Seeing through an ant's eyes: do entomopathogenic fungi extend their cognition to their hosts?

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Seeing Through an Ant's Eyes: Do Entomopathogenic Fungi Extend Their Cognition to Their Hosts?

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Abstract

Post-cognitivist approaches recognize cognition as a phenomenon that involves not just brains but all the sensorimotor apparatus of organisms. This means that brains are not always required for the emergence of cognition and that every organism can, in principle, be cognitive, unlocking a theoretical framework to explain the complex adaptive behavior of even non-neural organisms. This construct blurs the boundaries of cognitive processes, leading to what is known as the Extended Cognition thesis, where objects in the environment could become integral parts of an individual's cognitive system. Here, we explore the possibility that some species of entomopathogenic fungi in the families Cordycipitaceae, Ophiocordycipitaceae, and Clavicipitaceae could extend their cognition to the insects and other arthropods they infect. In this parasitism, the fungus takes possession of the sensorimotor apparatus of its host and coerces it to find the best places for fungal dispersal. We examine case studies where *Ophiocordyceps* spp. fungi induce ants to seek bright places in the forest. In this case, the fungus may be using the ant's sensorial and motoric apparatus to locate the places appropriate for its reproduction. This could be a remarkable example of extended cognition of a non-neural organism

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through a neural organism. However, empirical testing using a solid demarcating criterion is required to confirm this hypothesis.

Keywords: Fungal behavior; Fungal cognition; Cordycipitaceae; Ophiocordycipitaceae; Post-cognitivism; Extended mind; Cognitive ecology

1. Introduction

Cognition, as the process of perceiving the environment, processing and elaborating on the stimuli received, and acting to implement behaviors that overall increase chances of survival, has been considered a capability essential for the survival of all organisms by an increasing number of scientists (Souza, Toledo, & Saraiva, 2018; Bechtel & Bich, 2021; Shettleworth, 2010; Varela, Thompson, & Rosch, 2016; Lyon, Keijzer, Arendt, & Levin, 2021). Since the environment is variable and unpredictable, living organisms necessarily had to evolve mechanisms for monitoring environmental fluctuations and control their own behaviors accordingly. In this way, they can respond adaptively to the stimuli received and increase the likelihood of survival and enhancing fitness. In humans, this cognitive ability includes conscious experiences that enable us to make sense of the world. Yet, consciousness does not equate to cognition, and indeed, many cognitive processes are unconscious to us (Reber & Allen, 2022). Here, when we discuss cognition, we are referring to the process sometimes described as "basal cognition," which is a primitive capability that evolved differently in every group of organisms, with several degrees of complexity across the branches of the tree of life (Lyon et al., 2021). Understanding how cognition operates in different organisms, and its limitations and possibilities, may help in understanding our own cognition and how it relates to that of other organisms.

An increasing number of scientists understand that the cognitive process is inseparable from action (e.g., Keijzer, 2003; Stewart, Gapenne, & Di Paolo, 2010; Varela et al., 2016; Buzsáki 2019). Cognitive systems are active in seeking stimuli that allow them to accommodate their self-organization (e.g., their homeostasis) to the environmental variables they can sense with their sensory organs, ensuring that their self-organization is never disrupted. This is why many authors emphasize action as inextricable from cognition and consider cognition as a process of perception-action (Di Paolo & Thompson, 2014; Souza et al. 2018; Keijzer, 2003; Varela et al., 2016), that is, constant loops between perceiving the environment through action, and acting according to what is perceived. This idea is broadly known as enacted cognition (di Paolo & Thompson, 2014; Keijzer, 2003; Varela et al., 2016).

