

Unnerving Intelligence

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A variety of definitions of intelligence have been offered that are not exclusively human-centric. One, in particular, is taken as a starting point: end-directed behavior marked by the making of meaningful distinctions made possible by perception-action cycles. Specific examples of end-directed behavior are examined for evidence of three aspects of the kind of agency embodied in perception-action cycles, namely, *prospectivity*, *retrospectivity*, and *flexibility*. The chosen examples of behavior are nicely layered but otherwise unremarkable. Nonetheless, they all have an unexpected twist that challenges the kinds of explanations of intelligence qua agency that are rooted in neurobiology.

Imagine that I reject food because its odor indicates that its nutritional value is low. I don't even try it and I don't have to compare it against an alternative right now. I just reject it for the possibility that something better will turn up. How would you explain my behavior?

Imagine that I plant something that siphons the nutrients out of the soil in a location closer to my neighbor's garden than my own. Although this location is better for the long-term prospects of my garden, it's not neighborly. How would you explain my behavior?

Imagine that I'm cut by someone and I fight back with a volatile spray like mace. Or, alternatively, I set off an alarm that summons a kind of posse that dispatches my attacker. If the attacker comes back and hurts me again, I act even faster the second time. However, if I'm injured by someone who I do not identify as an attacker, I don't Mace them and I don't set off the alarm. How would you explain my behavior?

A current fashion in theorizing about adaptive behavior takes a Bayesian approach (e.g., Wolpert & Ghahramani, 2000, in press). Perception and action are taken to be statistical inferences based on stored knowledge about the probability that particular perceptual variables co-occur with particular natural scenes and particular actions

co-occur with particular end-effects. During perception, for example, many would argue that the brain refers to stored probability distributions in order to compute the likely identity of the current scene based on current variables. This thoroughly modern theory boasts clear echoes of Helmholtz: Assign to the proximal stimulus whatever distal stimulus is most likely to have caused it. That assignment, in turn, provides a model that will guide the selection of a likely motor program from stored probability distributions of actions. While one could, in principle, work out the details of the computations that would take this scenario from sensory input to motor output, we note what we take to be more than an oversight: Proponents of such computations don't typically address how one comes to possess the knowledge structures and inference machinery that not only support the computations but guarantee that they are correct. Nor do they address how the knowledge structures are precisely what the inference machinery needs and how the machinery manages to work on just those variables that are relevant to the problem of the moment (and not any of the infinite number of other variables that are present at the same time; cf. Turvey, Shaw, Reed & Mace, 1981; see also Malebranche, 1678/1997).

In some quarters, such “loans of intelligence” (Dennett, 1981; Turvey & Carello, 2012) are unsatisfying because they seem to presuppose, rather than explain, the capacities under examination. Anchoring the ability to make meaningful distinctions in rational capacities, knowledge structures, and inference machinery entails an infinite regress. But, philosophical considerations aside, the issue of computational capabilities is problematic in and of itself.¹ Not only are similar meaningful distinctions made by animals with widely varying nervous systems, they are made by organisms without nervous systems. For this latter point we note that our opening invitation to imagine how meaningful distinctions such as edible vs. inedible, self vs. other, and threatening vs. not threatening might be explained omitted one detail. Imagine that, in each case, I am a plant.

Example 1 describes the behavior of the five-angled dodder (*Cuscuta pentagona*), a parasitic leafless plant that must depend on drawing nutrients from a host to survive. It will coil around a good host or bend away from a poor host, and it will do so without first taking up any food from either host and without being in the presence of other potential

¹ Of course, philosophical considerations are also implicated in comparing perceiving and acting capabilities across phyla (or even across individuals), in particular, with respect to multiple realizability. Although a detailed treatment of such considerations here would obscure our larger point, it would likely turn on and around argument we make later: The capability of interest—agency, as defined below—is exactly the sort of thing that does not inhere in any specific neural or anatomical assembly.

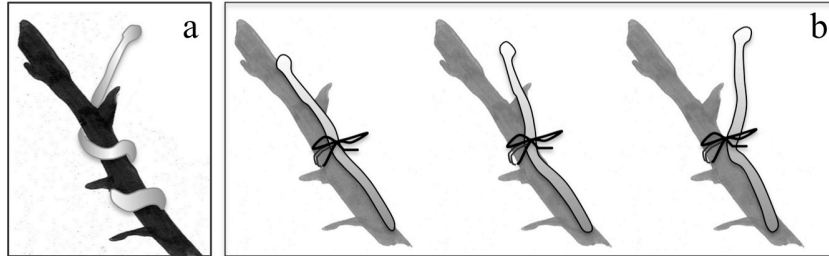


Figure 1. (a) Dodder coils around a hawthorn branch before tapping it to draw nourishment. (b) If dodder is tethered to a hawthorn branch that has been leached of nutrients, the tendril will grow away from the branch rather than coil around it (Kelly, 1992). Again, this behavior does not require tapping the branch. Information about edibility is available prior to eating-as-tapping.

hosts for comparison (Figure 1). Example 2 describes the behavior of the pea plant whose root development is such that it avoids competition with itself and increases competition with neighbors. Example 3 describes the behavior of the poplar leaf that deals with damage by exuding volatiles, air-borne chemicals of several types (Figure 2): toxic to an attacking caterpillar, attractive to predators of that unfortunate arthropod, or soothing if the leaf is cut with scissors rather than mandible. After a second caterpillar attack, the poplar releases those chemicals with a shorter latency, as do neighboring poplars who were not direct victims of the initial attack but were bathed in the chemical alarm call. And the poplar's behavior is not unusual: "Plants talking to their bodyguards is likely to be a characteristic of most, if not all, plant species" (Dicke, van Loon, & Soler, 2009).

Such examples have contributed to a burgeoning field referred to by some as *plant intelligence* (Calvo, 2007; Calvo & Keijzer, 2011, in press; Trewavas, 2003, 2005). More and more, scholars argue that the behaviors of plants—activities such as exuding chemicals, extending roots, bending stems—provide many parallels to the adaptive behaviors of animals (for other examples, see Dicke et al., 2009; Milius, 2009; Calvo & Keijzer, 2011). But adaptation is one thing; behaving in a way that could comfortably be labeled intelligent is quite another. If scientists are unwilling to believe that intelligence was an endowment on the 6th day, then how many days (or eons) are they willing to push it back? What are the generic principles that would allow intelligence to emerge (and in a very real sense to thereby be defined)? What some take to be a radical insight (cf. Hylton, 2009)—that intelligent behavior is non-algorithmic—does a lot of the heavy lifting in this endeavor. While this insight is radical it is not new; it is, in fact, fundamental ecological psychology (Gibson, 1958, 1959; Turvey & Carello, 2012). Ecological psychologists have long argued that animals' achievements of perception and action do

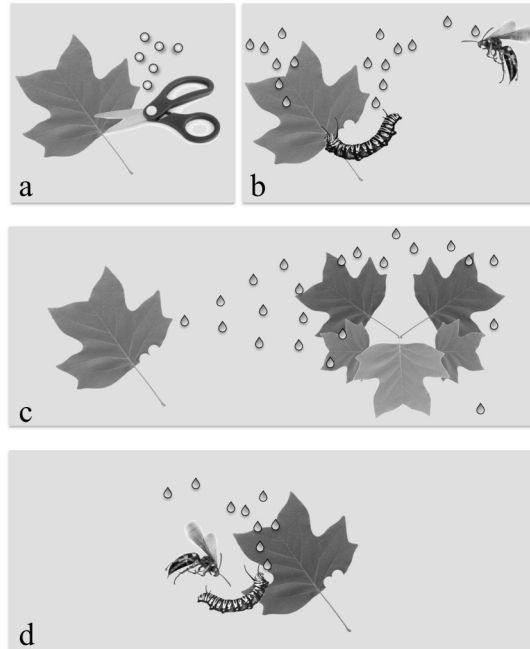


Figure 2. (a) A poplar leaf that is cut with scissors will exude a volatile that acts as a salve for its wound. (b) A poplar leaf that is bitten by a caterpillar will exude a different kind of volatile, one that attracts predators of the caterpillar, while (c) neighboring poplar leaves that are not under direct attack will exude the same kind of volatile. (d) If the poplar leaf suffers a second caterpillar attack, it exudes the predator-attractive volatile with a shorter latency (Dicke et al., 2009).

not take their character—neither the form of the problems nor the form of the solutions—from the sensory machinery, nervous systems, or brains of those animals. Whatever supportive role the hardware plays, it is not to define primitives and execute computations over them; it must be transparent to the lawful regularities at the ecological scale (Kugler & Turvey, 1987). The essence of ecological psychology is to anchor the character of perception and action in the animal-environment system. In particular, the focus is on how animals behave in the world, not how the world is built inside the animal (Reed, 1996).

