## PLANTS SENSE. BUT ONLY ANIMALS PERCEIVE.

## Mohan Matthen

### Introduction

All living things—plants, bacteria, and other non-animals included—adapt their behaviour to their surroundings. To do this, they have organs that are sensitive to environmental conditions. In short, all living things have sensory capacities. The question for philosophers of perception is this: How do these capacities relate to reality?

Now, many philosophers are inclined to deny—indeed, to deny emphatically—that plants could have *cognitive* capacities or be conscious. So, the story goes, they do not mediate response by coming to know it or by being conscious of it. These assertions typically do not take into account what we know about plants. Michael Tye (2021) for example, writes, entirely without citation, that the inner states of “tropistic organisms” such as plants:

. . are surely not phenomenal. There is nothing it is like to be a Venus Fly Trap or a Morning-Glory. . . The behavior of plants is inflexible. It is genetically determined and, therefore, not modifiable by learning. . . Plants do not learn from experience. . . are not subject to any qualia. Nothing that goes on inside them is poised to make a direct difference to what they believe or desire, since they have no beliefs or desires. (*ibid.*, §12)

The problem here is not so much that Tye’s conclusions are false. It is rather that, as we shall see, they are oblivious to relevant distinctions (some arrived at through decades, or even centuries, of empirical investigation) and are, as such, misleading or worse.[[1]](#footnote-2)

In the current state of scientific knowledge, it is becoming increasingly clear that plants have sensory systems and response effectors that are functionally similar in important ways to those that we find in animals, even “higher animals” such as fish, birds, and mammals. So, one should not slip into the once popular notion that plants are some kind of reflex machine. Yet, it is possible to go too far in the opposite direction. Some treat plants as if they were sessile versions of higher animals. But this neglects some important differences. In this chapter, I am concerned with one important difference. I argue that certain animals possess a sensory function that sets them apart from plants in a significant way. As we will see, this function is at the root of one of the most significant elements of the human self-conception.

### Othering Impressions: Sensing vs Perceiving

I have two chief aims here. The first is to show that plants and other non-animals *sense* in much the same way as animals—that is, their sensory systems have many of the same functions. My second aim is to display a difference. I will argue that plants are not capable of *perceiving*—only animals have this additional capacity.

Here is what I mean. I will say that:

A subject S *perceives* an entity X when S senses X as being distinct from S.[[2]](#footnote-3)

Here are some examples. I (S) *perceive* when I feel *a heavy spherical object* (X) in my hand or hear *a loud squealing sound* (X’) outside the window or catch sight of *a shady place to rest* (X’’) just down the road.

In each of these sensory states, I am presented with an entity that appears to be distinct from me. For first, each of these objects appears to be located in a common space beyond the boundaries of my body albeit in a common space in which my body also appears located. This means that if the above perceptions are concurrent, they appear to be located both relative to me and relative to one another in this space.

Moreover, these objects appear to be things my body can affect in certain ways. For example, I feel that I am supporting the heavy spherical object in my hand and preventing it from dropping out of my grasp. These appearances are of the objects in a sensorimotor framework, a “body schema” (Gallagher 1986, 2001) that enables me to handle and manipulate them.

Audition and vision also present me with othering impressions. That is, the things that I hear or see appear to be at a distance from me, located in a common space, and it seems that I can approach or move away from them.

These sensory states have the force of their objects being distinct from me. I cannot drop or approach something that is a part of my body. Things located in positions other than mine in a common space cannot be identical with me. Call them *othering impressions*.

To sum this up, I define *perception* as sensing that presents an othering impression of some entity. Mere sensing—sensing that is not perceiving—is not so marked. My thesis is that plants sense but do not have othering impressions. They do not perceive and have no use for perception. Only animals perceive.

### A Little History: Errors Along the Way

Before I get into my main line of argument, let me recount some history. Botany is a neglected subject in philosophy. Very few historical texts discuss plants, but when they do, they mostly pose the question of plant sensing in terms that suggest *perception.* As we shall see, modern scientific investigation does not conflate the notions in this manner. This corrects a bias that defines sensing in terms of othering and points to a conception of sensing that is more inclusive of plants. Just a little schematic history will help us understand the conceptual innovation that I am suggesting.

The dominant European tradition derives from Aristotle, who held that plants were alive but could not sense.[[3]](#footnote-4) Aristotle attributes to plants a “nutritive” or “vegetative” soul, but not a “sensitive” soul.

Each animal insofar as it is an animal has the capacity to sense, for it is by this that we distinguish between what is and what is not an animal. (*de Sensu* 1, 436b10-12)

In short, plants are by their very nature—i.e., by what it is to be a plant—unable to sense.

How did Aristotle arrive at this view? He seems to think that creatures that sense are subject to (a) hunger and thirst, which are forms of desire (*de Anima* II 3, 414a32-b16) as well as (b) sleep. Sleep is not relevant here, so let’s put it aside. Desire impels creatures to move, Aristotle says; there is thus no role for it in a sessile organism. This is why plants lack the power to sense, according to him. Notice how this is framed in terms that are better expressed by our term “perceive.” Plants are not capable of desire; desire is directed to objects at a distance; hence they do not sense anything that is at a distance. But since this argument allows that they might sense their own states, the properly drawn conclusion is that they don’t *perceive*, because they don’t sense anything outside.

