Hyphal and mycelial consciousness: The concept of the fungal mind

Nicholas P. Money*

Western Program and Department of Biology, Miami University, Oxford, OH, 45056, USA

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ABSTRACT

Like other cells, fungal hyphae show exquisite sensitivity to their environment. This reactivity is demonstrated at many levels, from changes in the form of the hypha resulting from alterations in patterns of exocytosis, to membrane excitation, and mechanisms of wound repair. Growing hyphae detect ridges on surfaces and respond to restrictions in their physical space. These are expressions of cellular consciousness. Fungal mycelia show decision-making and alter their developmental patterns in response to interactions with other organisms. Mycelia may even be capable of spatial recognition and learning coupled with a facility for short-term memory. Now is a fruitful time to recognize the study of fungal ethology as a distinctive discipline within mycology.

Sensitivity or irritability are not the same things as consciousness, but they are starting points in considering whether filamentous fungi have minds. We will begin this inquiry with single hyphae and move on to fungal colonies or mycelia. Hyphae are thin, pressurized tubes of cytoplasm adapted for invasive growth and feeding in solid materials. These microscopic threads elongate at their tips, where the exocytosis of thousands of vesicles per minute provides new membrane and cell wall components (Riquelme et al., 2018). The vesicles are produced by an endomembrane system that stretches along the hypha and they are guided by the cytoskeleton to a vesicle supply center (VSC) located close to the tip region. Vesicles move to the cell surface from this hub and new VSCs are organized behind the tip to support emerging branches. The sensitivity of the hypha is clear from the behavior of these VSCs, which are visible as clouds of vesicles called Spitzenkörpers in ascomycete and basidiomycete fungi (Riquelme and Sánchez-León, 2014). Spitzenkörpers form and dissolve as hyphae grow and stop growing, and variations in their size and position are correlated with changes in the rate of hyphal extension and the shape of the tip (Reynaga-Peña et al., 1997). There is nothing artificial about this intelligence. The continuous flow of information in the live cell would overwhelm the most complex robot.

Sensitivity is very evident when we manipulate the fungus in the lab. If the cell membrane is punctured with a glass micropipet, the hypha responds by mobilizing cytoplasmic vesicles to repair the leakage. When the hypha is sliced open with a scalpel blade, more radical repair mechanisms are deployed. Filamentous ascomycetes use organelles called Woronin bodies to seal-off hyphal compartments to prevent the whole hypha from rupturing and different defensive measures have evolved in other groups of fungi (Nguyen et al., 2021). These patching systems are comparable to blood-clotting mechanisms in animals.

Recordings of membrane potential using microelectrodes provide another illustration of hyphal sensitivity (Slayman and Slayman 1962). The membrane potential is responsive to physical perturbation of the cell and to changes in the surrounding chemical environment. Seemingly spontaneous waves of membrane depolarization followed by repolarization occur too (Slayman et al., 1976). These resemble the action potentials or nerve impulses in animals, but their function in fungi is a mystery. Changes in membrane potential may be features of a signaling mechanism that allows hyphae to detect microscopic ridges on surfaces. This behavior was discovered in rust fungi grown on microfabricated silicon wafers and serves the fungus in nature as it negotiates the surface topography of its host plants (Hoch et al., 1987).

Hyphae are reactive to more generalized physical contact between the cell surface and surrounding environment. Recent experiments have shown that the growth rate and branching patterns of hyphae are affected by confinement in microfluidic chambers (Baranger et al., 2020). Hyphae find themselves in similarly cramped situations in nature as they spread in soil and penetrate the tissues of plants and animals. Indeed, fungi may display unnatural...
behavior when they grow unconfined in liquid cultures or medium solidified with agar. These observations place a premium upon imaging fungal pathogens within the tissues of their hosts (Amich et al., 2020; Bain et al., 2015; Jones et al., 2016; Pfister et al., 2020).

Taken together, these illustrations of cellular sensitivity demonstrate that the living hypha is highly attuned and responsive to its surroundings. The same is true for all cells but has escaped the attention of mycologists as an evocation of consciousness. Arthur Reber (2019) has championed the cellular basis of consciousness and has made powerful arguments against the illogical privilege that has been accorded to human consciousness. Rather than seeing the human mind as a unique product of evolution, Reber regards our consciousness as one expression of irritability along a continuum of complexity. He is one of several scientists who propose that consciousness emerges from the perception of environmental conditions, discrimination between helpful and harmful stimuli, and other universal features of cellular behavior. The literature on this subject is vast and is rooted in research on protists in the early 1900s (Jennings 1904; Glasgow 2018). The theory of cellular consciousness is a work in progress, but it certainly encourages us to begin paying more attention to the behavioral sophistication of the fungi.