In order to behave effectively, the animal (or, more generally, the organism) needs to manifest *agency*. As summarized in the first special issue on physical intelligence (see also, Turvey, in press-2012):

Agency, scientifically explained, is the goal of ecological psychology: the manifest capability of all organisms to exhibit some degree of autonomy and control in their encounters (E. Gibson, 1994; Reed, 1996; Shaw & Kinsella-Shaw, 1988). Agency is constituted by (a) variation of means to bring about an end (*flexibility*), (b) coordinating

current control with emerging states of affairs (*prospectivity*), and (c) coordinating current control with prior states of affairs (*retrospectivity*) (Turvey & Carello, 2012, p. 4-5).

In what follows, we will consider the notion of intelligence from this perspective, which is perhaps uniquely untroubled by the lack of a special or exclusive causal role for a nervous system. Some have argued that this particular tranquility rests on grounding perception and action in a natural, physical context (Kugler & Turvey, 1987; Kugler, Turvey, Carello, & Shaw, 1985; Reed, Kugler, & Shaw, 1985; Turvey, 1990; Turvey & Carello, 1981; Turvey & Shaw, 1995), that perception and action are what they are because of thermodynamics (Swenson & Turvey, 1991). This means that the three-pronged definition of agency emerges from a natural-physical grounding. Of course, plants may have other limitations that will make meeting the demands of the label *intelligent* challenging. So we will provide an outline of what those demands are for a natural-physical approach to perception and action. We will then select a few examples of plant behavior to see if they are up to that challenge. We will end with a consideration of debates within the community of plant scientists as to whether the achievements of their organisms-of-choice ought to be considered intelligent. The debates are illuminating with respect to the broader goal of extending intelligence into the domain of the inanimate. While the possibility of intelligence in organisms other than humans and animals might be disconcerting—unnerving, if you will—it is demanded by the attempt to preserve principled continuity in a natural-physical account of effective behavior.

INTELLIGENCE AS INFORMATIONALLY-GUIDED PERCEPTION AND ACTION

A common understanding of intelligence is most assuredly a mental capacity or collection of capacities. It is close to what cognitive psychologists would call *declarative knowledge* or “knowing that.” Early attempts to find faculties of the mind in particular regions of the brain are echoed in the oldest theories as well as the most updated technologies that purport to do the same (e.g., dubbed neo-phrenology, Uttal, 2002). But when scholars confront the task of defining intelligence with care, their boundaries are not drawn according to domains of knowledge or specific skills but by relationships between the agent and the surrounding circumstances. They are closer to what cognitive psychologists would call *procedural knowledge* or “knowing how.” The breadth of these definitions not only accommodates but even invites a consideration of intelligence beyond the human. In his treatment of the evolution of

intelligence, Stenhouse (1974) aimed at a general theory of intelligence as “adaptively variable behavior during the lifetime of the individual.” The *MIT Encyclopedia of the Cognitive Sciences* (Wilson & Keil, 1999) requires a more active role for the agent: “the ability to adapt to, shape, and select environments.” Clearly, these definitions are not highlighting language or mathematics or strictly human skills. The colorful achievements of crows using hooks to scoop insects out of wells (even fashioning their own if none are available; Weir, Chappell, & Kacelnik, 2002) or Darwin’s worms selecting and bending leaves to line a burrow (Darwin, 1881) satisfy these broad definitions. The question is whether the invitation to consider intelligence beyond the human is also an invitation to consider intelligence beyond *Animalia*. Adapting is not the sticking point; behaving is, especially behaving that is variable, or that shapes and selects environments. The importance of knowing-how (see Turvey & Carello, 2012)² is conveyed by both of the preceding animal examples. Betty the crow knows what to do whether she has a branch or an experimenter-provided hook or she has to fashion a hook from a straight piece of wire. For the three cases, the behavior is necessarily different. Darwin’s worms know what to do whether the materials are leaves, bits of paper, or pebbles. Again, for the three cases, the behavior is necessarily different.

Before considering plant examples in more detail, let’s consider whether these kinds of definitions are satisfactory for the kind of natural-physical approach entailed by ecological psychology. We begin with the easy part: These definitions are already compatible with a focus on how organisms make their way in the world, not on how the world is made in organisms (Reed, 1996). So in that sense, they do not demand a representational/computational account (despite what their authors might have had in mind). But they do entail that intelligent agents have some degree of autonomy and control in their encounters. At minimum, for organisms to be considered intelligent, they cannot just be buffeted by forces—they must be able to act in a way that is orthogonal to local gradients. That is, they must not just follow the path of least resistance to a local source of energy; they must be able to avoid these so-called local potentials in favor of larger goals (Swenson, 2010). That criterion is already demanding but it is not enough. Selecting and shaping environments, not just adapting to them, requires that behaviors must be guided. A candidate generic definition of intelligence has been proposed: “end-directed behavior guided by meaning” (Turvey & Carello, 2012,

² This sense of knowing is as a natural phenomenon at a particular scale of magnitude (Turvey & Carello, 1981), as a coordinating of organism and environment, rather than as a property of mind. It is fundamentally framed in terms of behavior.

Guidelines 11 and 14). This definition requires an intelligent agent to make meaningful distinctions and to organize appropriate actions with respect to these distinctions.

Agency is manifest with respect to affordances (Gibson, 1979/1986; Turvey, 1992). Animals make meaningful distinctions—for example, perceiving something as edible or not, as a barrier to locomotion or not, as threatening or not—and organize their actions accordingly—to eat, to steer around, to defend oneself. We are rich with examples of affordance-effectivity couplings from a variety of creatures: the furry, the feathered, the scaly, and the shelled. Despite their variety, those wrappers enclose controllable segments—effectors—that allow the agent to move. And this, of course, is where plants are at a disadvantage. They are largely sessile. They may grow up or down or out, ramify or spread but, with a few exceptions, are otherwise anchored. “The plant has motion but not locomotion” (Bawden, 1919, p. 249).

Do they have enough means to exhibit autonomy and control in their encounters—do they do action? And in the absence of sensory machinery of whatever kind, are they capable of appropriate sensitivity to register states of affairs to make the kinds of meaningful distinctions that might guide them—do they do perception? Even if we find examples where a plant acts in response to something, is that all there is? Is a one-trick pony an intelligent pony?

