Fungal Ethology

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Abstract

The behavioral repertoire of the fungi includes expressions of sensitivity, problem solving, and memory by single cells and multicellular colonies. The search for food by species of filamentous fungi that decompose wood is particularly informative. These microorganisms produce tubular cells called hyphae that extend at their tips and branch to form elaborate three-dimensional colonies or mycelia. Information is transmitted through mycelia grown in culture over distances of many centimeters, resulting in changes in their growth patterns that favor expansion in places where food is detected. Problem solving is apparent in these reactions as the fungi negotiate physical obstacles and draw upon a rudimentary form of spatial memory. Behavioral complexity is also evident in the interactions between fungi and other organisms. These symbioses include the infection of plants and animals, and the formation of mutually-supportive relationships with plants called mycorrhizas. The proposition of fungal intelligence emerging from this research aligns with earlier behavioral studies on single-celled amoebas and slime molds. Together, these observations dissolve the supposed distinctions between conscious and unconscious organisms and support our ongoing liberation from Cartesian thinking about nature.

1. Aims and a road map for this chapter

This chapter describes recent research on the behavioral ecology or ethology of fungi. At a time of renewed interest in the subject of basal cognition in non-brained species, this work has added to the wider examination of the theory of cellular consciousness (Section 2). We look at the sensitivity and growth responses of fungal cells called hyphae (Section 3), and extend this inquiry to the cooperation between multiple hyphae in fungal colonies or mycelia (Section 4). Sensory mechanisms and signaling processes within fungal cells are addressed in Sections 5 and 6, before we consider communication within plant-fungal networks in Section 7. This research has attracted a good deal of illogical interpretation and one of the aims of this chapter is to discriminate between the reliable science and misleading ideas about fungal behavior.

2. The context for research on fungal behavior

More than a century before mycologists began to examine the possibility of volition in the fungi, mobile protists like the iconic cell, *Amoeba proteus*, had been the subject of remarkable experiments on cellular behavior (Verworn, 1889; Schloegel & Schmidgen, 2002). Studies on protists, which used to be called protozoans, revealed that they engaged in decision-making as they searched for food, evaded predators, and withdrew from noxious chemicals (Jennings, 1906). The stochastic or individualistic nature of these simple actions seemed comparable to the problem solving and goal orientation normally associated with animal behavior. This early work on cell biology caught the attention of Friedrich Nietzsche, who viewed this cellular

sensitivity as a simple expression of his "Will to Power" (Moore, 2003), writing, "Self-consciousness [das Ich-Geistige] itself is already present in the cell. Before the cell there is no self-consciousness."

Interest in protist behavior increased at the beginning of the twentieth century and then subsided as the study of cell biology was revolutionized by the techniques of electron microscopy, biochemistry, and molecular genetics. Research on protistology continued during this period without gaining wider attention, but there were some exceptional experiments on learning in *Paramecium* (reviewed by Gershman et al., 2021). The discovery of the elaborate mating dance in another protist called *Stylonychia* (Grell, 1951) was another landmark in the study of the behavioral sophistication of these single-celled organisms. Work on plant sensitivity or irritability also waxed and waned, but few botanists took plant sentience seriously until very recently (Calvo & Lawrence, 2023; Hansen, 2024).

Slime molds, which are related to amoebas and classified as protists, were incorporated into the niche of research on cellular intelligence when experiments revealed their responsiveness to the locations of food and other environmental stimuli (Reid, 2023). Fungi, which are unrelated to slime molds, were not part of this work and their developmental behavior was not contemplated as a form of basal cognition until novel lines of experimental analysis began to point in this direction (Fukasawa et al., 2020; Money, 2021; Aleklett & Boddy, 2021). Fungi grow in the form of colonies of branching filaments called hyphae that feed by absorbing nutrients from their surroundings. Their reliance on growth versus movement from place to place for

feeding was one of the reasons that they were ignored in the earlier studies on cellular intelligence, but this distinction has been overrated. Although fungal hyphae are not motile like amoebas and protists that swim using cilia (vibrating hairs), their irritability is apparent as they extend at their tips, form unique branching patterns, maneuver around obstacles, converge on food, and unite in mating reactions. This continuous expression of sensitivity through growth is comparable to the reactiveness of a swimming cell like *Paramecium*, or, at least it is not fundamentally different. In the fungus and the ciliate, the behavior of the organism involves individual, goal-oriented or purposeful responses to internal (cytoplasmic) and external (environmental) cues. The energy needs of the fungus, for example, guide the transfer of nutrients from well-fed parts of the colony to distant hyphae that are extending in a nutrient-poor microenvironment (Section 4). There is an obvious purpose to this cytoplasmic reaction.

