirect communication. Here one ant may deposit pheromone to send a signal, such as the location of a food source. A conspecific can then encounter this trail and receive the signal, which enables it to discover the food source the first ant found. Similar to vascular signalling in plants, these ants can communicate without direct contact.

In addition, ants leave species- and colony-specific chemical footprints wherever they walk [35]. Whilst pheromone trails can typically only be sensed by conspecifics, the presence and intensity of these footprints can also be sensed by other ant species [35]. In this way, these ants can gain information about the presence and nearness of other colonies, as well as the potential location of exploited food sources [35]. They can then either avoid these places to evade costly fights, or move toward exploited food sources. Since exploited food sources are likely to be of higher quality than non-exploited ones, it may pay off to either slip in and harvest some food, or oust the current occupiers by force.

Although these footprints may be used by competitors, not leaving these signals likely involves a fitness cost, though its precise nature can vary between species. Firstly, the footprints are produced by tarsal pads that also enhance adhesion to smooth surfaces [35]. This introduces a trade-off: smaller pads may leave less concentrated footprints for competitors to follow, but also reduce grip in for example trees. Secondly, different colonies of the same species use the same pheromone chemicals to make their trails [35]. Since footprints are colony-specific, ants may use these to recognise trails made by nest-mates [35].

Conclusion

In both plants and ants, movement enables long-distance communication: neither the cells nor the ants meet each other directly. However, they differ in whether the message moves, or the sender and receiver do [17]. Plant cells remain at a fixed position in the plant, and the signalling molecules travel between the cells. In ant colonies, on the other hand, the pheromone trail remains at a fixed position in space, while the ants wander around.

Each plant function of long-distance communication we have discussed can be matched to an ant analogue. Functionally, pheromone trails correspond closely to the plant vascular network: they enable efficient transport of nutrients within the colony. Likewise, both ants wandering off the trail and volatiles can bypass the vascular or pheromone topology. They can take shortcuts to sites that are close in 3D space, but far away on the vascular or pheromone paths. Lastly, the interaction with other plants or ant colonies is mediated by volatiles and chemical footprints, respectively. In both cases eavesdropping occurs, but silent mutants may also incur fitness costs.

Plant tropisms and ant architecture: computations which influence input

So far, the information processes we have considered take input and produce output, and that is where the process we considered ended. However, biological computations do not occur in a vacuum, and output of a previous information process often influences the current input. Here we ask which mechanisms can create such an output-input coupling?

As an example, a plant can move toward or away from various stimuli, to maximise available light, space, water, nutrients, and so on. These **tropisms** are increasingly studied by representing them as input-processing-output systems, where the processing step is often modelled with simple

descriptive equations [36]. These models may then be tested against data to see whether their equations are complete, or whether important factors may be missing. In this way, [37] found that shoots reorienting in response to gravity must be sensing their own local curvature as well as the direction of gravity. This expands the accepted 'sine law' view of gravisensing with **proprioception**, where the plant senses its own internal state [36], [37].

Proprioception is very important in both plant development and tropisms [30]. This mechanical feedback of a plant's own form allows plants to produce each new leaf or root with a consistent shape [30], as well as control their movement. Proprioception is not a purely internal process: for example, plants vibrate in the wind with frequencies dictated only by their own weight, stiffness, and shape [30]. This external movement may allow plants to sense their own shape, and so modulate branching lengths to avoid breakage [30] (also compare with [9]). As we can see, the sessile plants need to use external movement to sense their own internal state, which is an example of how plant embodiment shapes proprioception processes.

We can also see proprioception at work in ant colonies, if we view them of existing of not just ants but also their nest. The nest performs essential functions for the colony, such as ventilation [38]. Moreover, both structure-encoded and social feedbacks drive the colony to adapt the nest over time, so that it continues to fit its needs [38]. As an example, volatile pheromones around queen or brood allow ants to enlarge their chambers as they grow [38]. In both function and adaptability, the nest can be seen as analogous to a living tissue.

Ant colonies do not coordinate their nest construction by direct ant-ant communication [38]. Instead, each ant adds material to or removes it from a piece of the building, and this local structure modification serves as a blueprint for the next construction effort [38]. On the colony level, these local proprioception feedbacks add up to a sophisticated nest architecture [38].

Both plant tropisms and ant nest building are the output of information processes, but they also qualitatively change the input of future computations. For example, only once a seedling has broken through the soil by negative gravitropism, it has light available as an input. The red/far-red ratio in this light can then be an input for a shade avoidance computation, so that the seedling can compete with other plants for this light [33]. Likewise, the construction of nest entrances is a result of colony-level information processing. Yet, as we saw before, the number and position of these entrances also influence the coordination among foragers, and thus the colony's success in computing the optimal food intake strategy [26], [28].