PROSPECTIVITY, RETROSPECTIVITY, AND FLEXIBILITY IN PLANT BEHAVIOR

A seed is planted in the soil. If the soil has enough nutrients and water, the seed will germinate and grow. Climates of one kind will be favorable to the survival of a particular collection of characteristics; climates of a different kind will favor the survival of a different set of characteristics. Such coarse adaptations are not what we mean by intelligence. Plant-as-agent has to show the ability to be forward-looking, changing its behavior in anticipation of what will be, reflective of what has been, and with options as to how it can behave to accomplish its end. In other words, we are looking for evidence of prospectivity, retrospectivity, and flexibility in examples of plant behaviors. We are not providing an exhaustive inventory of intelligent behavior by plants. Such compendia are available from expert sources (e.g., Chamovitz, 2012; Trewavas, 2003). Nor will we get into issues of specific mechanisms (e.g., which gene or protein is involved) that might support those behaviors. Our interest is in providing existence proofs for such behaviors in plants that might be categorized in terms of the demands for agency. It should be noted that our descriptions of plant behavior use the

language of agency, construed as the manifesting of prospectivity, retrospectivity, and flexibility—the capabilities that, we argue, are the hallmark of successful action. Consequently, we purposely eschew phrases like “a stimulus elicits a response” in favor of end-directed phrases like “steers by detecting.”

First, it has to be established that plants can legitimately be said to behave. Although it may not be obvious to those familiar only with animal behavior, the examples in the opening paragraphs demonstrate that plants, too, move and act. Silvertown and Gordon (1989) offer the following definition of behavior as one that covers plants as well as animals: behavior is “...morphological or physiological responses to events or environmental changes that are rapid relative to the lifetime of an individual.” Though plants seem to be almost entirely sessile, this definition highlights that their behavior may simply go unnoticed because it does not occur on the scale of most animal behaviors. Consideration of the relationship between behavior and lifespan fits with the Gibsonian [cf. Gibson, 1979/1986; Warren & Shaw, 1985] emphasis on events as nested and occurring on multiple, interconnected timescales. With no clear-cut distinctions between fast and slow events, discounting plants because they move more slowly than humans is scientifically untenable. Further, Silvertown and Gordon’s emphasis on morphological change also sheds light on the issue of plant behavior: whereas an animal may move toward food or away from something inimical, a plant may grow toward or away from environmental features depending on its needs (Trewavas, 2005). Plants and animals differ in morphology, needed resources, and ways of obtaining resources, as do species within phyla and individuals within species. The relevant, and ecologically minded concern is with an organism’s constraints and possibilities for interaction with its environment. It is under these terms that behavior must be assessed for prospectivity, retrospectivity and flexibility.

Examples of prospective behavior are the easiest to come by. As already noted, dodder will bend away from a poor host on the prospect that a better one will come along in the future. The pea plant develops roots in such a way to avoid future competition with itself while increasing competition with neighbors. And the poplar leaf coordinates current control of its volatiles to bring about the arrival of a vespid posse. It seems clear that these behaviors are end-directed. Examples of retrospectivity are less prevalent, but also available in the literature. As already noted, the poplar exudes its volatiles with a different latency depending on its history. Crop plants like sorghum and pasture grasses acclimate to drought or cold when exposed to mild water deprivation or low temperatures (Kramer, 1980). Another example is that of pea tendrils that require combined mechanical stress and blue light to coil. The plant

coils under blue light even if mechanical stress happened hours before (Jaffe & Shotwell, 1980). A last example is found in Scots pine (*Pinus sylvestris* L.) that express differential stem growth depending on mechanical stress applied during their dormant period (Valinger, Lundqvist & Sundberg, 1994). Flexibility is a challenge. It does not just require a variety of behaviors but a variety of ways of bringing about an end. Here we appeal once more to the poplar. It can use different volatiles to combat the immediate attacker toxically or to summon the attacker's predators. Siratro (*Macroptilium atropurpureum*), a twining legume, exhibits compounded flexible-prospective resource seeking behavior, orienting its leaves toward the sun when the soil is water-rich but away when the soil is dry (Ludlow & Björkman, 1984). In other words, Siratro is not only sensitive to both its need for water and its need for sunlight, but also to how the pursuit of each resource may interfere with the pursuit of the other. As a last example, the primary root of *Arabidopsis thaliana* can maintain general downward expansion while avoiding obstacles (Figure 3) by changing its gravity-informed growth according to touch information about barriers (Massa & Gilroy, 2003). This satisfaction of goals in the face of competing constraints is analogous to rational choice behavior in other organisms lacking neural machinery, such as the slime mold (*Physarum polycephalum*; Dussutour, Latty, Beekman, & Simpson, 2010; Latty & Beekman, 2010), as well as reminiscent of other efforts to couch plant resource-seeking in economic terms (Kelly, 1990; Cain, Dudle & Evans, 1996).

It seems clear that that plant behaviors can be forward-looking, reflective of what has been, and versatile in accomplishing ends. But our generic definition of intelligence requires that these behaviors be guided by meaning. The behavior of the poplar has been characterized by the scientists who study this plant-herbivore relationship in a way that seems to enforce this parallel: "Plants release airborne chemicals that can convey *ecologically relevant information* to other organisms" (Mescher,

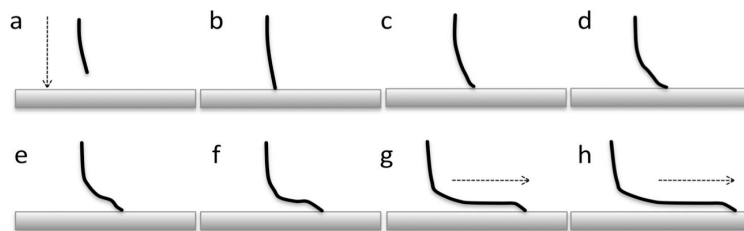


Figure 3 The primary root of *Arabidopsis thaliana* (a) grows downward, informed by the gravitational gradient. (b) It encounters a glass barrier, whereupon it grows a step-like structure (c, d, and e). Only the root tip touches the barrier (the main axis does not) and the root does not buckle; it grows at the same rate as before contact (f, g, and h). This suggests that the root tip actively senses the obstacle and modulates the growth informed by the gravitational gradient. (Massa & Gilroy, 2003).

Runyon, & DeMorais, 2006, emphasis added; see also Runyon, Mescher, DeMorais, 2008). There are a few things going on in the poplar example so let's focus on the ecologically relevant information for other poplars. In the domain of perception-action cycles in humans and animals, we look for structured energy distributions specific to a state of affairs. Given this specificity, these structured energy distributions are meaningful in the sense that they inform about the state of affairs. A particular optic flow morphology, for example, is specific to, and thus informs about, one's direction of heading. For meaning-guided behavior, we are looking for field properties (in the physics sense) such as gradients, which might inform the plant about current, emerging, and past states of affairs. The fact that plants steer and orient and ramify and spread on the basis of gradients of various kinds, whether exuded by other plants, or encountered in the soil, the light, or mechanical vibration, simply seems to generalize this intuition.

For dodder, the relevant information specifying inedible seems to be carried in the airborne chemicals exuded by the nutrition-poor host (Kelly, 1992). Potential hosts that vary systematically in nutrient level (produced by first leaching them of all nutrients and then seeding them with different proportions) will be encircled by dodder with a likelihood that parallels the specific nutrient level. The pea-plant steers by detecting chemical concentrations in the soil. And the poplar plant is guided by chemicals in the saliva of their predators (which are not carried in the scissors of a gardener) as well as in the air of their attacked neighbors. Large-scale meaning-guided behavior is apparent in how the chemical components of smoke prompt the germination needed to reforest after a fire (Flematti, Ghisalberti, Dixon, & Trengove, 2004).