In India, the question of plants was more widely discussed, and opinion was more divided. Many Indian philosophers realized that plants are alive. According to the Upanishads (followed by the Jains in this respect) they are “sprout-born,” though many Buddhists said that they were not “breathing beings,” which caused them to equivocate about their animate nature (Findly 2002). Quite commonly, they are designated as *ekindriya*, or “possessors of a single faculty,” that of touch—presumably, on the grounds that they are sensitive to conditions that (in humans) are sensed by tactile contact. According to Findly, there is a tradition in the *Mahabharata ­*that ascribes “all five sense faculties to plants”—a tradition also taken up by the Jain philosopher, Jinabhadra, who says (as Piotr Balcerowicz puts it in private correspondence) that plants “experience (or react to) colour, sound, smell and taste through special capacities.”[[4]](#footnote-5)

One point of interest to note right away is that both traditions identify sensing with the external sense modalities by which animals perceive—primarily, the traditional five. For them, the question “Do plants sense?” is just the question, “Do plants touch, hear, see, smell or taste?” And we have three answers to this question.

1. Aristotle says no, they do not touch or hear or see, etc.
2. Most Jains and some early Buddhists say that they exploit touch but no other modality; plants are *ekindriya*.
3. Jinabhadra says they have all five senses.

However, posing the question in this way—i.e., in terms of the five senses that animals possess—is already an error, as I’ll argue in a moment.

But before I get to this, let me note a further, equally damaging error. Since verbs of perception normally take a direct object, the question whether plants touch, hear see, etc. becomes “*What* (if anything) do plants touch, hear, see, etc?” By this very natural-seeming slide, this transforms the inquiry into one about external perception. For Aristotle, who (rightly) links external perception and motility, plants cannot see, hear, touch etc., because they have no use for awareness of edible things at a distance from themselves, things that they desire to move towards or away from, and so on—they don’t sense these external things, and so they don’t sense at all. For a philosopher like Jinabhadra, however, the question is one of *sensitivity*—for him, I assume, the question “Can a plant see?” reduces to the question whether plants are sensitive to things that animals like ourselves see. Since they are—they are sensitive to light and dark, for example—a philosopher like Jinabhadra would be disposed to conclude that the question has a positive answer. They see, and it follows that they see something. Minimally, they see light and darkness.[[5]](#footnote-6)

Here's the thing, though. An organism might be sensitive to some stimulus without perceiving that stimulus. For example, it might be sensitive to darkness, but this sensitivity might express itself simply by making it sleepy. In other words, it might sense darkness and thus become sleepy without sensing *that* it is dark. In both Europe and India, the transitivity of perceptual verbs obscured this possibility.

The fallacious inference from sensitivity to X to perceiving X is still with us. For example, Paco Calvo and Karl Friston (2017) powerfully argue that, as they put it: “Plants respond in a fast, and yet coordinated manner, to environmental contingencies” (*ibid.* 5). This is surely right—it is agreed territory. Calvo and Friston argue that predictive processing is involved here. In other words, the system responds to a proximal stimulus in a manner befitting a distal stimulus anticipated in the near future. They write: “plant perception entails predictive hypotheses *as to what is out there*: it could be a herbivore representing bad news, it could be a stream of water, or what may” (4, emphasis added). What they have actually established is this: at time *t*, a plant may initiate a response that is appropriate to water (or some other distal stimulus) at t + ∂. Let us grant that this might be true. It still does not entail that the plant locates the water in a body scheme, or common space, or that in some other way others it. Sensing something is not necessarily to have an othering perception of it.

Aristotle and Jinabhadra have opposed views on the subject of plant sensing—one thinks that lack any sense faculty, including the most basic one of touch, while the other thinks that they possess them all. And so, at first glance, it seems that Aristotle has a demanding criterion of sensing—that it must be associated with desire, for example—and that Jinabhadra has a permissive criterion—one that demands only sensitivity to the stimuli characteristic of a particular modality. Their positions are appropriate to their criteria, but the fact remains that neither poses the question properly. The question should *not* be: Do plants possess *our* five external modalities? This encourages an inappropriate zoocentrism. When considering plant sensing, the question should rather be:

Do plants have dedicated systems that are (a) sensitive to circumstances that require differential response for the maintenance of life, and (b) capable of initiating response to these circumstances as they occur?

This question is more accommodating. It allows for specialized sensory mechanisms that have nothing to do with the traditional five.[[6]](#footnote-7) And it does not require othering representations of sensory objects.

### Scientific Investigations

The modern conception of sensing seems to emerge slowly from scientific investigations of plant behaviour from the late eighteenth century onwards. The investigators of this period were looking at how plants adapt to change. This was widely thought to be mediated by sensory organs.

In 1779, the Genevan philosopher of nature, Charles Bonnet reported[[7]](#footnote-8) that if you lay a potted plant on its side, its stem bends and reorients to the vertical as it grows. Bonnet believed in a chain of being that ascends from “subtle matter” at the bottom to humans at the top. According to him, powers of sensing emerged in plants, which he placed nearly half-way up his chain. He took the gravitropism of his potted plants to be evidence of this. We now know more about the sensory capacity that mediates this behaviour. Plants have cells known as statocysts, which contain organelles known as statoliths. When these cells are tilted off the vertical, the statoliths “sediment.” This change induces the statocyst to emit an ionic signal. This initiates the turn of the stem. Thus, the statoliths function as receptors and the statocysts as transducers that emit sensory signals for gravitropism.

Following investigators such as Bonnet, sensing came to be seen as a mediator of variable response with no assumption made about othering impressions. The new attitude is evident in the work of Charles Darwin and two of his sons who, building on the work of a number of botanists,[[8]](#footnote-9) conducted extensive experiments on plants. (Figure 1 is a trace of plant movement by the Darwins.) These culminated in a book entitled *The Power of Movement in Plants* (1880) with the stated aim of giving a unified account of “several large classes of movement, common to almost all plants.”