There is a natural tendency to consider an organism conscious if it appears to engage in decision-making that results in a unique behavioral outcome. Whether or not humans have free will, we take actions that seem willful: she finished her coffee, whereas her friend left her cup half full. On a simpler level, fungi express the same kind of individualistic behavior all the time. Because the precise timing and position of branch emergence from a hypha varies, every germling assumes a unique shape (Hewitt et al., 2016). This stochastic quality of development is evident from the shape of clonal colonies growing on a surface and is amplified when the hyphae proliferate in three dimensions. Although there is a high degree of predictability in the overall time-dependent form of the emerging fungus, it seems likely that its detailed shape is irreproducible. These behavioral differences arise from something akin to decision-making: the location of a branch is determined by its point of emergence on the circumference of the primary hypha and the timing of its inception. Consciousness is a product of the interaction between the genetic controls that underlie this developmental process and the responsiveness of the fungus to the physical environment. The fungus is not thinking in the sense that a brained animal thinks, but some of the underlying cellular processes of signal transduction are bound to be homologous.

Fungi that operate as opportunistic pathogens of humans shift to different growth forms when they enter host tissues, with the classic yeast-mold transition facilitating invasive growth. More subtle changes occur in response to the low levels of free iron within animal tissues. These have been described as anticipatory behaviors because they offer protection from host immunological defenses before they are presented to the fungus (Brown et al., 2019). Pathogens also shield themselves from the host by masking molecules on their cell surfaces that are recognized by the innate immune system. Anticipatory behaviors are not comparable with the classical conditioning of Pavlov’s dogs because they appear to be hard-wired genetically programmed routines that are always deployed when the fungus enters the host. Nothing is learned by the individual fungus, whereas Pavlov’s dogs began to salivate independently at the sound of the ringing bell during reward-response experiments. On the other hand, the behavioral processes in the dogs and the fungi are founded on the intrinsic genetic characteristics of their species.

If individual hyphae are conscious, what happens when an interconnected colony, or mycelium, of thousands of these cells forms in the soil? Is a mycelium more than a sum of its parts? Can it be regarded as an integrated conscious entity? Beautiful studies with radioactive isotopes have demonstrated that materials are transported between locations across a mycelium, so that one part of the colony that accesses food can feed distant hyphae that have exhausted the available nutrients (Fricke et al., 2008). This is an impressive illustration of resource allocation within a single mycelium. Source-sink dynamics may explain this process, with materials simply flowing in response to concentration gradients, but information may be flowing too (Fricke et al., 2017). Competition between mycelia of decomposer fungi is likely to be one interaction that involves a good deal of signaling between clonal colonies, which can fuse, and different genets that fight for food. Communication is also essential for the formation and maintenance of mycorrhizal symbioses between fungi and plants (McCLean et al., 2017; Pellegrin et al. 2019; Simard et al., 2012).

Beyond sensitivity and responsiveness, learning and memory may be regarded as expressions of higher consciousness. These processes have been explored in slime molds for many years (Vallverdú et al., 2018) and mycologists are playing catch-up at last. Mycelia of grassland fungi that are incubated at elevated temperatures grow more swiftly after they are exposed to a second, more severe heat shock than controls that have not experienced the initial heat shock (Andrade-Linares et al., 2016). This suggests that compensatory heat shock mechanisms adopted during the first period of stress are activated immediately when the second shock occurs. The fungus can remember the first stressful experience for up to 12 h. Other experiments have shown that a mycelium growing within a wood block that serves as a home base, or inoculum, can memorize the relative position of a second wood block that is used as a bait (Fukasawa et al., 2020). When the original wood block is removed from its soil tray, disconnecting the inoculum from the bait, and placed in a fresh soil tray, the mycelium will tend to reemerge from the side of the wood block from which it had located the bait. This is an illustration of a simple form of spatial navigation, memory, and, arguably, intelligence.

Studies on mycelia and mycorrhizas have encouraged the concept of the forest as a kind of super-organism with a “wood wide net” formulated by fungal connections between trees. This awkward allusion to the World Wide Web has some usefulness as a metaphor, and is an attention grabber, but it does a disservice to the fungi. In this brief essay I have considered fungal expressions of consciousness, including sensitivity, decision making, learning, and memory. This rich behavioral repertoire allows fungi to adapt in real time to changes in environmental circumstances. Our internet shows none of this inherent flexibility. It is a network of pathways that generates nothing on its own. Life outshines the limitations of this drab technology in every cell. With the wealth of research revealing the sensitivity and responsiveness of individual hyphae to their environment, coupled with the novel studies on mycelial learning and memory, now is a fruitful time to recognize the study of fungal ethology as a distinctive discipline within mycology.

References


In some sources the term mycelium (plural mycelium) has been stretched from its original scientific use as a count noun (each mycelium [singular] expands by branching/mycelium [plural] expand by branching) into a mass noun that is used, sloppily in my opinion, as a singular or plural commodity (mycelium [sing. or pl.] expands by branching). Language evolves, but this swerve in the vocabulary of mycology needs to be recognized.