Another clear example of coordination of current control with an emerging state of affairs specified by ecologically relevant information in the chemical gradient is induced by an attack on a plant's conspecifics. Willow trees can be planted in pots so that their roots are isolated from each other and either sharing air in the same sealed room or completely isolated in separate sealed rooms. If a willow is infected with caterpillars, it will engage its own defenses against the leaf-eaters. This direct action is not surprising. More noteworthy are the same kinds of defensive adjustments by willows in the same room, adjustments that are not engaged by willows that are isolated by root and room (Grady & Suzuki, 2004).

Volatiles mediate important ecological interactions among plant species, not only for defense but also for nourishment (Runyon, Mescher, DeMorais, 2006). When a dodder is placed in the middle of an arena with no potential hosts, it will grow in all directions with equal frequency. If any of a variety of potential hosts (e.g., tomato plants, impatiens) is

introduced, dodder grows in its direction. Dodder also grows toward “tomato extract” but not toward a plastic tomato plant that casts the same shadow as a real plant, suggesting that the relevant energy gradient is chemical. If a potential host is of low quality, such as a wheat plant, dodder will grow toward it but with less enthusiasm (i.e., a lower proportion of forays in its direction). Given a choice between the high-quality tomato and the low-quality wheat, growth is towards the tomato (Figure 4). As it turns out, wheat gives off one compound that dodder finds repellent, a compound that tomatoes give off when infested with pests (Runyon et al.)!

Chemical gradients are not the only medium that conveys ecologically relevant information. Touch responsiveness (thigmotrophism) is

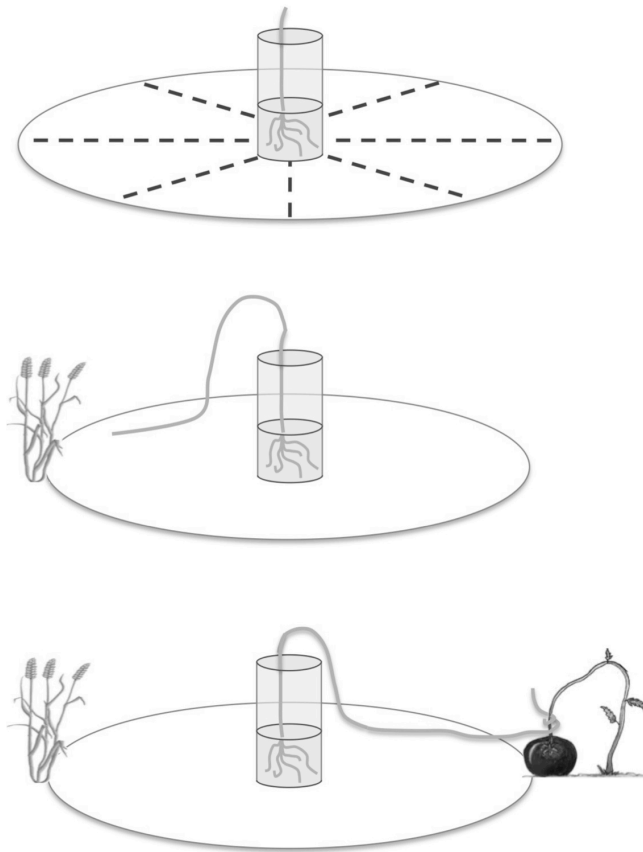


Figure 4 (top) A dodder placed in the middle of an arena with no potential hosts will grow in all directions with equal frequency. (middle) If a viable but not ideal host such as a wheat plant is placed at one location in the arena, dodder will grow in that direction preferentially. (bottom). If both a preferred host such as a tomato plant is also available in the arena, dodder will grow preferentially toward the tomato (Runyon et al., 2006).

common in tendrils, as pointed out before, which will coil around a stem, and roots, which will steer around (Vartanian, 2011) or through a barrier (Braam, 2005). A plant stem that is stroked a few seconds per day grows a thicker stem, which makes it more wind-resistant (Jaffe & Shotwell, 1980). Sensitivity of plants to gravity has long been appreciated (Knight, 1806). Gravitational gradients may be construed as informing shoots about orientation relevant to efficient photosynthesis and informing roots about orientation relevant to finding water and nutrients (Chen, Rosen, & Masson, 1999). Light sensitivity, not unexpectedly, abounds. The flowering plant *Malvastrum* orients its leaves to follow the sun throughout the day. Although it ends up facing west, it assumes a neutral posture at sundown. Just before dawn, however, it faces where the sun will be (Ford, 1999). Specific portions of the spectrum appear to inform plant behavior. For example, some nightshade species (*Solanum nigrum* and *Solanum ptycanthum*) adjust their rate of stem elongation based on the ratio of red to far-red radiation, which is important information for shade-avoiding plants (Crotser, Witt, & Spomer, 2003). Lastly, it has recently been demonstrated that young roots of corn (*Zea mays L.*), orient toward the source of water-borne sound, with the speculation that such acoustic structure may provide information about resource location (Gagliano, Mancuso, & Robert, in press). Not unexpectedly, much research in this domain is subject to spirited debate. The nature of the debate tends to center on the mechanisms, however, not on the fact of sensitivity to particular gradients. What is especially intriguing about the possibility of multiple gradients is that they may provide a basis for the same functional behavior. For example, not only does the foliage of *Mimosa pudica* close during darkness and reopen in light (Raven, Evert, & Eichhorn, 2005), the leaves also close with touching, warming, blowing, or shaking (e.g., Simons, 1981).

IS PLANT INTELLIGENCE POSSIBLE?

The foregoing characterization of plants as agents capable of prospective, retrospective and flexible behavior guided by meaning has elicited three types of reactions in the scientific community: (1) seeking a plant counterpart to the kind of neurobiology presumed to be necessary to allow intelligent behavior, (2) denying the possibility that the kinds of behaviors exhibited by plants can be considered intelligent because plants do not have a nervous system, or (3) accepting the absence of nervous system or an analogue in plants, but invoking rational capabilities to explain their behavior.

Plant analogues for the nervous system exist. The logic behind the quest for nerve-like structures in plants appears to be the following: The

complex adaptive behavior that, in animals, is called intelligence is made possible by the power of the central nervous system to process information. Plants clearly have complex adaptive behavior: They forage for food in competitive circumstances; they demonstrate concerted responses to changing environmental circumstances that maximize their fitness. If only something akin to a nervous system could be found, then the claim of plant intelligence would be legitimized.

The first reaction is not new. Darwin (1875) had suggested that:

It is hardly an exaggeration to say that the tip of the radicle thus endowed [...] acts like the brain of one of the lower animals; the brain being situated within the anterior end of the body, receiving impressions from the sense-organs, and directing the several movements.

Bose, the radio pioneer, devoted a good deal of attention to plant physiology (1907, 1926), including identifying what he took to be “nervous system-like response in all parts [of a plant] that recoil from shock just like an animal would.” This kind of reaction is the foundation of plant neurobiology, a recent field that focuses on the interaction of plants with their environment, specifically, on the plant’s integral response to perceived signals. Plant neurobiology (e.g., Baluska, Mancuso, Volkmann, 2006; Roshchina, 2001; Stahlberg, 2006) assumes the existence in green plants of structures equivalent to those known from animal physiology, such as synapses, neurons, rapid signaling and communication systems, and may even assume an organization managed with intelligence by a sort of central brain. Focus of research has been on long-distance electrical signals and molecules homologous to the neuroreceptors and neurotransmitters found in the nervous systems of animals (Brenner, Stahlberg, Mancuso, et al., 2007).

How literal are we supposed to consider the foregoing analogies? Trewavas (2007) argues that they are instructive metaphors. A kind of mission statement for the journal *Plant Signaling and Behavior* seems to agree with this characterization:

This Plant Neurobiological view sees plants as information-processing organisms with complex communications of various types occurring throughout the individual plant. What we need to find out is how their information is gathered and processed, what routes do data take (*if not via 'nerves' sensu strictu*), and how are adaptive responses integrated and coordinated, how are these events 'remembered' in order to allow realistic predictions of future using past experiences (<http://www.plantbehavior.org/neuro.html>; italics added).