Examples of the relationship between perception and action are many and are distributed across a wide range of taxa. An interesting example is vision. Vision itself provides little useful information about the environment unless it is matched with movements (action). For instance, with our own stereoscopic vision, the only way of understanding the distance between two objects and ourselves is by moving the head to achieve parallax (Kim, Angelaki, & DeAngelis, 2016). Another well-known example is the experiment by Held and Hein (1963) involving kittens raised in complete darkness, except for daily 3-h experimental sessions. In each session, one kitten was allowed to walk freely in a cage while harnessed to a gondola that carried another kitten that could not move. The movements of the active kitten propelled the gondola, ensuring that both animals received identical visual stimulation. However, the stimuli were active in one case and passive in the other. Following the experimental period, the actively moving kittens exhibited normal locomotion, whereas the passive kittens behaved as if they were blind (Held & Hein, 1963). For them, perception was never matched with action, disrupting the loop that sustains an important cognitive capability.

Action and movement are also needed for non-neural organisms such as bacteria. When the bacterium *Escherichia coli* finds chemicals in the medium that indicate a source of resources (e.g., a gradient of glucose), movement is the only way the bacterium can acquire information about the source of the gradient, for most of the receptors are highly polarized, located at one end of this prokaryotic cell. Therefore, swimming is necessary to establish the relation between distance and concentration of attractants (Bechtel & Bich, 2021; Sourjik & Wingreen, 2012). With these examples, we would like to highlight that movement (and actions) are inextricable from cognition, regardless of the presence of a neural system. In other words, cognition is enacted (di Paolo & Thompson, 2014; Varela et al., 2016).

A different, but related, theory to explain cognition deals with the material substrate of the cognitive process. It originally described part of human cognitive behavior and proposes that our cognitive processes are not restricted to the limits of our skin (or central nervous system); rather, they are often extended to objects we manipulate to increase our own cognitive capacities. This is known as the Extended Mind Thesis (Clark & Chalmers, 1998; Menary et al. 2010). According to this hypothesis, when we interact with objects of the environment that aid our cognitive processing, like using notes to remember something or our cell phone to navigate somewhere, these objects become an integral part of our cognitive process, having an active role functionally as relevant as our neurons. However, these objects are only part of the extended cognitive process insofar as we interact with them (Rowlands, Lau, & Deutsch, 2020).

This hypothesis has received much criticism, partly because it implies that cognition is not based only on neurons, and because it lacked a clear, mechanistic criterion to demarcate what is considered cognitive (e.g., Adams & Aizawa, 2001; Allen-Hermanson, 2013; Ludwig, 2015; Rupert, 2004). Nevertheless, extended cognition was at least partly incorporated into a model of cognition that does not deem neurons as strictly necessary to the manifestation of this phenomenon, and that sees cognition as a process enacted through the actions of agents embedded in their environments (Newen, de Bruin, & Gallagher, 2018).

To solve the issue of delimiting the boundaries of cognition, raised by critics of this hypothesis, Kaplan (2012) proposed the elegant mutual manipulability (MM) delimiting criterion (Craver, 2007), later redeveloped as the concept of Matched Interlevel Experiments (Craver, Glennan, & Povich, 2021). This criterion would help scientists to establish a clear method to test empirically hypotheses on extended cognition. Indeed, the MM criterion is commonly used, albeit often inadvertently, in the neurosciences to establish relations of constitutive relevance of different neurons or sets of neurons to the animal cognitive process (Kaplan, 2012). However, the MM can, in principle, be used outside the neurosciences to delimit cognitive processes in general, and in particular, extended cognitive processes.