A diagram of a constellation

Description automatically generated

Figure 1: The movement of a cabbage radicle, one of many such tracings in Darwin (1880). Darwin established that the tip of a radicle received “impressions from the sense-organs” and directed the movement of the shoot.

A plant’s growing parts spread in ways that benefit the plant. Its roots must overcome the resistance of the earth; its stem grows vertically upwards; its tendrils need to find support; its leafy branches seek light. The Darwins realized that these movements were actively managed.

When light strikes one side of a plant, or light changes into darkness, or when gravitation acts on a displaced part, the plant is enabled in some unknown manner to increase the always varying turgescence of the cells on one side; so that the ordinary circumnutating movement is modified, and the part bends either to or from the exciting cause. (1880, 547-548)

The primary movement of the growing parts that Darwin studies is “circumnutation,” the more or less random circling of roots, tendrils, etc. “to all points of the compass” (*ibid.* 1)—“every growing part of every plant is continually circumnutating, though often on a small scale.” Circumnutation is an underlying random substrate of directed movement—random in the sense that it is not *toward* or *away from* any source of benefit. Additional motions are superimposed on circumnutation in accordance with need; a root’s circumnutation is biased in the direction of gravity, for example, and a shoot’s is biased in the opposite direction. “There is always movement in progress, and its amplitude, or direction, or both, have only to be modified for the good of the plant in relation with internal or external stimuli” (4).

Darwin realized that movements directed by “internal or external stimuli” implied sensing those stimuli. He attributed sensory function to the tip of a plant’s radicle. Amputate this, and the root’s environmental responsivity is eliminated, and it behaves in an inflexible way.

It is hardly an exaggeration to say that the tip of the radicle . . . having the power of directing the movements of the adjoining parts, acts like the brain of one of the lower animals; the brain being seated within the anterior end of the body, receiving impressions from the sense-organs, and directing the several movements. (*ibid.* 573)

This is Darwin’s ground for attributing sensory function to plants.

The message we should take from Darwin is that all living things respond in a functionally appropriate way to occurrences and circumstances that affect their well-being. In order to be able to do this, organisms generally have to transition to an “effector state” that initiates action appropriate to the circumstances they encounter. To achieve the right match between effector states and prevailing circumstances, organisms need to possess receptors that are receptive to the chemical, mechanical, and electromagnetic influences of their environment and organs that transduce these influences into signals that initiate their response. In short, they need sense receptors, transducers, and sensory systems.

### Plant Behaviour Is Complex But Does Not Employ Othering Representation

Tye says that plants are “tropistic organisms.” Is Bonnet’s phenomenon a “tropism?” Yes, because a tropism in plants is defined as “directional growth in response to a directional stimulus” (Gilroy 2008, R275). Gravity is a directional stimulus, and plants grow directionally in response. But one should not assume (as Tye apparently does) that tropisms are simple, genetically determined reflexes. In fact, they are quite complex. Gravitropism in particular is not a simple bend to the vertical. The upward bend of a shoot is achieved by adding extra growth at the lower side. (Plants bend towards one direction by adding auxin, the growth hormone to the opposite side of the stem.) But the shape of the shoot is maintained throughout; the growth on the lower side of the bend does not carry through in the form of a lump or thickening. Accordingly, there is a “decurving” process that ensures that the shoot *above* the bend has normal dimensions. In addition to decurving, there is also phototropism and other natural tendencies. Each of these processes requires input from dedicated sensors (Bastien, Douady, and Moulia, 2015; Moulton, Olivetti, and Goriely 2020). As a consequence, plant behaviour integrates the output of multiple sensors. As one recent paper on gravitropism in wheat coleoptiles notes:

Coleoptiles respond not only to sums but also to differences between stimuli over different timescales, constituting evidence that plants can compare stimuli—crucial for search and regulation processes. (Rivière and Meroz 2023)

Coming to another sensory complexity, plants appear to learn. Pea tendrils coil if they sense contact in the light but stay uncoiled if they are rubbed while in the dark. (See Engelberth 2003 for a review.) In a classic study, M. J. Jaffe (1977) showed that the effects of rubbing are “stored;” tendrils that were rubbed in the dark immediately coiled when exposed to light up to two hours later. Gagliano et al (2014) found that when *M. pudica* (see note 8) is subjected to continuous and identical disturbances, such as drops of water, it modulated its initial response, which was to close it leaves. Gagliano and her co-authors suggest that this modification of behaviour “exhibits clear habituation, suggesting some elementary form of learning” (*ibid* 63). (See also Affifi 2013.)

There is no doubt, then, that plants are able to detect changing environmental conditions, and that their responses “greatly transcend the phenomenon of cellular irritability” (Binet 1888, quoted by Trewavas 2014). Plant behaviour is not, in other words, a simple passive reaction to events on their surfaces (as Aristotle and his successors believed); it requires at least the classification and comparison of these events and the activation of internal processes.

Though plant sensing is complex in these ways, I want to argue that it does not require othering representation of the outside environment. Even if the statoliths are presentations of the direction of gravity, and even if gravity is outside and distinct of the plant, plants do not have othering representations of gravity or its direction. Their growth behaviour does not, in other words, require gravity to be represented as something outside and distinct from the plant. This, I suggest, is universally true of plant sensing. The sensory regulation of plant behaviour does not depend on making a distinction between self and other. It does not require othering representations.[[9]](#footnote-10)

Now, this might seem counter-intuitive. Many years ago, I argued (Matthen 1988) that:

A perceptual state is a presentation of *F* if and only if its function is to detect *F.*

This “teleosemantic” approach to representational content implies that plant sensors represent external circumstances—if a sensor drives response to an external circumstance, it leads us to say that it represents that circumstance. The function of statocysts is to drive response to gravity. So, should we not say that statocysts represent *gravity*, which happens to be a force external to the plant? Is this an othering impression? Not necessarily. For representing an external circumstance does not entail representing it *as* external. The plant changes state when certain external circumstances are detected, but there is nothing in its state that makes it respond as to an external thing. As complex as it is, then, the gravitropism described above does not imply that gravity is represented as a force outside the organism.