Proponents of the “plant neurobiological” view claim that the application of these concepts to plants is a necessary move for an advancement of the scientific understanding of plant behavior.

Plant analogues for the nervous system do not exist. The idea of plant intelligence has been attacked on the basis of the frailty of the evidence for nerve-like structures in plants (Struik, Yin & Meinke, 2008). This attack represents the second reaction to mounting evidence of the richness of plant behavior. In a collective action, dozens of researchers published a letter disavowing the idea of plant neurobiology (Alpi et al., 2007). They expressed serious concerns about the idea of plant intelligence, backing up their arguments with the claim that there is no evidence for the existence of neurons, synapses or brains in higher plants or for the neurotransmitter-like long-distance transport of plant hormones. They argue that general principles for signal propagation and signal processing of plant systems do not justify the far-fetched interpretations and analogies used by the proponents of plant neurobiology. In reference to the claim of the necessity of such analogies for scientific progress, the title of the letter provocatively asked, “no brain, no gain?” It is interesting that the question raised seems to apply also to the authors’ own reasoning. That is to say, the authors of the letter essentially argue that without evidence for a nervous system, claims of intelligence are unfounded. This itself is a frail argument. It assumes that a nerve-like system is, indeed, necessary in order for intelligent behavior to manifest. But what nerve action is required? Could the open/closed action of a calcium signaling system (Calvo & Keijzer, 2011) adequately mimic the on/off action of neurons, thereby settling—affirmatively—the debate on whether intelligence is an appropriate term to describe the behavior of plants? If one agrees that complex end-directed adaptive behavior guided by meaning is to be called intelligence, and that plants exhibit such behavior, then whether or not plants have neuron-like structures or synapse-like activities seems to be quite beside the point.

Intelligence is a special animal characteristic. The third reaction to plant behavior as intelligent behavior focuses on the nature of intelligence and intelligent beings. Whatever it is that plants are doing and however they are doing it, plants are just the wrong kind of being with the wrong kind of wherewithal. In a brief, but multi-faceted critique, Firm (2004) presents arguments that would no doubt buttress the common understanding of intelligence. An appeal to the Latin root of the word intelligence appears to take the concept even further afield from what plants do (and what the word was originally intended to encompass):

The word intelligence comes from Latin (from *intellegere* to discern, comprehend and, literally, ‘choose between’, from *inter-* and *legere*, to choose). The key words in this definition are *discern*, *comprehend* and

choose, all of which are terms that are meaningful in the context of human behaviour. These terms, and the concept of intelligence, were adopted by those participating in the development of the English language to describe actions, and to express thoughts, about their own behaviour. The terms discern, comprehend and choose each imply a considerable degree of mental processing of more basic sensory information. There is rather little evidence that plants (or maybe more accurately plant cells) do anything other than rudimentary processing of sensed information and that alone should caution us against adopting the term 'intelligence' when discussing the abilities of plants (Firn, 2004, p. 346).

The essence of this view is that, while there may be sensing by plants, their machinery is not up to the task of executing what is presumed to be mental-like processing of whatever data might be sensed. Their adaptations are simple, their flexibility merely developmental. Many systems—some artificial, some biological—accomplish complicated tasks but only those that bring about their behaviors in a particular way, should be considered intelligent systems. Labeling plants as intelligent would presume too much about their capabilities and violate the parsimony principle (Struik, Yin & Meinke, 2008). The fact that proponents of plant intelligence appeal to a generic definition of intelligence such as that offered by Stenhouse (1974) is considered a retreat by this faction because it does not demand cogitative ability. It is not clear what they would think of the similarly generic offering of the *MIT Encyclopedia of the Cognitive Sciences* (Wilson & Keil, 1999).

Naturally, advocates of plant intelligence argue against reserving the intelligent label only for humans or animals with human-like abilities, painting such arguments as unjustifiably anthropocentric (Chamovitz, 2012, Trewavas, 2003). Instead of defining intelligent behavior with regard to characteristics considered important from a human standpoint, Trewavas argues that we should acknowledge that the success (fitness) of an organism depends on its performance in its own particular niche and that intelligence is essential to its success (cf. Turvey & Carello, 2012, Guideline 11). Despite warning against anthropocentrism, however, Trewavas cannot avoid being entrapped by it (making him a strange bedfellow for the third reaction to plant intelligence). From their sensitivity to the array of environmental variables and their coordinated, frequently anticipatory responses, he infers the presence, in plants, of rational processes advocated by cognitivism to underlie human capabilities: internally set objectives, internally specified information and memory, internal representations, computations to assess and correct errors, calculations of cost-benefit functions, predictive modeling of the future and subsequent choices and decisions. The purported presence of

these mechanisms is used to substantiate the claim for plant intelligence (in spite of the absence of neurons), in an obvious question-begging appeal to rationality.

Mechanism is the lure for Chamovitz (2012) as well. Against the backdrop of a popular encoding, storage, and retrieval model of human and computer memory, for example, he asserts, “If we’re going to look for the existence of even the simplest memories in plants, these are the processes we need to see happening” (p. 116). It is somewhat surprising that these scholars do not confront the likelihood that characterizations of human memory and perception³ might be just as contentious as characterizations of the achievements of plants. We believe that the arguments of both of these proponents of plant intelligence would be best served not by an appeal to mechanisms but by an appeal to principles. We turn to such an appeal next.

A NATURAL-PHYSICAL PERSPECTIVE ON COMPLEX ADAPTIVE BEHAVIOR

An alternative not yet considered in the community of plant scientists is the one that is thoroughly grounded in a natural-physical approach to perception and action. Intelligence as effectively guiding behavior in an environment, whether in plants or animals or humans or any other kind of system, need not and cannot have anything to do with the mechanisms instantiated in nervous systems or human minds (taken to be computational systems). The kind of purposeful behavior we want to label intelligent cannot depend, for its explanation, on the specifics of the kind of physiological machinery that one kind of intelligent creature happens to have, or the kind of psychological mechanisms usually purported to explain the intelligence of that kind of creature. A primary concern for this kind of perspective is the development of a psychological theory that covers all organisms (Turvey, 2012). Organisms across all phyla successfully confront problems of adaptation, resource location, growth, and self-maintenance among others, and a theory that takes human capabilities as its only proper explananda is not sufficient for a general theory of intelligent adaptive behavior. Intelligent

³ Chamovitz (2012) notes that “within the field of memory numerous models and theories exist” (p. 152), but that acknowledgment seems not to extend to the presumed processes. He also treats it as problematic that “Although plants see a much larger spectrum than we do, they don’t see in pictures. Plants don’t have a nervous system that translates light signals into pictures” (p. 23). Despite the best efforts of ecological psychologists over the past 50 years or so, he accepts that “photoreceptors allow our brains to make pictures that enable us to interpret and respond to our changing environment” (p. 24).

behavior must be a product of physics not physiology, or cognitive science for that matter.

Perception-action is possible because an invariant relation exists between higher-order properties of structured energy distributions and perceiver/actor–environment systems. Directed behavior is in the relation between the detection of information⁴ that guides the activities that, in turn, facilitate that detection. The perceiver/actor becomes attuned to the information by being immersed in the lawfully structured energy distributions. If that structure were not sufficiently regular, there would be no attunement. The particular machinery that does the attuning and the detecting does not impart its character on the explanation of the behavior.