Nevertheless, the behavioral repertoire of the fungi does not amount to the condition of consciousness according to some definitions. Mallatt et al. (2021) posited a fundamental distinction between conscious organisms that act upon predictions about future events, and unconscious ones that do not. Plants, they argued, cannot be regarded as conscious because they lack the capacity for anticipatory behavior: plants react to stimuli, but they do not operate in a proactive fashion. The same critique applies to the fungi and Mallatt et al. (2021) suggested that consciousness is limited to species of arthropods, cephalopods, and vertebrates. This proposition is weakened when we consider examples of anticipatory behavior in microorganisms that modify their molecular responses to a repeated stimulus. The resulting biochemical changes place the cell in a state of readiness to ride out a subsequent

environmental stress. Responses to osmotic stress in yeast (a single-celled fungus) are a good example of this cytoplasmic preparation (Meriem et al., 2019). Although the stress response of yeast is limited to an automatic routine of genetic controls, the single cell is operating in a proactive fashion which seems to rank as a primitive form of consciousness using the criteria of Mallatt et al. (2021).

In light of the difficulties in defining cognition, intelligence, volition, and related phenomena (Lyon et al., 2021), it makes sense to regard consciousness as a flavor of information processing with differing expressions along a spectrum of behavioral complexity. Allen (2017) refers to this as a stance of "relaxed pluralism," which allows multiple lines of objective inquiry. This approach allows room for studies on the behavioral ecology or ethology of the fungi. Evidence for goal-oriented or purposeful behavior, learning, and memory in these microorganisms has become part of the growing field of research on the cellular basis of consciousness (Reber et al., 2024).

3. Hyphal sensitivity

The hypha is the exploratory and feeding apparatus used by filamentous fungi. This dual role requires sensitivity to the physical and chemical nature of the surrounding environment and is apparent in the way that hyphae negotiate surfaces, wend their way through porous soils, and penetrate all manner of solid materials (Bedekovic & Brand, 2022; Figure 1). Hyphae produced by saprotophic fungi decompose and digest the tissues of dead plants and other organic debris, endophytes insinuate themselves within the tissues of living plants, and parasites and

pathogens attack plants and animals. Other fungi include commensals that grow on the human body and support our health through their interactions with bacteria and the immune system. Most of these fungi grow as yeasts, but species of filamentous fungi are also important players in this complex ecosystem called the human mycobiome.
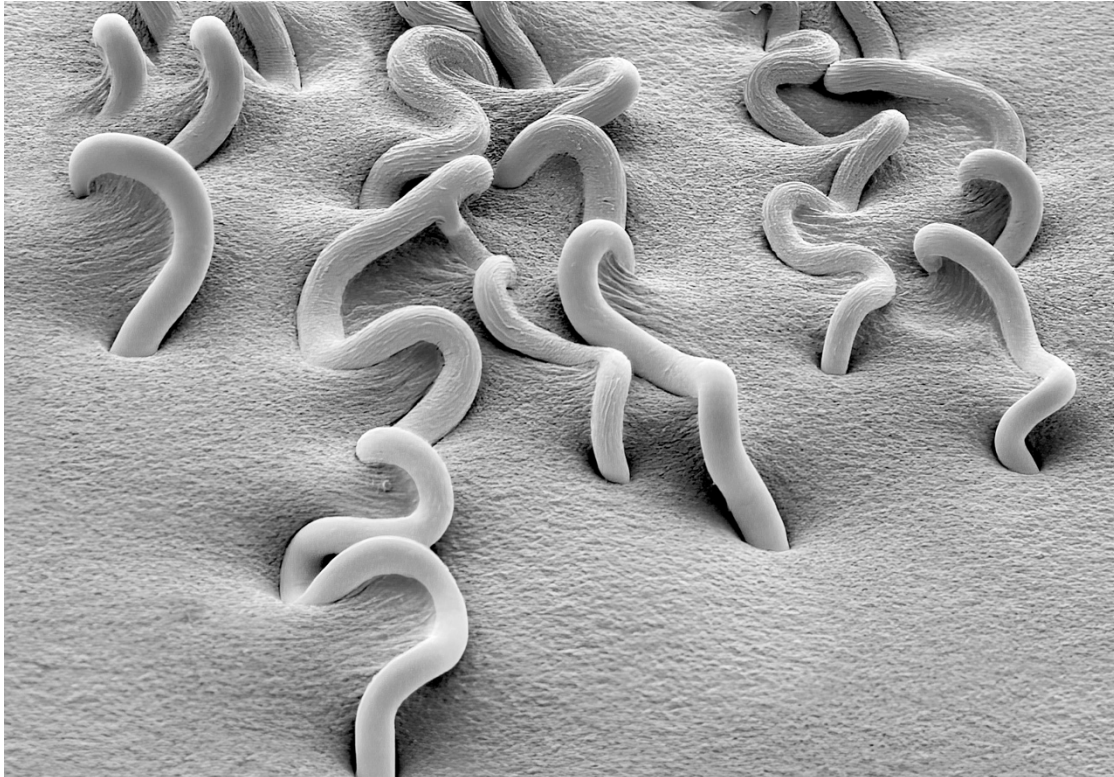

Figure 1. Hyphae of a pathogenic fungus that infects human tissues. Source: Science Photo Library.