### Perception and Othering in Higher Animals

Higher animals *perceive*. That is, their sensory processes yield othering representations of entities located by means of “cognitive maps” of the space outside the organism itself. When I take my seat in a crowded subway car, carefully maintaining a polite distance from the person already sitting there, I am acting in sensory awareness of this other person and where she is, relative to me and also relative to the other things and people I see.

There are two features of othering awareness that are important here.

First, I am aware of the things around me as items that I could bump into or otherwise interact with. That is, I possess a sensorimotor awareness of these things, relative to my limbs and their movements, including a space-like framework that enables my limbs to effect action on nearby things. Shaun Gallagher (1986, 2001) called this framework the “body schema”—a sensorimotor system that “constantly regulates posture and movement . . . without the necessity of perceptual monitoring” (2002, 149).[[10]](#footnote-11)

And second the things I externally perceive appear to me as possessing metric location relative to one another and to me. This implies a “cognitive map”[[11]](#footnote-12) or distance- and direction-based location scheme for everything externally perceived (including my own bodies).

The bodily scheme and cognitive map are the foundations of othering impressions—these things are presented as distinct from me in consequence of the above spatial features of their appearance.

Why *spatial* representation? The crucial point here is that higher animals are freely motile: they move through their environment towards or away from points of their choosing. They keep track of the things they have to navigate to, around, and away from. Plants, by contrast, are sessile: they merely “grow through their environment” (Gilroy 2008, R275). In higher animals, such as birds and mammals, motility brings environmental challenges that require locational awareness and navigational skills.[[12]](#footnote-13) This is why these animals perceive—why they have sensory representations of things as located in the space outside themselves.

The contrast that I am making here provokes a sceptical question. Concede that plants act on the basis of the condition of their own sensors. After all: what other source of information do they have? But, says the sceptic, isn’t exactly the same true of animals? We experience visual, auditory, tactual, olfactory, gustatory impressions. These impressions are the products of our senses. Since we have no other source of information, we must be acting on the basis of these alone. (This, in fact, is the point of view of Thomas Reid, to whose distinction between sensation and perception I am indebted—see note 1.) How are we different from plants? Whence do othering impressions arise?

The answer to this question is, perhaps, surprising. Birds and mammals (and possibly have *innate* spatial frameworks—they have inner representational organs that impart spatial form to sensory output. They do not place things in external space by somehow inferring spatial relations from non-spatial sense impressions. Rather, their sensory organs are genetically constructed to place all external objects in a spatial matrix with themselves at the origin or universal reference point. With respect to sensorimotor action, this matrix is Gallagher’s (1986, 2001) “body schema.” With respect to navigation, mammals and birds (and perhaps some fish[[13]](#footnote-14)) array external perceptual sources in the hippocampus. This organ serves as a map of the external sources relative to the organism itself. Both kinds of representations are othering because they locate things at measured distances away from the organism. Plants have no facility that generates othering representations. They operate just on the state of their sensors without sorting out the self and other.

### What is Sensing?

In light of the discussion so far, I offer the following as a definition of sensing *without* any assumption of othering representation.

*Sensing* is a capacity *S* of an entity *E* to:

1. be in a state mediated by distinct receptive and transducing organs that
2. covaries with variable circumstances, where

(b) eachsuch state has the biological function of triggering *E*’s normal responseto the circumstance to which it corresponds.

The definition is apt for:

1. the traditional cases, where the responses are epistemic. For example, colour vision is the capacity of an organism to be in different states for the different colours that it can discriminate by means of colour sensors, where each of these states has the biological function of triggering different belief tendencies about the colour of seen objects.

The definition also fits:

1. sensory capacities that serve bodily regulation. For example, thermal sensors are in different states when exposed to different temperatures and serve to trigger thermoregulatory actions (such as sweating or shivering) appropriate to those temperatures.

And it accommodates:

1. sensory systems (such as appetite) that generate motivational states (such as hunger) that impel an animal to act in a manner that is appropriate to the circumstance detected.[[14]](#footnote-15)

### Chance: Growth that Goes Against Gradients

Now, let’s consider behaviours that suggest spatial representations in plants and why these behaviours do not in fact require spatial representation.

Plants send roots towards areas of greater moisture and nutrition content. If a root is growing toward such an area and encounters an obstacle, it grows around the obstacle and resumes its growth toward its initial destination. How do they determine where these better areas are? It might seem that in order to do this it must explore its surroundings with the aim of finding the resources it needs. And this would imply that it represents the spatial region around it. I will argue that this is not so. There are two forms of behaviour that achieve the said result while only requiring a sampling of proximal values within, or at the surface of, an organism’s body. These do not require a representation either of external space or of the locations of distal objects in external space. Plant act simply on the basis of the state of their own sensors.