To explain the MM in simple terms, if an organism's cognitive process involves an environmental element, altering the organism's cognitive state should correspondingly modify that element (this is known as top-down manipulation). Conversely, altering the environmental element should influence the cognitive process in turn (bottom-up manipulation). For example, Japyassú and Laland (2017) proposed that spider webs are an extended element of spider cognition. Among the examples they provide to support their claim, they mention some experiments showing that spiders alter the tension of the threads of their webs to better detect prey, especially if hungry (Nakata, 2010; 2013; Watanabe, 2000). The altered cognitive state of hungry spiders changes the structure of the web and the spider's own capacity to perceive, which is considered a top-down manipulation. Conversely, experimentally pulling the threads of the web makes the spider direct its attention toward specific areas of the web, even if there is no reason for the spider to expect food in those areas (Watanabe, 2000; Nakata, 2010), and this is considered a bottom-up manipulation (Japyassú & Laland, 2017). This is a very simple explanation, and the reader is invited to refer to Japyassú and Laland (2017), Kaplan (2012), and Craver et al. (2021) for more details. What is key here is that the mutual relationship between a cognitive system and objects that might be part of the cognitive process could be inferred by experimental manipulations. The MM criterion bestows researchers a tool for testing extended cognition in different organisms and has been endorsed by some authors as a valid criterion to determine the boundaries of other organisms' cognition, like spiders (Japyassú & Laland, 2017), plants, termites, slime molds, and any organism potentially able to extend its cognitive process (Parise, Gubert, Whalan, & Gagliano, 2023).

Here, we tackle an unexplored possibility: that entomopathogenic fungi could extend their cognition to the insects they parasitize. These are fungi that infect insects and other arthropods, taking possession of their sensorimotor and cognitive apparatus, and coercing them to behave in a way that eventually kills the host while increasing the fungus' ability to disperse. This includes a range of neural and motoric manipulations, from stimulating insects to climb toward light, to increasing their sexual drive (see review by de Bekker, Beckerson, & Elya, 2021). We propose that there is evidence to suggest that these fungi, when using the sensorimotor system of an insect, effectively extend their own cognition to that insect. To explore this, we dissect case studies where entomopathogenic fungi use ants to find bright places in the forest, usually high ones, which likely improves the dispersion of fungal spores. This will illustrate how perception and action are only accomplished when the tight coupling of fungi and ants occurs.

2. Insect and fungal cognition

The cognitive capabilities of insects have been documented for many years (e.g., Dujardin, 1850), and the body of evidence for their cognition continues to increase (e.g., Dhein, 2023; McFarland, 1991; Solvi, Baciadonna, & Chittka, 2016; Webb, 2012). Perhaps one of the most striking examples is the ability of honeybees to codify information about the environment with dance movements (Visscher, 2009). Bumblebees have been used as models to study insect learning, and it was demonstrated that they can be trained to complete tasks in exchange for a sugary reward (Loukola, Solvi, Coscos, & Chittka, 2017). Perry, Barron, & Chittka (2017) reviewed the studies on bee cognition, highlighting that they have sophisticated cognitive abilities like spatial navigation ability, selective attention, social learning and cultural transmission, emotion-like states, and even metacognition (Perry et al., 2017). Selective attention was also observed in other insects like *Drosophila melanogaster* (Sareen, Wolf, & Heisenberg, 2011).

Ants also present rather advanced cognitive capabilities (Czaczkes 2022), including associative learning, where they associate a neutral smell with a source of sugar (Piqueret, Sandoz, & d'Ettorre, 2019), using tools for absorbing sugary liquids and bringing them to the nests (Lőrinczi, Módra, Juhász, & Maák, 2018), and dropping stones onto the head of ground-nesting bees to lure them to leave the nest, subsequently attacking them (Schultz, 1982). Ants seem to evaluate their own certainty about environmental cues, modulating their behavior accordingly (Czaczkes 2022). Of particular interest for our case is that some ants rely more on light cues when light is available, but with decreasing levels of light, they tend to depend more on pheromones for navigation (Jones et al. 2019).