Hyphae sense ridges on surfaces and negotiate obstacles by changing their growth direction and use a combination of enzymatic digestion and physical force to penetrate solid materials (Money et al., 2004; Brand & Gow, 2009). They narrow themselves to grow through constrictions and alter their patterns of branching in search of food. Recent advances in

microscopic imaging techniques allow investigators to monitor the extension of hyphal tips and the underlying molecular activities that support the mechanism of tip growth (Money, 2022; Kakizaki et al., 2023; Kawatomi et al., 2024). The development of living hyphae can be studied on solid surfaces, inside microfabricated growth chambers, and even within living plant tissues. Through these experiments we are discovering an extraordinary level of sensitivity, flexibility, and adaptability in the growth responses of individual hypha. Additional illustrations of this sensitivity include a variety of wounding responses of hyphae that contain leakages from damaged cell walls. Rhythmic changes in the electrochemical potential across the cell membrane that have been described as action potentials are also interesting from the perspective of cellular irritability (Section 5). The activities of the individual hyphae multiply through growth and branching into the complex behavioral characteristics of mycelia that are formed by these interconnected filaments.

4. Networking within multicellular fungal colonies

Fungal mycelia develop when single or multiple hyphae emerge from germinating spores. These hyphae branch repeatedly as they elongate, forming new growth axes and radiating away from one another in a way that maximizes coverage of the available space (Figure 2). This involves the mutual repulsion between growing hyphal tips and results in the formation of a circular colony on a surface, and a spheroidal mycelium when the fungus is able to explore a three-dimensional space from its starting point. Branches remain connected to their parent hyphae, producing a fluid continuum of filaments. This integration is supplemented by the formation of

cross-bridges between the radiating hyphae of some fungi (Figure 3). The density of these

connections, called anastomosis tubes, is very variable. This is important because limited

bridging will constrain the transmission of any information within the mycelium to the two-way

traffic of signals from edge to edge of the colony (Hammadeh et al., 2022).
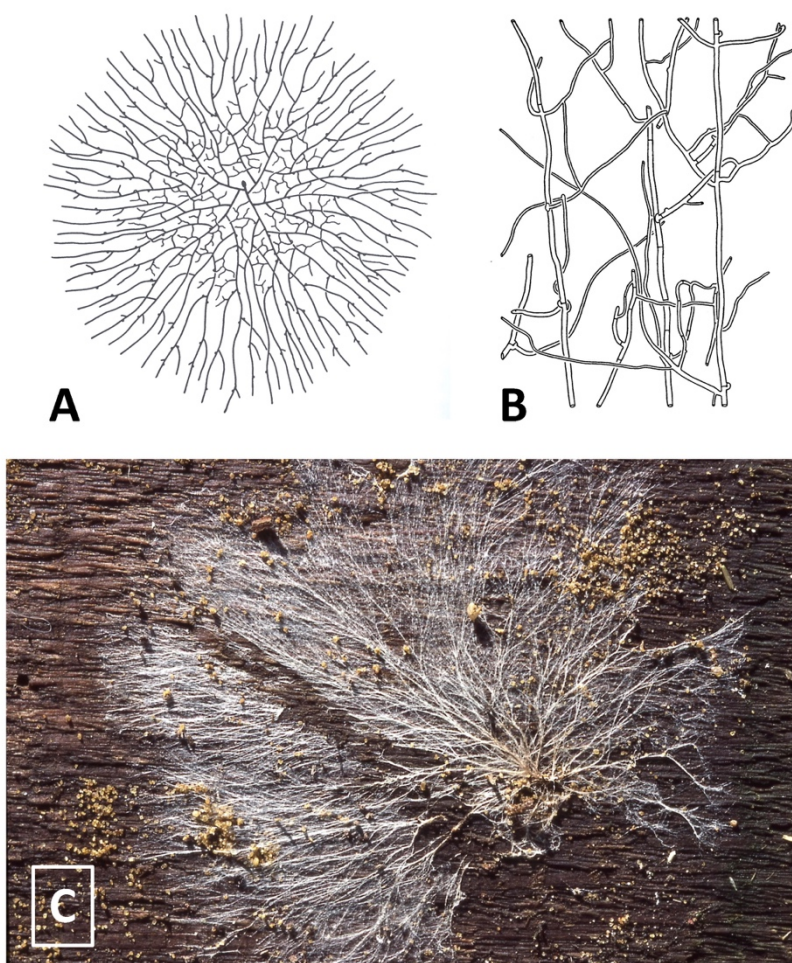

Figure 2. Fungal colonies or mycelia. A. Young colony that has grown from a single spore at

the center. B. Magnified view of hyphae within a colony. C. Mycelium spreading over wood.