In summary, though both plant tropisms and ant nest construction can be viewed as input-computation-output processes, they are described more accurately by a closed feedback loop, where the output of previous computations shapes the input for the next information process.

Proprioception plays an important role in both processes, which may be no coincidence. After all, for this output-input coupling to exist, the environmental effects of the previous computation cannot be disrupted too much before the next information process takes these as input. In other words, controllable environments are better candidates for input based on previous output, and one of the most controllable environments is the internal one of the plant or colony itself [9].

Conclusion

We have seen that embodiment is an essential part of distributed information processing for both plants and ant colonies. Firstly, these networks exist on a solid-liquid scale. Solid brains, such as plant tissues, use structure to compute, whereas ant colonies and other liquid brains use movement instead. Secondly, embodiment constraints and the trade-off between construction cost and

transport speed shape the developing vascular and pheromone trail networks. Thirdly, local communication is enough to integrate information across the entire tissue or colony and do complex information processing. The various long-distance communication methods enhance signalling reliability, allow signals to arrive faster by taking shortcuts in 3D space, and enable plants and colonies to interact with their neighbours. Lastly, biological information processes typically are part of a closed feedback loop, where previous output moulds the input for the current computation. Proprioception processes often generate part of the input, since the plant or colony's internal state is a highly controllable environment.

When people think of cognition, information processing usually is at its heart. Since plants can compute, a logical follow-up question is whether plants are cognitive. Much of the plant cognition debate is taken up by two competing perspectives: plant neurobiology and its opposite, which we can call the collection-of-parts perspective [39]. This latter perspective views the plant as a non-cognitive collection of parts [39]. Here the individual cells, leaves, roots, and so on, each process information and make separate decisions [39]. In this view, any whole-plant behaviour is simply a by-product of interactions between these components [39].

In contrast, proponents of the plant neurobiology perspective view the plant as an individual organism, endowed with consciousness and intelligence [39]. This perspective makes extensive use of comparisons to animal brains [39]. For example, the root tip is viewed as a brain-like decision centre, which then communicates with the rest of the plant body through the vascular system [39]. These vascular signals are not only chemical and hydraulic, but also electrical, and thus the xylem and phloem vessels are typically likened to neurons [39]. In this view, the rapid electrical signals are key to plant intelligence [39].

The plant neurobiology perspective is a controversial one, and has been since its inception, with the debate now spanning two decades and showing no sign of being resolved soon [39]. Plant neurobiology has been criticised among other things for relying on speculations instead of testing hypotheses through experiments, and trying to fit plant behaviour into a neural animal mould [39]. This latter criticism becomes even more poignant now we have seen how important embodiment is to information processing: plant bodies and neural animal bodies are subject to different constraints, so why would we expect to find strictly analogous structures and methods for information processing?

If plants are cognitive, then this cognition must arise from distributed processes that not only shape, but are also shaped by, the plant body and environment. [9] argues that in such a setup, cognition would arise not from computation (i.e. information integration) itself, but from the synchronisation between local computations. This implies that if we are to search for plant cognition, we should not try to identify decision centres. Instead, we may need to turn our focus to patterns emerging from the interplay between the various local decisions. If plants are cognitive, then neurobiology may be entirely the wrong model for this cognition.

Although the plant neurobiology seems a poor fit, the examples of embodiment we have seen also show that a plant is more than the sum of its parts. Hence, the collection-of-parts perspective does not correspond with our evidence either. Instead, this paper fits well with a third perspective discussed in [39], which we can call the 'distributed-computing' perspective. This perspective also sees plants as more than the sum of their parts, but eschews brain-like comparisons [39]. Instead, novel whole-plant behaviours emerge from the interaction between plant parts [39], a process that is almost by definition embodied (i.e. constrained by body and environmental properties).

For example, as a plant grows and ages, it usually acquires an increasing number of leaves and roots. These parts are also typically more distant from each other. Therefore, we can imagine that this lengthens communication times and increases the complexity of signal integration. These two factors can change the effects of feedback loops and so fundamentally change the computation being done. Whilst plant branching patterns have been extensively studied (see e.g. [22], [40], [41]), to our knowledge the precise effects of growth on processing delays and signal integration are still unknown. As a fundamental part of any plant-wide computation, elucidating the influence of these factors would be a definite benefit to our understanding of plant information processing and decision making.

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