First, I’ll give an account of gradient-based behaviour, or tropisms. Think of a *field* as a spatial distribution of some physical variable: for instance, electromagnetic strength, gravitational force, velocity and volume of water flow, chemical concentration, and so on. What do you do when you are trying to track down the source of a foul odour in your kitchen? You sniff and move, following your nose to higher odour concentrations. In effect, you sample and compare odour field strength at various points and to follow increasing or decreasing strength depending on your purposes. The object that interests you is located where the field strength is greatest. You rely on *field gradients* in order to get to or away from it.

How, in general, does an organism detect a field gradient, given that its sensors can only detect the strength of the field at a given point? There are two possible ways. The first is the one just mentioned: it samples field strength at successive locations and compares these readings over time. The second is that the strength of its gradient-directional orientation is determined by the strength of its field vector reading. For example, it might be more strongly pulled in the direction of the vector when the field is stronger. Thus, where the field is weak, it might waver with respect to that direction, but as the field-strength increases it might fix on the gradient with less and less wavering. This second method requires only one reading at a time—no comparisons over time. I suggest that the second would be the one followed by plants, there being no evidence of them being able to make comparisons over measured time.

Gradient-based change has been extensively discussed in the literature on evolution by natural selection, raising issues that are relevant to us now. Natural selection is gradient based on a metric constructed in the following way. Graphically array all possible genotypes available to a population of organisms so that similar genotypes are close to one another along the independent axes of the graph and dissimilar ones far apart.[[15]](#footnote-16) Each genotype has a fitness-value, and this is represented in the graph as the “height” of that genotype along the dependent axis. Figure 2 is a simplified example of such a graphical representation of fitness: it assumes only one dimension of similarity. The “landscape” shown in Figure 2 is, in effect a field-map that represents fitness as a function of a single genotypic variable. Populations will (with high probability) transition from states of lower fitness to adjacent states of higher fitness but will *not* (again with high probability) transition from states of high fitness to adjacent states of lower fitness. This is a consequence of the Principle of Natural Selection. Looked at in this way, natural selection is a tropism—the directional movement of a population in response to a directional stimulus.

Now consider the population marked by the circle near the trough between A and B in Figure 2. At the trough, this population is at a local minimum, meaning that its fitness is lower than that of any similarity-adjacent point. Any mutation, or change in its genotype, would result in an increase of fitness. Now, remembering that this landscape varies in only one respect, and assuming for the sake of simplicity that the slope of the fitness curve is equal in both directions, this population is as likely to move towards B as it is towards A. Once it starts up either slope, it has only one way to go to increase its fitness, because any change in the opposite direction would then be a decrease in fitness. So, if we were to assume that populations *always* ascend a fitness gradient, some populations in the trough of a curve like that of Figure 2 will miss the global maximum. On our assumptions, each such population is equally likely to ascend only to a local maximum, such as A, even though this is not the highest fitness point in the entire landscape. And an ascent to A is irreversible on these assumptions. There is no way it can get from A to B without first reducing its fitness, and natural selection makes it highly unlikely that any such reduction could occur.

This yields a general point that made by Jon Elster (1979), which I recount in David Gauthier’s (1983) felicitous summary:

Although natural selection yields local maxima, it does not in general yield global maxima . . . it can not wait; it can not refuse a favourable mutation so that it may later be able to accept a more favourable one. And it cannot accept an unfavourable mutation [that takes it downhill from A] so that it may later accept an even more favourable one [that takes it upward to B from the trough between A and B] (134)

According to Elster, the achievement of non-local maxima requires a representation of the distant terrain. If a population at A could represent B as a distant non-local maximum, then it could accept an unfavourable mutation in order to get to B. But this is, of course, what a population under natural selection cannot do. It does not represent the whole fitness landscape; it merely moves along fitness gradients.

A diagram of a mountain

Description automatically generated

Figure 2: A diagram of fitness values (y-axis) that attach to phenotype variation (x-axis) in a population.

One might reach a similar conclusion about the gradient based growth of a plant’s root system. Reinterpret Figure 2, now, as the nutrient concentration height of adjacent locations. The pink circle in Figure 2 is now the position of a root tip following a nutrient gradient. Suppose that the root found its way to A, a local nutrient maximum. Then its path to B would be blocked. This happens more frequently than you might think. Suppose a root is following an ascending nutrient gradient when it comes upon an impenetrable obstacle—a granite rock, say. Its best course is to grow around the rock and pick up the interrupted gradient on the other side. But by Elster’s argument as presented above, it cannot do this. It cannot accept a reduction of nutrient concentration so that it may later accept a more favourable increase. Any change of direction would be along a negative gradient. In effect, the place where it meets the rock is a local maximum—every step taken from there represents a reduction of nutrient concentration. Consequently, the gradient following root is simply stuck there. The problem is, of course, that root systems *don’t* get stuck when they meet obstacles. They *do* go around them. So how does this happen?

Situations of this type were debated by R. A. Fisher and Sewall Wright. Both thought that it was indeed possible to get from A to B in Figure 2. Both their views are relevant. Fisher’s idea was that it was easy to underestimate the dimensionality of the fitness landscape. Figure 2 records fitness values for one dimension of genotype variation. But what if there were another dimension. Then, there could be an ascending path from A to B that lies “behind” the plane diagrammed above. Call this the “added dimension” solution.

Wright, for his part, pointed out that genetic drift could solve the problem. Evolving populations engage in a fitness-weighted “random walk;” they do not evolve monotonically to the fittest alternative, but rather fluctuate back and forth in the overall direction of that alternative. If selection were deterministic, a population could never descend from A in order to get to the global maximum, B. However, chance occurrences could make it drift to the trough between A and B and then ascend to B. Call this the “random walk” solution.