Sources: A, B, adapted from Buller (1931); C, Alamy Stock Photo.

Figure 3. Detailed view of fungal hyphae that have grown from spores and formed cross-connections to form an integrated network of cells. Source: Adapted from Buller (1933).

Studies on mycelial development have led to the metaphorical description of the feeding colony as the brain of the fungus. The fact that the mycelium is the whole fungus and not part of a larger organism is one of the limitations of this idea, but the colony does operate as a computational device that assumes an optimal geometry in response to nutrient availability. The sheer number of hyphae in mycelia has encouraged these ruminations. Mycelia produce

billions of microscopic threads in a kilogram of rich grassland soil and approach the density of neurons in our brains, but any networking in the fungus is completely eclipsed by the number of synaptic connections between nerve cells. The mycelium is an abacus rather than a supercomputer.

Evidence for networking comes from experiments in which the movements of fluorescent dyes and radioactive tracers are tracked for distances of millimeters to centimeters across mycelia grown in culture (Fricker et al., 2008, 2017). Passive diffusion is fast enough to transmit these compounds over a few millimeters, but the mass flow of cytoplasm is the primary mechanism for transport across longer distances through hyphae (Herman & Bleichrodt, 2022; Figure 4). Mass flow propels the hyphal contents along at speeds of 10 to 20 mm per hour. Together, diffusion and mass flow redirect the distribution of materials from different parts of the mycelium according to nutrient availability.

The operation of larger mycelia is complicated by the aggregation of dozens of hyphae to form thickened assemblages called cords and rhizomorphs that resemble the root systems of plants. These structures serve as supply lines, allowing parts of mycelia that have run out of food and water to connect with distant groups of fully-hydrated hyphae with access to nutrients. Saprotrophic fungi that specialize in wood decomposition have been the leading models for experiments on mycelial development. Their responses to the placement of wood blocks in cultures provide the strongest evidence for fungal intelligence.
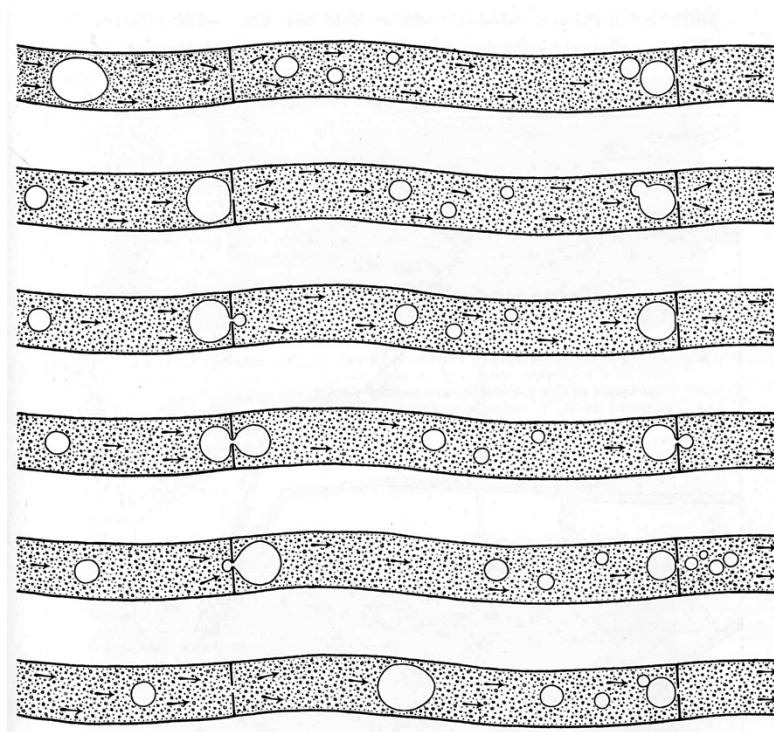
Figure 4. Mass flow of cytoplasm within hyphae from left to right, showing fluid-filled vacuoles squeezing through pores in septa. Successive images of hyphae from top to bottom of the figure are separated by 10 seconds. Source: Adapted from Buller (1933).