While insect cognition seems strongly supported by evidence, fungal cognition has been relatively neglected. Only recently have researchers demonstrated interest in this possibility (see Aleklett & Boddy, 2021; Fukasawa, Hamano, Kaga, Akai, & Takehi, 2024). However, as living organisms (and following the all-inclusive definition of basal cognition that we adopt here), fungi should be considered cognitive, and research has just begun to unravel the prospects. For example, Fukasawa, Savoury, & Boddy (2020) showed that the saprotrophic *Phanerochaete velutina* has memory capacity, and their hyphae presumably can remember the direction where a wooden bait was previously located. *Saccharomyces* also have molecular mechanisms to remember past experiences and use them to optimize mating (Caudron & Barral, 2013) and withstand stress (Ben Meriem, Khalil, Hersen, & Fabre 2019). *Candida albicans*, a parasitic fungus, monitors several environmental parameters and integrates this information to make decisions about continuing as a yeast or developing into the pathogenic filamentous form (Shareck & Belhumeur, 2011; Zhao & Rusche, 2021). Fungi seem able to codify environmental stimuli in electrical signals (Adamatzky, 2023; Olsson & Hansson, 1995), and the connections between the elements of this bioelectrical network, in principle, could present the logical gates necessary for Boolean processing of information (Adamatzky, Ayres, Beasley, Roberts, & Wösten, 2022). Research on fungal cognition and behavior is just beginning, but it is promising. Slime molds, which are not fungi, but are structurally and functionally similar, have a long history of cognitive studies like problem-solving (Nakagaki, Yamada, & Tóth, 2000; Reid, Latty, Dussutour, & Beekman, 2012) and learning by habituation (Boisseau, Vogel, & Dussutour 2016), and have been proposed to extend their cognition too (Sims & Kieverstein 2022).

It could be argued, therefore, that fungi are cognitive, despite the scarcity of empirical evidence. If they are indeed cognitive, would fungi extend their cognitive process, like other organisms (Parise et al., 2023) seem to do? We propose that at least a very special group of fungi could potentially do this: entomopathogenic fungi in the order Hypocreales (families Cordycipitaceae, Ophiocordycipitaceae, and Clavicipitaceae). There are approximately 1300 entomopathogenic species within these families (Dong et al., 2022; Sung et al. 2007). As mentioned before, when infecting an arthropod, they control and manipulate most of the bodily elements that sustain the cognition of their hosts. In order to be considered as extending fungal cognition, the fungus would need to perceive through its host, and not just manipulate it like a marionette. Below, we explore alluring case studies from the tropical jungles of the world.

3. Seeing through an ant's eyes

It is impossible to infer if fungi have a subjective experience of seeing through ants' eyes, so this title should be taken metaphorically. However, it is possible to infer how an ant's vision can be constitutively relevant to the cognition of an entomopathogenic fungus if these cues are used to locate and reach the best places for fungal reproduction. When these fungi infect their hosts, there are many different ways they can control host behavior, like growing hyphae between the muscles or the central nervous system, mechanically altering their movements, and releasing chemical substances that will change the behavior of the host (de Bekker et al., 2021). The result is that the host is compelled to behave according to the fungus' needs, for example, by finding a place in the environment with the appropriate level of humidity to presumably maximize fungal fitness (Cardoso Neto, Leal, & Baccaro, 2019). These control mechanisms are still understudied, and there is much to be discovered, in particular about how the cognitive systems of both organisms interact. For example, it is known that ants use solar cues to gauge their position in the environment and navigate through it (Wehner, 1984; Wystrach & Graham, 2012), while the effects of light on most entomopathogenic species are largely ignored. Yet, in a study with a species of carpenter ant (*Camponotus leonardi*) infected by the entomopathogenic fungus *Ophiocordyceps unilateralis sensu lato* in a tropical forest in Thailand, Hughes et al. (2011) found that once infected, these ants, normally canopy-dwelling, would descend to the understory and then reascend to a height of ca. 25 cm to finally bite a leaf in a process known as "death grip." This is the final action of an infected ant before being killed to allow the growth of the stroma (also known as the fruiting body) from the ant's dorsal pronotum. Hughes et al. (2011) noticed that the death grips happened around noon (11:00–13:30 h), when the sun was highest in the sky, suggesting that the fungi could be using a direct solar cue to induce the biting behavior, although alternative explanations like indirect cues (e.g., temperature, humidity) or circadian cycles were not tested.