Both these solutions are relevant to the gradient based directionality of growth that we have been discussing. Consider Fisher’s added dimension solution first. We assumed that the root would follow a nutrition gradient, but as we have seen, there are other relevant gradients for it to follow. The root that is stuck at the granite obstacle might have no ascending nutritional gradient to follow, but at that point it might follow an ascending wetness, gravitational, or (as it actually happens) thigmotropic or pressure gradient.[[16]](#footnote-17) In fact, it might all along have been following an integrated gradient that does not peak at the rock obstacle—we noted earlier that plants integrate their sensory inputs. Sensory integration creates gradients in multiple dimensions.

Now consider Wright’s random walk solution. A root that has nowhere to grow but downwards on a nutrition gradient may grow in random directions. This too is consistent with plant behaviour. Just as an evolving population moves about the fitness landscape randomly with an overall direction superimposed by selection, so also a plant’s roots and tendrils constantly “circumnutate.” As we saw, Darwin thought that movements along field gradients were superimposed on circumnutation. Circumnutation can carry the root anywhere, but sensed gradients bias its growth in the direction of field gradient vectors. The stronger the field, the greater the bias toward the field-gradient. Like a tracking dog it’s growth would waver back and forth at first but become straighter and straighter as the field became stronger. This could carry a root tip down a field gradient to a point where it has a clear path to a global nutrition maximum.

To summarize, then, a root that encounters an obstacle along its ascending gradient could either grow along another gradient or grow randomly until it found a point from which it could resume its ascending path. Elster supposed that natural selection, operant conditioning, and supply-and-demand market forces are governed entirely by field gradients and are thus doomed to get stuck in local maxima. (He thought, by the way, that this is an argument in favour of state planning.) But he was wrong: gradients of higher dimensionality and random walks disturb a system’s stable equilibrium at local maxima, clearing their path to non-local maxima.

The conclusion that we can draw about plant behaviour is that internal controls are, first of all, multidimensional. And in addition to all of the force fields that constitutes these dimensions, there is an underlying random motion on which the force fields are superimposed. Plant growth integrates all of these.

### Object-Targeted Behaviour

Earlier, I said that certain organisms have no interest in *objects*. The root system of a plant doesn’t care where the nutrition in the soil comes from—e.g., a dead animal that is decomposing in the soil or a drip of moisture that is dissolving minerals in the soil. It simply maximizes (or rather optimizes) the nutrition available to it. However, there are plant behaviours that seem to target objects. Do these behaviours require a representation of these objects?

Consider the behaviour of carnivorous plants such as the Venus flytrap. It is easy to think that they *are* concerned with the insects that alight on their leaves; their behaviour is as much directed to eating their prey, as mine might be to the buffet table at the other end of the room. But the flytrap doesn’t have to represent the insect or its location in order to attain its goal. Here’s a description of how it operates:

The whole central zone which is covered with digestive glands. Among these are bristles known as trigger hairs, usually three to a lobe. When an insect crawls along the ventral surfaces and bumps into the three small trigger hairs, the trap snaps shut. Two touches of a trigger hair activate the trap which snaps in a fraction of a second at room temperature. (Pavlović, Demko, and Hudák 2010, 37).

Here’s how this could work without a representation or measurement of outside objects, or of space and time. Let us say that the flower is in a “resting state” *R*. At this point, trigger hair *H* is touched. *H* responds by causing the flower to enter into an “alert state” *A*. When the flower is in state *A* and a trigger hair *H* is disturbed, the plant’s leaves snap shut*.* Since the alert state decays rapidly, the trap shuts only when trigger hairs are disturbed twice in a short time period.

The above can be represented as a machine program for trigger hairs:

If the flower is in state *R*, and trigger hair *H* isdisturbed, then switch the flower to state *A*.

If the flower is in state *A* and trigger hair *H* is disturbed, then activate the snap-shut routine.

If the flower is in state *A* for more than t (t ≌ 20s), then revert to R.

Each line of the program involves a conditional action. We may suppose that these are realized by chemical means; for instance, the switch-to-A might be achieved by the rapid propagation of some chemical, and the reversion to R by the decay of this chemical. (The snap-shut routine is more complex.) In this way, sessile organisms can react to a spatiotemporal pattern occurring on their bodily surfaces (or interiors) without needing to represent the outside causes explicitly. Their internal states mediate behaviour that is sensitive to spatiotemporal patterns without representing those patterns. There is no need for the Venus flytrap to sense the fly as distinct from other objects in the vicinity; there is no need for it to represent where the fly is.

### Targeted Motility and Its Demands

As complex as detection and choice functions are in sessile organisms, organisms that move themselves from one place to another are faced with problems that demand a different kind of sensory function. Organisms that are motile in this way need and are equipped to search for food not just in contiguous soil and air, but also in regions that are some distance removed from themselves. I walk across the crowded reception room to greet the friend I haven’t run into for a long time. In doing this, I not only make choices based on what I perceive distally, but also plot a course through space to the person I thus single out. I don’t follow a gradient in order to do this; I plot a course to an object identified at a distance and correct my course as I go. Behaviour that targets distant objects demands a different kind of perceptual representation of space.

Let us now consider a particular form of motility, which is likely what Aristotle had in mind when he said that the soul “pursues and flees” sensed objects that are pleasant or aversive. *Targeted* motility, or *t*-motility,is self-actuated, self-propelled motion *toward (or away from) a distant object or location* through terrain that might require an indirect path around obstacles or course-correction as new circumstances arise.

I’ll give three kinds of evidence that shows that animals are *t*-motile.