The most compelling research on this subject has been published by a Japanese investigator, Yu Fukasawa, and his collaborators, including Lynne Boddy, a British mycologist and distinguished fungal ecologist. In the earliest of these experiments, Fukasawa et al. (2020) showed that mycelia of the fungus *Phanerochaete velutina* growing over soil memorize the position of small blocks of wood that serve as their food. The test began by placing a wood block (block #1) colonized by a mycelium on a soil tray. The fungus responded by spreading in all directions until

it made contact with a second wood block (block #2) placed as a bait at the margin of its colony. At the end of the first phase of the experiment, the mycelium had colonized wood blocks #1 and #2. In the second phase of the experiment, the original wood block (block #1) was transplanted to a fresh soil tray. Growth resumed from all four sides of the wood block, but, crucially, more hyphae extended from the bait side of the wood block from which the fungus located block #2 in the first phase of the test (Figure 5). This behavior suggests that the mycelium memorized the successful growth pattern and "retraced its steps" in search for fresh food.
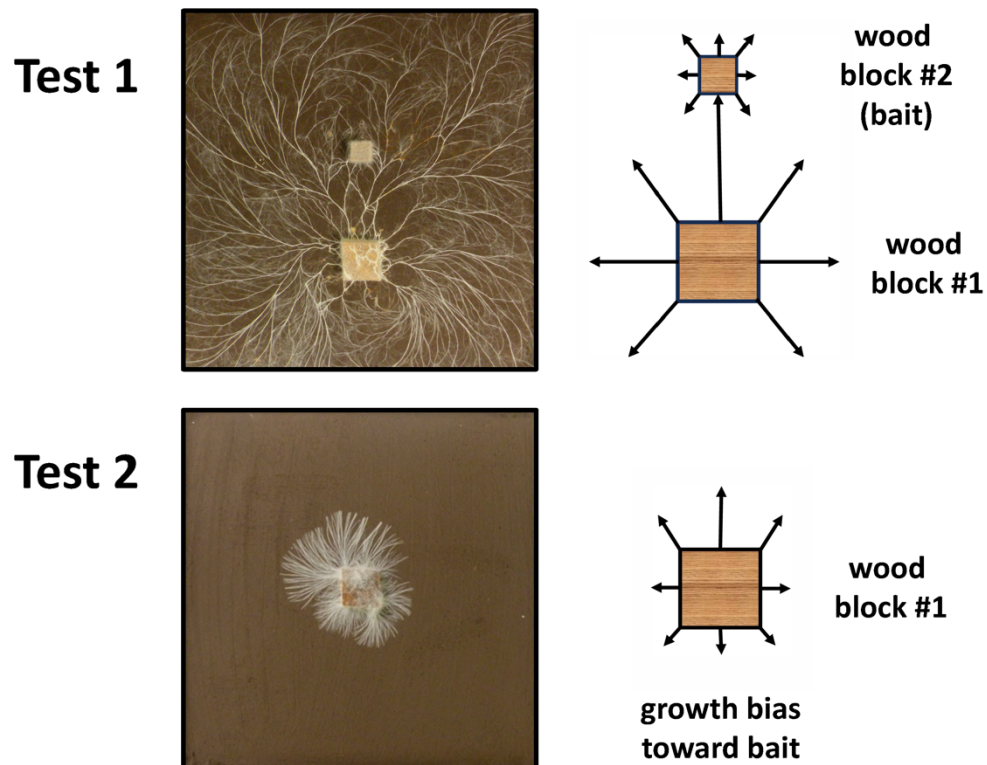

Figure 5. Wood block experiments showing regrowth of the fungus after transfer to a fresh culture dish in Test 2 toward the bait that it had located in Test 1. Source: Photographs from Yu Fukasawa with permission.

The pattern of mycelial development in this experiment is quite subtle, but the fungus must have stored information on the bait side of wood block #1 that was closest to wood block #2 in the first phase of the experiment. This could be a structural memory in the form of more concentrated growth of hyphae within the wood block on the bait side, or perhaps the fungus responded to a molecular marker deposited in the hyphae oriented toward the bait. The behavior of the fungus in this simple experiment seems a long way from recollecting where we left our keys, but, again, elementary cellular processes must be responsible for both memory tests.

Additional experiments provide evidence that mycelia are capable of making strategic decisions about their growth according to the availability of nutrients in different locations. Fukasawa & Kaga (2021) used the wood block #1 and #2 set up from the earlier experiments and studied the effect of timing on the colonization process. If wood block #1 was incubated for 2 weeks before baiting with wood block #2, the mycelium extended from both wood blocks in search of more food when they were transplanted to fresh soil trays. If wood block #1 was incubated for 14 weeks before baiting, regrowth occurred only from wood block #2 after transplantation. The investigators interpreted this result as an indication of decision making on the part of the mycelia, but the absence of regrowth from wood block #1 in the second test may also have been due to the death of the hyphae after so many weeks of activity. Because the mycelium in wood block #2 arrived from the well-colonized wood block #1, the hyphae in this location had not had sufficient time to exhaust the nutrients in the bait and were able to resume growth.