The nonalgorithmic nature of perception and action is old-school Gibson (1958, 1959) and has become profoundly apparent in research and theorizing for the past 60 years (e.g., Bingham, 1988; Carello, Turvey, Kugler, & Shaw, 1984; Mace, 1977, 1986; Shaw, 2003). As noted at the outset, for the last 30 years or so, some ecological psychologists have considered the grounding of that non-algorithmic approach to be thermodynamics (e.g., Kugler, Kelso, & Turvey, 1980; Kugler, Turvey, Carello, & Shaw, 1985; Michaels & Carello, 1981; Turvey & Carello, 1981). The issue, in essence, is how perception-action cycles could have arisen. The answer, in essence, is that they must have emerged from thermodynamic processes (Swenson & Turvey, 1991; Turvey, in press-2012; Turvey & Shaw, 1995). This perspective allows and, perhaps, even demands continuity in the treatment of intelligence across all phyla.

To address that demand, we take a modified version of Swenson's (2010) three-step "physical intelligence certification" as our basis for grounding a general account of agency in natural-physical terms (see also Swenson, 1998, 2009). First, the system in question must be autocatakinetic (ACK). An ACK system is one that maintains itself through the dissipation of potentials or resources (see Stepp & Srinivasa, this issue; Turvey & Carello, 2012, Guidelines 6 and 7; see also Chemero, 2012, for how ACK systems differ from autocatalytic and autopoietic systems). If a system is solely determined by its originating potential and that resource is used up, such a system would go out of existence. But less dramatically, as noted earlier, agency requires flexibility. A system with agency, cannot be a slave to local potentials. Such a system's behavior must be different even when the originating potential is the same. Secondly, therefore, the system must be able to act in a way that is orthogonal to those potentials (cf. Shaw & Kinsella-

⁴ Information as used here is in the Gibsonian, specificational sense and not the information-theoretic sense of Shannon (see Turvey & Carello, 2012, Guidelines 17 and 18).

Shaw, 2012), by accessing other potentials. But how are new potentials accessed? The autokinetics must be enriched in such a way that they make possible the system's sensitivity to, and opportunistic linking to, information about non-local, even novel, potentials. This last requirement for a kind of generic foraging is the most difficult challenge. Certification as a physically intelligent agent requires the perceptually guided search for potentials useful to the agent (where the primary sense of *useful* is with respect to increasing the rate of entropy production; Swenson & Turvey, 1991; Turvey & Carello, 2012, Guidelines 14 and 15).

How do plants fare in this treatment of intelligence as agency? Let us consider the poplar example. They maintain themselves through the dissipation of resources, making them ACK. They are not passive under the attack of herbivorous arthropods. They fight back locally with defenses that affect the attacker directly and they fight back non-locally by attracting distant carnivores. And they discriminate damaging attacks from non-attacking damage. Check, check, and check!

For such a perspective, the effort to “create a physically-grounded, evolutionary understanding of intelligence” (Hylton, 2009), an understanding that is grounded in first principles, is not a quirky exercise; it is part and parcel of the enterprise. And it is clearly not new. As it happens, a sentiment endorsing physical constraints on the evolution of intelligent behavior dates to the early decades of the last century. In a treatment of the evolution of behavior, the philosopher Bawden (a functionalist who studied with Dewey) wondered “whether the beginnings of behavior are to be carried back to the physical and chemical elements on this earth” (Bawden, 1919, p. 248). Given his concern for the evolution of behavior, he thought it necessary to consider activities that humans have in common with lower organisms. As fundamental activities, he identified nutritive and reproductive functions. In light of the foregoing certification of physical intelligence, his characterization of these functions is particularly interesting: “The food process and the sex process both involve the seeking of the distant object, movement toward it, grappling with it, and appropriating it” (Bawden, 1919, p. 249). His further interesting conjecture was not only that these two functions perhaps wholly determined the behavior of lower organisms but also that the complex, even rational, behaviors of higher animals and humans are refinements of these. While the necessary refinements might be a bit remote (he anchored economic and military activities in the nutritive function, art and religion in reproduction, and literature, education, philosophy, and science in both), the attempt at principled continuity is admirable. A similar sentiment is expressed by Kugler and Turvey (1987): Nervous system properties per se are only the properties of a medium in which a variety of natural laws are manifested.

A principled continuity is to be found in these laws rather than in the particular tissue that happens to embody them for some creatures. Anatomical specificities are to be considered only boundary conditions on the realization of laws at the ecological scale. Therefore no particular anatomical or physical assembly is privileged—it is just that some “condense out a larger variety of lawful regularities” (Kugler & Turvey, p. 254). It is not by means of nervous systems that agency is expressed; rather, it is through such assemblies (of which animal nervous systems are only one example) that agency is instantiated.

EPILOGUE

The fact that the end-directed behaviors of plants are consistent with the kind of perspective that demands continuity in the treatment of intelligence across all phyla is comforting to us. But others are no doubt discomfited by such a demand. Some would argue that combining intelligence with a modifying label such as *plant* or *bacteria* (or the even more outré *physical*) “...is clearly not *animal intelligence*. Hence we have reached a definition of intelligence that has no meaning unless combined with another word or used in a precise context in a sentence” (Firn, 2004, p. 346). We disagree on two fronts—with the assertion that a labeled intelligence is necessarily of a different kind than the ultimately privileged intelligence that is unlabeled *human*, and with the assertion that a general definition has no meaning. Both assertions have been addressed in other attempts to come to terms with what it means to characterize intelligence from first principles:

If we allow the phrase *biological intelligence* to mean “biological systems that exhibit intelligent actions,” then the corresponding phrase attendant to a quest for intelligence from first principles would be *physical intelligence*. Its corresponding meaning would be “physical systems that exhibit intelligent actions.” Phrased this way, *type of system* is separated from *intelligent actions*. Also, by calling actions “intelligent” it seems natural to infer that other actions might not be intelligent. “Biological” and “physical” denote the *kind of embodiment* of the system in question (Shaw & Kinsella-Shaw, 2012, p. 63).

On this view, *plant intelligence* denotes the kind of embodiment; the actions, not the embodiment, are the target for evaluation as intelligent. This elaborates the point raised in Kugler and Turvey (1987) with respect to nervous systems. The importance of the actions was also highlighted in Kondepudi’s examination of physical intelligence (PI) in terms of self-organization and entropy production: “Because PI, however defined, is

better conceived as ‘process’ than ‘state,’ it must have its origins in basic thermodynamic forces and flows” (Kondepudi, 2012, p. 43).

So what are we to do with our gut feelings that physical and bacteria and plant intelligence are all different from animal intelligence, which is itself different from human intelligence? We reinforce the search for principled continuity, perhaps with an eye to how these different embodiments might be ordered. Amplifying Kugler and Turvey’s (1987) conjecture about nervous systems, embodiments might differ with respect to the variety of lawful regularities they manifest in perceiving and acting. A related argument is found in Kondepudi where the embodiments might support different numbers of organized, or nonequilibrium, states. In particular:

As the system’s complexity in terms of thermodynamic forces and flows increases, the number of possible organized states also increases. When this happens, the system can respond to its environment in new ways by making transitions between the available organized states in response to changes in the environmental factors (Kondepudi, 2012, pp. 39-40).

He continues:

[It] is supposed that for a complex system to be capable of PI it must have a large number of accessible nonequilibrium states and the system must be capable of making transitions between them. These states are metastable because an appropriate perturbation or interaction with the environment can drive the system to another state (Kondepudi, 2012, p. 41).