Start with the phenomenological. Organisms that are *t*-motile are equipped to search for food not just in contiguous soil and air, but also in regions that are some distance removed from themselves. Behaviour that targets distant objects demands a perceptual representation of space. Let’s suppose that you start from A and set a course to B, which you can initially see. The straight path to B is blocked and so you have to plot an indirect trajectory. Moreover, there are objects along the way that obscure your view of B when you are up close to them. (See Figure 3.)





Figure 3: Finding your way around an obstacle

T-motile organisms keep track of B while detouring around the objects in the way. At many points, B is out of sight behind the obstacle, but they are able to track their own position relative to B despite this. They do this by updating their position on an internal map on which the position of B is marked. Input to the update is perceptual movement information. This information is in a form that allows it to update the map. They cannot achieve this by sampling the strength of some field that maxes out at B.

The above was phenomenological evidence. It seems, subjectively, that we are capable of *t*-motile action. Now here are two performance-based criteria.

The first such criterion was devised by E. C. Tolman (1948) and colleagues. It is meant to show that animals represent their surroundings in the form of a “cognitive map," a mental representation that enables them to store and recall geometrical features of recalled environments.[[17]](#footnote-18) As Michael Rescorla (2018) reports, scientists defend the existence of these maps by showing that animals are able to “take novel detours and shortcuts.” “A recurring experimental paradigm . . . is to displace the animal to an unfamiliar point within a familiar environment. In many cases, the animal travels directly from the release point to the goal” (*ibid*. 35). For example, Tolman, Ritchie, and Kalish (1946) trained rats to find food in a maze like that in Fig 4:

A diagram of a circular object with lines and text

Description automatically generated

Figure 4: Maze used to train rats to find food located at point H

Having done so, they then removed the maze, replacing it with an apparatus of radiating chutes with the starting point and food reward unmoved (Fig 5).

A diagram of a sun

Description automatically generated

Figure 5: Radiating chutes that replace the maze shown in Figure 4. Note the start-point on the circular platform and the end-point, H, as in Figure 4.

The result was that the rats were to run straight to H, or at least come close. This shows that they could, in Rescorla’s words, take novel shortcuts.

C. R. Gallistel (1990) relates a similar performance in a human child. He recounts how Barbara Landau and Lila Gleitman (1985) brought a congenitally blind child of 31 months into their lab and guided her from a point of origin (where her mother was seated) to various objects in the lab—a table, a basket, and so on—always bringing her back to Mother after visiting each object. Once the child had become familiar with the paths from Mother to each object, they guided her to one of the objects, the table, and asked her to find her way to another object, the basket. She was able to trace a more or less straight line between these objects, not having to travel via Mother. Gallistel remarks: “In holding its course, the child was presumably entirely dependent on dead reckoning, calculating changes in her position from vestibular, kinaesthetic, and efference copy signals” (1990, 101). The child did not find the basket by muscle memory; she had no muscle memory of the table-to-basket path. She also did not use a field created by some signal emanating from the basket; in particular, she could not use the fact that the destination object loomed as she approached it. Rather, her spatial sense was able to construct an internal map of the objects from the paths traversed earlier, which she then used to trace a direct path from one object to another by-passing the earlier circuitous routes via Mother. She used motion signals from her vestibular, kinesthetic, and motor systems encoded her own movement vectors to distinct located objects; she had no access to a field strength gradient for the purpose.

There are many other phenomena of this sort. Foraging animals—ants, bats, honey-bees—take a random exploratory path from their home base in search of food. When they have found food, they are able to return to their home by a direct path.

Finally, there is direct evidence from the brain of cognitive maps contained therein.

John O’Keefe and Lynn Nadel (1978) and co-workers showed that the hippocampus contains an array of so-called “place cells,” each of which is associated with a specific place in the environment. Workers in later years, many in O’Keefe’s research groups at University College, London, slowly discovered that these place cells are supported by a variety of location-indicating cells such as grid cells (which fire when the animal is at an intersection of lines that make up a grid that covers the environment), border cells (corresponding to walls and other limits to the animal’s environment) and head-direction cells (which mark the animal’s heading).[[18]](#footnote-19) Together, the array of place-cells and border-cells thus constructed constitutes an allocentric map of a remembered place, with head-direction cells providing a translation from egocentric to allocentric coordinates.

The hippocampus is an organ that structures sensory input from the external senses in a matrix that corresponds to external space, thus enabling us to perceive objects as possessing allocentric location in a single framework. Recall the sceptic who questions how it is possible for an organism to possess information that goes beyond what is given by sensory receptors. The answer is that the hippocampus imposes spatial structure on this information. This is not an arbitrary imposition. The spatial structure works to provide the organism with the phenomenological structure of *t*-motility which, in addition, meets the performance requirements sketched above. As O’Keefe and Nadel (1978) argue, the hippocampus is an organ that imposes a Kantian *a priori* onto the sensory substrate of the eye, ear, and so on.

### Conclusion

In perception, animals make contact with a world arrayed in three spatial dimensions. They do so in two ways. First all motile animals have a body schema for sensorimotor interaction. Second, higher animals such as teleost fish, birds, and mammals have cognitive maps for the allocentric location of perceived entities. Spatial sensory states of this sort are othering—entities appear distinct from the perceiving subject in virtue of perception.

Plants do not perceive; they simply regulate their own bodies in accordance with programs based on the input of their sensors. We should not underestimate the claims of such self-regulating sensing. Plants are not passive lumps of organic matter. But we should not overestimate it either. Plant sensing is not the same as external sensing, consciousness, or agency. It is entirely self-regarding.