The colonization process in these wood block experiments is complicated by the observation that the distance between the wood blocks determines the investment in growth (Fukasawa & Ishii, 2023). Mycelia migrate to baits (wood block #2) that are close (1 cm) to the inoculum (wood block #1) more frequently than baits that are farther away (15 cm). Full migration of the fungus is indicated in these experiments by the transfer of mycelial biomass from wood block #1 to wood block #2 such that the mycelium is no longer active in wood block #1. This makes sense from the perspective of the energetic investment made by the fungus as it forages for food. Migration to a nearby wood block obviously requires less "foraging effort" than moving to a distant wood block. In another series of experiments, Fukasawa et al. (2024b) studied the decomposition of wood baits placed in a circle versus a cross pattern. They found that the fungus formed fruitless connections to baits that it had already colonized when it reached the wood blocks at the end of the cross. It was also more effective at decomposing the wood blocks in the circular arrangement. Again, it is questionable whether the behavior of mycelia in these tests represents decision making based on the size, proximity, and arrangement of resources, or that the fungus is simply following its programming in reaction to each contact with the little blocks of wood in the experiments. To understand the decision-making process, we need to examine the signaling mechanisms that operate within mycelia as they engage in wood decomposition. How do mycelia detect the nutrient levels in wood baits and how are the responses of the hyphae in one location conveyed to other parts of the colony?

5. Information transfer within mycelia: chemical and electrochemical processes

The operation of stretch-activated and stretch-inactivated ion channels in the cell membrane is one of the sensory mechanisms in hyphae (Morris & Sigurdson, 1989; Lange & Peiter, 2020). Perturbation of the hyphal tip, for example, can trigger calcium influx through stretch-activated calcium channels, turn on calcium signaling pathways, and result in hyphal reorientation (Brand et al., 2007). Another plausible signaling mechanism in fungi involves changes in the electrochemical potential across the cell membrane. All cells maintain a voltage across their membranes that is established by a combination of the passive diffusion of ions from the cytoplasm to the surrounding fluid, and vice versa, and the transport of ions through integral membrane proteins that act as channels, carriers, and pumps. The passive flux of potassium ions through the cell membrane creates a net negative charge (this is the cation diffusion potential) and active ion pumps amplify this membrane potential. The fungus *Neurospora crassa*, which has been used as a model for studies on membrane physiology, has a resting membrane potential of -180 mV (Slayman & Slayman, 1962; Slayman, 1965). This voltage is generated by passive ion flux and the active expulsion of protons by a transmembrane H^+-ATPase or proton pump (Slayman et al., 1973; Young et al., 2024).

Clifford Slayman, who pioneered the research on *Neurospora* physiology, discovered that the hyphal membrane potential was lost (depolarization) in a seemingly spontaneous fashion and reestablished (repolarization) on the timescale of 1 to 4 minutes (Slayman et al., 1976). This temporary collapse of the voltage could be explained by a sudden increase in membrane

permeability to protons and chloride ions, or by a brief and reversible slump in H^+-ATPase

activity. The physiological mechanism remains unsolved. Either way, the resulting sinusoidal

waveform of the oscillations in membrane voltage in the fungus is comparable to the shape of

the classic action potential in animal neurons, although action potentials in nerve cells occur on

a millisecond timescale. Another difference between the action potentials in hyphae and

nervous systems is their speed of transmission. Nerve impulses are propagated along neurons

at maximum speeds in excess of 100 meters per second, but is not known whether the action

potentials in *Neurospora* are conducted along the length of the hypha at all. Given the

limitations in the available data, the recordings made by Slayman et al. (1976) suggest that any

mobile voltage pulses in *Neurospora* could be one million times slower than a nerve impulse

and comparable to the speed of chemical communication along hyphae via the mass flow of

cytoplasm (Section 4).

These results do not discount the possibility of mycelial communication via electrical impulses,

but they certainly limit the usefulness of comparisons between hyphal and neuronal activity.

Action potentials have also been detected in the non-neuronal cells of other organisms

including single-celled protists. In some cases, these voltage changes appear to reflect the

inherent instability of the semipermeable membrane and the operation of homeostatic

mechanisms to restore the balance of ions after leakage, with no hint of a signaling process

(Brunet & Arendt, 2015).