So the variety of lawful regularities that a system exploits and exhibits, or the number of nonequilibrium states it can access, both speak to the kind of ordering of intelligent actions that tap our common understanding of intelligence. It should be noted that while both phrasings seem to imply that a counting is possible that might lead to a new kind of intelligence quotient, the very nature of possibilities for action might make them uncountable. Certainly this is true of affordances, which we have argued, are central to agency. Here is the problem: Environmental properties and the behavioral adjustments to them are nested at multiple spatiotemporal scales and an organism must perceive both in order to control its activity (Turvey & Carello, 1981). Nonetheless we might wonder whether different orders of magnitude of uncountable perception-action couplings might provide an approximate index of intelligence.

AUTHORS' NOTES

This work was supported, in part, by the Defense Advanced Research Projects Agency (DARPA) Physical Intelligence Program through a subcontract with HRL Laboratories (HRL 000708-DS). The views, opinions, and/or findings contained in this article are those of the authors and should not be interpreted as representing the official views or policies, either expressed or implied, of DARPA or the Department of Defense.

REFERENCES

- Alpi, A. et al. (2007). Plant neurobiology: no brain, no gain? *Trends in Plant Science*, *12*, 135-135.
- Baluska, F., Mancuso, S., Volkmann, D. (Eds.) (2006). *Communication in plants: neuronal aspects of plant life*. Berlin: Springer Verlag.
- Bawden, H. H. (1919). The evolution of behavior. *Psychological Review*, *26*, 247-276.
- Bingham, G. P. (1988). Task-specific devices and the perceptual bottleneck. *Human Movement Science*, *7*, 225-264.
- Bose, J. Ch. (1907). *Plant response as a means of physiological investigation*. London: Longman, Green & Co.
- Bose, J. Ch. (1926). *The nervous mechanism of plants*. London: Longman, Green & Co.
- Braam, J. (2005). In touch: plant responses to mechanical stimuli, *New Phytologist*, *165*, 373-389.
- Brenner, E. D., Stahlberg, R., Mancuso, S., Vivanco, J., Baluska, F., & Van Volkenburgh, E. (2006). Plant neurobiology: an integrated view of plant signaling. *Trends in Plant Science*, *11*, 413-419.
- Cain, M. L., Dudle, D. A., & Evans, J.P. (1996). Spatial models of foraging in clonal plant species. *American Journal of Botany*, *83*, 76-85.
- Calvo, P. (2007). The quest for cognition in plant neurobiology. *Plant Signaling & Behavior*, *2*, 208-211.
- Calvo, P., & Keijzer, F. (in press). Cognition in plants. In F. Baluska (Ed.) *Plant-environment interactions: Behavioral perspective*. Amsterdam: Elsevier.
- Calvo, P., & Keijzer, F. (2011). Plants: Adaptive behavior, root-brains, and minimal cognition. *Adaptive Behavior*, *19*, 155-171.
- Carello, C., Turvey, M. T., Kugler, P. N., & Shaw, R. (1984). Inadequacies of the computer metaphor. In M. Gazzaniga (Ed.), *Handbook of cognitive neuroscience* (pp. 229-248). New York: Plenum.
- Chamovitz, D. (2012). *What a plant knows: A field guide to the senses*. New York: Scientific American Books.
- Chemero, A. (2012). Modeling self-organization with nonwellfounded set theory. *Ecological Psychology*, *24*, 46-59.

- Chen, R., Rosen, E., & Masson, P. H. (1999). Gravitropism in higher plants. *Plant Physiology*, *120*, 343-350.
- Crotser, M.P., Witt, W.W., & Spomer, L.A. (2003). Neutral density shading and far-red radiation influence black nightshade (*Solanum nigrum*) and eastern black nightshade (*Solanum ptycanthum*) growth. *Weed Science*, *51*, 208-213.
- Darwin, C. (1875). *The movements and habits of climbing plants*. London: John Murray.
- Darwin, C. (1880). *The power of movement in plants*. London: John Murray.
- Darwin, C. (1881/2004). *The formation of vegetable mould, through the action of worms*. Whitefish, MT: Kessinger Publishing.
- Dennett, D. C. (1981). *Brainstorms: Philosophical Essays on Mind and Psychology*. Cambridge, MA: MIT Press.
- Dicke, M., van Loon, J. J. A., & Soler, R. (2009). Chemical complexity of volatiles from plants induced by multiple attack. *Nature Chemical Biology*, *5*, 317-324.
- Dussutour, A., Latty, T., Beekman, M., & Simpson, S. J. (2010). Amoeboid organism solves complex nutritional challenges. *Proceedings of the National Academy of Science*, *107*, 4607-4611.
- Firn, R. (2004). Plant intelligence: an alternative point of view. *Annals of Botany*, *93*, 345-351.
- Flematti, G. R., Ghisalberti, E. L., Dixon, K. W., & Trengove, R. D. (2004). A compound from smoke that promotes seed germination. *Science*, *305*(5686), 977.
- Ford, B. J. (1999). *The secret language of life*. NY: Fromm Intl.
- Gagliano, M., Mancuso, S., & Robert, D. (in press). Towards understanding plant bioacoustics. *Trends in Plant Science*.
- Gibson, J. J. (1958). Visually controlled locomotion and visual orientation in animals. *British Journal of Psychology*, *49*, 182-194.
- Gibson, J. J. (1959). Perception as a function of stimulation. In S. Koch (Ed.), *Psychology: A study of a science, I* (pp. 457-501). New York: McGraw-Hill.
- Gibson, J. J. (1979/1986). *The ecological approach to visual perception*. Hillsdale, NJ: Lawrence Erlbaum Associates. (Original work published 1979).
- Grady, W., & Suzuki, D. (2004). *Tree: A life story*. Vancouver: D&M Publishers.
- Hylton, T. (June 2009). *Physical intelligence*. Physical Intelligence Proposers Workshop.
- Jaffe, M.J., & Shotwell, M. (1980). Physiological studies on pea tendrils, XI. Storage of tactile sensory information prior to the light activation effect. *Physiology of Plants*, *50*, 78-82.
- Kelly, C. K. (1990). Plant foraging: a marginal value model and coiling response in *Cuscuta subinclusa*. *Ecology*, *71*, 1916-1925.
- Kelly, C. K. (1992). Resource choice in *Cuscuta europaea*. *Proceedings of the National Academy of Science*, *89*, 12194-12197.
- Knight, T. A. (1806). On the direction of the radicle and germen during the vegetation of seeds. *Philosophical Transactions of the Royal Society of London—Biological Sciences*, *99*, 108-120.