When humans are conscious, they are self-conscious. When I think, I have an idea of myself as the agent of thinking. Such a mode of thought implies a distinction, an idea of *non*-self.When I think of the outside world, I think of it as real inasmuch as I think of it as something outside myself. These notions of self, of self and other, and of independently existing reality are all founded on sense impressions that present the targets of action as outside the agent’s body. These impressions are the “othering” impressions that I have discussed in this book. These impressions are what set perception aside from mere sensation. Only animals are capable of perception. If plants are conscious, then they are solipsists.[[19]](#footnote-20)

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1. I would like to say what may not be obvious—Tye’s work on perception is generally admirable. [↑](#footnote-ref-2)
2. This definition is inspired by, but a little different from, Thomas Reid’s classic conception. According to Reid, a *sensation* is a sense impression I that has no object distinct from Iitself (*EIP* I 1 12). A perception, for him, is a mental state P formed on the basis of sensations that has an object distinct from P. In my view, Reid’s conception of sensation is a bit odd—it suggests that sensations might be reflexive in some manner. I believe that this suggestion is irrelevant to Reid’s intention—he simply wants to assert that perception is about external objects but is derived from sensory states that carry no information about external objects. My definitions are intended to capture something like this distinction. My version is more demanding for *perception* (and by implication, less demanding for sensation (which I call “mere sensing”)*.* For a subject S to perceive is for S to have a sense-based impression P of something distinct from S (not merely distinct from P itself). [↑](#footnote-ref-3)
3. Aristotle’s doctrine is well documented in Coren (2017). For an excellent discussion of the medieval tradition, see Christina Thomsen Thörnqvist (2022). [↑](#footnote-ref-4)
4. For information and discussion about the Indian traditions, I am grateful to my colleagues, Elisa Freschi, Nilanjan Das, and Jonardon Ganeri, as well as to Piotr Balcerowicz. [↑](#footnote-ref-5)
5. I hasten to say that I do not know whether this was Jinabhadra’s position. It is, however, an undeniable tendency throughout the history of philosophy. [↑](#footnote-ref-6)
6. Some would respond to this by saying that there are more senses than five—see, for example, Fiona Macpherson (2011). She would say that gravisensing is just an example of an “extra” (as we might say) sense modality. Macpherson is certainly correct to say that there are sense modalities over and above the five (for example, the infrared “vision” that some snakes possess). But her list—“hunger, thirst, wet and dry, the weight of objects, fullness of the bladder, suffocation and respiration, sexual appetite, and lactiferousness” (*ibid* 126)—contains a number of special purpose sensory capacities that regulate the body without an associated impression. These are not really full-fledged “senses.” [↑](#footnote-ref-7)
7. Bonnet’s work referred to by Moulton, Oliveti, and Goriely (2020). [↑](#footnote-ref-8)
8. Darwin cites a number of other plant physiologists: Hugo De Vries, Sydney Howard Vines, A. B. Frank, and Julius von Sachs. Forty years after Darwin, Jagdish Chandra Bose, a Bengali physicist, studied electrical signalling in *Mimosa pudica*. Every Indian child has taken delight in this plant’s habit of closing its leaves when touched. Darwin notes that this behaviour of *M. pudica* resembles sleep but says that the cause is different; this in itself indicates this behaviour is actively managed. (See Trewavas 2014, 16-18,for an account of Bose’s work and <http://tinyurl.com/gn6p2r4> for a story in the *Independent* on the Google Doodle that commemorates Bose.) [↑](#footnote-ref-9)
9. The same could be said, for example, about the way ants use the polarization of the Sun’s light to determine direction and bearing. The navigational states of these animals depends on the states of their polarization detectors; however, this is *not* tantamount to representing the Sun or its light as objects distinct from themselves. (Thanks to an anonymous referee for requesting this clarification.) [↑](#footnote-ref-10)
10. The body schema is implicit in dorsal stream visual processing, or what I have called “motion-guiding vision” (Matthen 2005, ch. 13). [↑](#footnote-ref-11)
11. The term “cognitive map” was introduced by Tolman (1946, 1948) and made canonical by O’Keefe and Nadel’s (1978) classic work on the hippocampus. [↑](#footnote-ref-12)
12. Some “lower” animals, such as hymenopterans, move about their habitat, but *navigate* (or move relative to a target) primarily to a home base (such as a nest). It is somewhat controversial whether such navigation demands a full cognitive map or spatial layout, as opposed to a single homing vector. See Wang et al (2023) for discussion and for compelling evidence that honey-bees possess a full cognitive map. However this may be, it is clear that these animals have sensorimotor othering impressions. For they pick up and transport food from distant locations to their nest. [↑](#footnote-ref-13)
13. See Rodriguez et. al.(2021). Rodriguez suggests that teleost fish have a homologue of the hippocampus. [↑](#footnote-ref-14)
14. For a discussion of hunger along these lines, see Matthen (2023). [↑](#footnote-ref-15)
15. Let’s say, for the sake of simplicity, that genotype A is more similar to B than to C if it takes fewer mutations to get from A to B than from A to C. [↑](#footnote-ref-16)
16. See Massa and Gilroy (2003) suggest that pressure on the root deactivates the gravisensors and thus causes the root to grow along the barrier. Of course, this doesn’t ensure that the root will emerge on the other side of the barrier relative to the nutrition or wetness gradients. [↑](#footnote-ref-17)
17. See Tolman (1948) for discussion. [↑](#footnote-ref-18)
18. May Britt Moser’s (2014) Nobel Prize Lecture gives a good and accessible narrative account of these discoveries. [↑](#footnote-ref-19)
19. I am very grateful to Peter Schulte and an anonymous referee for extremely helpful and constructive comments. [↑](#footnote-ref-20)