6. Questionable studies on neuronal-type communication within mycelia

Unfortunately, there has been relatively little critical research on hyphal electrophysiology since the studies by Clifford Slayman and colleagues. Faster oscillations or spikes in membrane potential were recorded from the mycelia of species of *Pleurotus* and *Armillaria* (fungi that form mushrooms), but these were not characterized as clearly as the action potentials in *Neurospora* (Olsson & Hansson, 1995). There have also been some questionable studies on fungal electrophysiology that do not justify the extraordinary claims of nerve-like communication within mycelia made by their authors. Mishra et al. (2024) created biohybrid robots whose movements were coupled to the electrophysiological disturbances within mycelia growing in culture dishes. The fungus used in these experiments is an edible mushroom called the king oyster, *Pleurotus eryngii*. Needle electrodes were inserted into the cultures and signals from the mycelia were relayed to motors that controlled the wheels and legs of the robots. Spontaneous voltage spikes in the microvolt range were recorded from the electrodes and additional voltage swings were recorded from mycelia exposed to ultraviolet light. The resulting erratic movements of the robots led the investigators to dream of future fungal machines that respond to environmental variables and could be useful in crop management and other applications.

The voltage spikes recorded by Mishra et al. (2024) were three orders of magnitude smaller than the shifts in hyphal membrane potential measured with intracellular electrodes in the earlier electrophysiological studies on fungi. They were also at odds with the earlier extracellular electrical activity in the millivolt range measured with extracellular electrodes by

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Olsson & Hansson (1995). Although Mishra et al. (2024) described the voltage fluctuations as "action potentials," these were not resolved into any recognizable waveforms in their analyses. It seems more likely that the electrophysiological signals from *Pleurotus* were nothing more than random noise resulting from the insertion of the electrodes into the cultures. It would be instructive to carry out control experiments using slices of potato or beetroot to see whether these vegetables show comparable levels of intelligence.

Similar flights of the imagination at the expense of logic are found in other studies on fungal electrophysiology. Using needle electrodes for extracellular recordings from mycelia of various fungi, Adamatzky (2022) measured voltage spikes ranging from 30 microvolts to 2 millivolts. Analysis of these signals revealed trains of electrical activity that the author interpreted as evidence of communication using a fungal language, with a little bracket fungus called the split gill offering the most complex sentences. This study and related publications make a mockery of the emerging objective research on fungal behavior and the processing of information by mycelia.

Within this milieu, there have been some more thoughtful studies on fungal communication that deserve closer scrutiny. For example, Fukasawa et al. (2024a) reported oscillations in electrical potential between hyphae feeding on a bait and other parts of the mycelium in their culture studies. Again, these recordings were made using extracellular electrodes, but it seems plausible that changes in mycelial growth associated with the availability of nutrients may be communicated through changes in membrane permeability that is detected with these

electrodes. In this instance, of course, the electrophysiological signals may be a consequence of other physiological changes in the fungus rather than any evidence of messaging. Wernet et al. (2023) provide more compelling evidence for communication in their measurements of oscillations in calcium and signaling proteins in single isolated hyphae and the synchronization of these patterns when hyphae fuse. The authors describe the synchronization process as monologue becoming dialogue.

7. Communication within plant-fungal networks

Plant-fungus communication is an area of very active research that spans different kinds of mycorrhizal relationships as well as the study of plant colonization by pathogenic and endophytic fungi (Zeilinger et al., 2016; Lu et al., 2021). The development of mycorrhizal symbioses between mycelia and the root systems of plants requires inter-species communications that permit the fungus to penetrate the plant tissues without stimulating the destructive interactions that occur when pathogenic fungi infect their hosts. In the ectomycorrhizal relationship between the mushroom-forming fungus *Laccaria bicolor* and poplar trees, the mycelium releases signaling molecules that activate ion channels in the root cells (Cope et al., 2019). The resulting flow of calcium ions initiates a cascade of gene expression in the plant that supports the formation of a stable symbiosis. The molecular interactions between mycelia and plants raise the same questions about developmental complexity versus expressions of intelligence that arise with the wood-decomposing fungi discussed in Section 4. Greater controversy is raised by suggestions that mycorrhizal fungi may act as conduits for

communication between plants, for which there is very limited evidence (Henriksson et al., 2023; Karst et al., 2023; Robinson et al., 2024).

8. Conclusion: developmental programming or consciousness?

Critical studies on fungal development began with experiments on the growth patterns produced by expanding mycelia and their interactions during mating reactions. Oscar Brefeld (1839-1925) was one of the pioneers in this field of research, who provided detailed accounts of hyphal development following spore germination and the formation of mushrooms. Brefeld's drawings of mushroom formation reveal one of the most complicated anatomical modifications that takes place in the fungi (Figure 6).