- Kondepudi, D. (2012). Self-organization, entropy production and physical intelligence: preliminary remarks. *Ecological Psychology*, 24, 33-45.
- Kramer, P. J. (1980). Drought stress, and the origin of adaptations. In N. C. Turner & P. J. Kramer (Eds.), *Adaptations of plants to water and high temperature stress* (pp. 7-20). New York: Wiley.
- Kugler, P. N., Kelso, J. A. S., & Turvey, M. T. (1980). Coordinative structures as dissipative structures I. Theoretical lines of convergence. In G. E. Stelmach & J. Requin (Eds.) *Tutorials in Motor Behavior* (pp. 1-47). Amsterdam: North Holland.
- Kugler, P. N., & Turvey, M. T. (1987). *Information, natural law and the self-assembly of rhythmic movement*. Hillsdale, NJ: Erlbaum.
- Kugler, P. N., Turvey, M. T., Carello, C., & Shaw, R. (1985). The physics of controlled collisions: A reverie about locomotion. In W. H. Warren, Jr. & R. Shaw (Eds.), *Persistence and change* (pp. 195-230). Hillsdale, NJ: Lawrence Erlbaum Associates.
- Latty, T., & Beekman, M. (2010). Food quality and the risk of light exposure affect patch-choice decisions in the slime mold *Physarum polycephalum*. *Ecology*, 91, 22-27.
- Ludlow, M. M., & Björkman, O. (1984). Paraheliotropic leaf movement in *Siratro* as a protective mechanism against drought-induced damage to primary photosynthetic reactions: damage by excessive light and heat. *Planta*, 161, 505-518.
- Mace, W. M. (1977). James J. Gibson's strategy for perceiving: Ask not what's inside your head but what your head's inside of. In *Perceiving, acting, and knowing* (pp. 43-65). Hillsdale, NJ: Lawrence Erlbaum Associates.
- Mace, W. M. (1986). J. J. Gibson's ecological theory of information pickup: Cognition from the ground up. In T. J. Knapp & L. Robertson (Ed.), *Approaches to cognition: Contrasts and controversies* (pp.137-157). Hillsdale, NJ: Lawrence Erlbaum Associates.
- Malebranche, N. (1997). T. M. Lennon & P. J. Olscamp (Eds.). *The search after truth: With elucidations (Cambridge texts in the history of philosophy)*. Cambridge, UK: Cambridge University Press. (Original work published in 1678)
- Massa, G. D. & Gilroy, S. (2003). Touch modulates gravity sensing to regulate the growth of primary roots of *Arabidopsis thaliana*. *The Plant Journal*, 33, 435-445.
- Mescher, M. C., Runyon, J. B., & De Moraes, C. M. (2006). Host finding by parasitic plants: a new perspective on plant to plant communication. *Plant Signaling & Behavior*, 1, 284-286.
- Michaels, C. F., & Carello, C. (1981). *Direct perception*. New York: Prentice Hall.
- Milius, S. (2009). No brainer behavior. *Science News*, 175, 16-20.
- Raven, P. H., Evert, R. F., & Eichhorn, S. E. (2005). *Biology of plants*. New York: Freeman.
- Reed, E. S. (1996). *Encountering the world*. Oxford: Oxford University Press.
- Reed, E. S., Kugler, P. N., & Shaw, R. E. (1985). Work group on biology and physics. In W. H. Warren & R. E. Shaw (Eds.), *Persistence and change*:

- Proceedings of the first international conference on event perception* (pp. 307-345). Hillsdale, NJ: Erlbaum.
- Roshchina, V. V. (2001). *Neurotransmitters in plant life*. Enfield, NH: Science Publishers.
- Runyon, J. B., Mescher, M. C., & De Moraes, C. M. (2006). Volatile chemical cues guide host location and host selection by parasitic plants. *Science*, *313*, 1964-1967.
- Runyon, J. B., Mescher, M. C., & De Moraes, C. M. (2008). Parasitism by *Cuscuta pentagona* attenuates host plant defense of insect herbivores. *Plant Physiology*, *146*, 987-995.
- Shaw, R. E. (2003). The agent-environment interface: Simon's indirect or Gibson's direct coupling? *Ecological Psychology*, *15*, 37-106.
- Shaw, R. E., & Kinsella-Shaw, J. M. (2012). Hints of intelligence from first principles. *Ecological Psychology*, *24*, 60-93.
- Silvertown, J., & Gordon, D. M. (1989). A framework for plant behavior. *Annual Review of Ecology and Systematics*, *20*, 349-366.
- Simons, P. J. (1981). The role of electricity in plant movements. *New Phytologist*, *87*, 11-37.
- Stahlberg, R. (2006). Historical overview on plant neurobiology. *Plant Signaling and Behavior*, *1*, 6-8.
- Stenhouse, D. (1974). *The evolution of intelligence—a general theory and some of its implications*. London: George Allen and Unwin.
- Struik, P.C., Yin, X., & Meinke H. (2008). Plant neurobiology and green plant intelligence: science, metaphors and nonsense. *Journal of the Science of Food and Agriculture*, *88*, 363-370.
- Swenson, R. (1998). Spontaneous order, evolution, and autokinetics: The nomological basis for the emergence of meaning. In G. van de Vijver, S. Salthé, & M. Delpo (Eds.), *Evolutionary systems* (pp. 155-180). Dordrecht, The Netherlands: Kluwer.
- Swenson, R. (2009). The fourth law of thermodynamics: The law of maximum entropy production (LMEP). *Chemistry*, *18*, 333-339.
- Swenson, R. (June, 2010). *Physical intelligence: the evolutionary epistemology of entropy production maximization*. Presentation to the UConn Workshop on Physical Intelligence.
- Swenson, R., & Turvey, M. T. (1991). Thermodynamic reasons for perception-action cycles. *Ecological Psychology*, *3*, 317-348.
- Trewavas, A. (2003). Aspects of plant intelligence. *Annals of Botany*, *92*, 1-20.
- Trewavas, A. (2005). Green plants as intelligent organisms. *Trends in Plant Science*, *10*, 413-419.
- Trewavas, A. (2007). Response to Alpi et al.: Plant neurobiology – all metaphors have value. *Trends in Plant Science*, *12*, 231-233.
- Turvey, M. T. (1990). The challenge of a physical account of action: A personal view. In H.T.A. Whiting, O. Meijer, & P. van Wierengen (Eds.) *A natural-physical approach to movement control*. Amsterdam: Free University Press.
- Turvey, M. T. (1992). Affordances and prospective control: An outline of the ontology. *Ecological Psychology*, *4*, 173-187.

- Turvey, M. T. (in press, 2012). Ecological perspective on perception-action: What kind of science does it entail? In W. Prinz, M. Bessard, & A. Herwig (Eds.), *Action science: Foundations of an emerging discipline*. Cambridge MA: MIT Press.
- Turvey, M. T., & Carello, C. (1981). Cognition: The view from ecological realism. *Cognition, 10*, 313-321.
- Turvey, M. T., & Carello, C. (2012). On intelligence from first principles: guidelines for inquiry into the hypothesis of physical intelligence (PI). *Ecological Psychology, 24*, 3-32.
- Turvey, M. T., & Shaw, R. E. (1995). Toward an ecological physics and a physical psychology. In R. Solso & D. Massaro (Eds.), *The science of the mind: 2001 and beyond* (pp. 144-169). Oxford: Oxford University Press.
- Turvey, M. T., Shaw, R. E., Reed, E. S., & Mace, W. M. (1981). Ecological laws of perceiving and acting: In reply to Fodor and Pylyshyn. *Cognition, 9*, 237-304.
- Uttal, W. R. (2002). Précis of The New Phrenology: The limits of localizing cognitive processes in the brain. *Brain and Mind, 3*, 221-228.
- Valinger, E., Lundqvist, L., & Sundberg, B. (1994). Mechanical stress during dormancy stimulates stem growth of Scots pine seedlings. *Forest Ecology and Management, 67*, 299-303.
- Vartanian, S. (2011). Thigmotropism in tendrils. <http://biology.kenyon.edu/edwards/project/steffan/b45sv.htm>
- Warren, W. H., & Shaw, R. E. (1985). Events and encounters as units of analysis in ecological psychology. In W. H. Warren & R. E. Shaw (Eds.), *Persistence and change: Proceedings of the first international conference on event perception* (pp. 1-27). Hillsdale, NJ: Erlbaum.
- Weir, A. A. S., Chappell, J., & Kacelnik, A. (2002). Shaping of hooks in New Caledonian crows. *Science, 297*, 981.
- Wilson, R. A., & Keil, F. (Eds.) (1999). *MIT encyclopedia of the cognitive sciences*. Cambridge, MA: MIT Press.
- Wolpert, D.M., & Ghahramani, Z. (2000). Computational principles of movement neuroscience. *Nature Neuroscience, 3*, 1212-1217.
- Wolpert, D. M., & Ghahramani, Z. (in press). Bayes rule in perception, action and cognition. In R. L. Gregory (Ed.). *Oxford companion to the mind*. Oxford, UK: Oxford University Press.