Beginning with the aggregation of a small number of hyphae, the fungus organizes a template for the fruit body with minimal visible differentiation among the cells. What can be seen, as Brefeld showed, is the outline of the mushroom cap and stem that emerges from the orientation and shaping of hyphae in the middle of the aggregate. This structure is produced by the same kinds of filamentous hyphal cells that form the feeding mycelium, whose individual and collective behavior is evident from the feeding experiments described in Sections 3 and 4. But when these cells weave themselves into the fruit body there is tendency to dismiss their sensitivity and responsiveness. With the loss of their individuality and conformation to a genetically-prescribed series of developmental steps in mushroom formation, the apparent self-possession of the hyphae seems to fade from view.
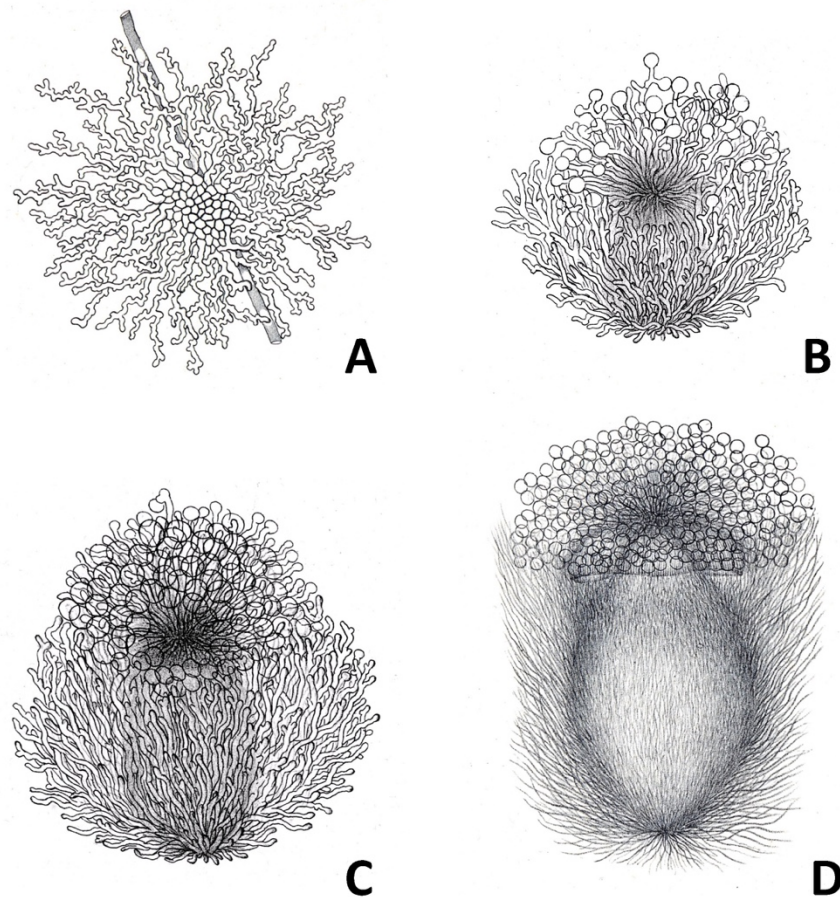
Figure 6. Drawings of the early development of the ink cap mushroom, *Coprinopsis stercorea*. (A) The fruit body is initiated as a knot of hyphae. (B, C) Hyphae in the center of the aggregate form a recognizable growth axis from which (D) the cap and stem of the mushroom differentiate. Source: adapted from Brefeld (1877).

This judgment is illogical. Each of the hyphae participating in mushroom development senses its positioning relative to the surrounding cells and adjusts its growth in response to developmental signals that craft the multicellular fruit body. The hyphae are constrained in their

growth responses, but the same is true of hyphae in a feeding colony that grow toward their food. We are misled by our bias toward identifying goal-oriented behavior in the hyphal response to *external* stimuli, such as nutrient availability, as the principal signature of cellular consciousness. Goals are also met in response to *internal* signals in the mushroom. We pursue similar thinking when we privilege the independent behavior of human cells growing in tissue cultures and believe that they subsume their autonomy in favor of cooperation to create the embryo. The cells in developing mushrooms and humans are regarded as automatons because they respond to genetically-encoded programs from which any divergence can be catastrophic.

Whether we regard the behavioral repertoire of cells as a form of elementary consciousness is a question for philosophers, but one thing is certain. Every expression of cognition in animals with brains is reliant on the sensitivity of cells whose biochemical and physiological mechanisms are common to all organisms, even fungi. In the end, even the most complex manifestations of predictive and purposeful behavior, including those predicated on the human belief in free will, are founded on elementary cellular processes common to all life. There is no ghost in the machine, only ions moving across membranes.

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