In a later study in Taiwan, Chung et al. (2017) found a strong correlation between the head orientation of dead *Dolichoderus thoracicus* ants infected by *O. pseudolloydii* and the position of canopy gaps, suggesting that significant numbers of ants died facing the brightest areas of the canopy. This could indicate that the infected ants were guided by light cues. To investigate this effect further, Andriolli et al. (2019) manipulated light conditions in experimental plots in the Amazon rainforest by covering the plots with a shading screen. They observed that *C. atriceps* (another species of carpenter ant) infected by *O. camponoti-atricipis* died more frequently in the control plots that received normal light levels, whereas the ants found in the shaded plots preferentially died at the edges of the plot, where light could come from the sides. The few ants found dead inside the shaded plot were found at a higher elevation than the ants in the control treatment or the ones that died at the edges of the shaded plot. Importantly, apart from light intensity, other environmental variables like humidity and temperature did not differ significantly between the treatments (Andriolli et al., 2019), which challenges the alternative hypotheses excluding solar cues raised by Hughes et al. (2011) to explain infected ant placement.

What the studies above show is that these fungi appear to be using the ants' sight to find the best places for fungal reproduction. Curiously, fungi often avoid light, but when within an ant's body, the behavior seems to be the opposite. In this case, the accomplishment of a complex cognitive behavior, that is, sensing the environment, perceiving light direction, integrating this information, and implementing the correct movements to climb a plant to the brightest spot—all of them arguably very cognitive we stress (Bechtel & Bich, 2021)—is only possible when ant and fungus are coupled intimately.

Intriguingly, Hughes et al. (2011) found extensive hyphal growth inside the head and between mandibular muscles of *C. leonardi* infected with *O. unilateralis s.l.*, but no hyphae were seen within the brain, only around it. A similar result was observed by Fredericksen et al. (2017) with electron microscopy to investigate the distribution of fungal tissues in *C. castaneus* colonized by *O. unilateralis s.l.* Again, the authors found no evidence of fungal colonization of the ant's brain. Instead, the fungal hyphae invaded the rest of the body, forming structures around the muscles and only feeding on the brain once the ant had been coerced into anchoring itself in a place that was beneficial for fungal spore dispersal.

This is why we propose that the cognition of the fungus might be extended to the ant's sensorimotor apparatus. The ant would become part of the fungus' cognition, opening up to the fungus a plethora of new possibilities of interactions with the environment that were previously unobtainable. Gibson (1977) proposed that the environment offers possibilities of action to an organism, which he called "affordances," and that these guide cognitive behavior. However, what determines the affordances to engage with is the organism, depending on its sensory and motoric apparatus. In other words, the structure of the organism (e.g., eyes, muscles, tentacles, antennae) determines how it will engage cognitively with its surroundings (Maturana & Varela, 1980). What we see in these entomopathogenic fungi is an extraordinary explosion of affordances, or possibilities of interaction with the environment, caused by the parasitism of an ant. A fungus in its filamentous form would never be able to walk long distances following light gradients, climbing bushes, and exploring the best niches for future dispersal. This is likely achieved when it extends its cognition to a vehicle that allows it to develop these behaviors.

It could be counterargued that the phenomenon observed in ants infected by these entomopathogenic fungi is not a case of extended cognition, but simply of an extension of motoric capacities, without the need for cognition to be involved. In other words, the ant's body and sensorimotor apparatus is a *causal background condition* but not *constitutively relevant* to the cognition of the fungus (Kaplan, 2012). However, as argued above, action (including movement) is inseparable from cognition. Locomotion is a property absent in fungi—they grow to places but are overall sessile—yet this absence is overcome through the coupling with a vehicle: the ant's body, which they presumably control. Furthermore, it must not be forgotten that a simple act like walking is a formidable cognitive task, so complex indeed that every movement of every limb must be continuously controlled and compared to the organism's situation in the environment in real-time. This is a hurdle long acknowledged in robotics, and is one of the reasons why it is so difficult to replicate animal locomotion in bioinspired robots (Burden, Libby, Jayaram, Sponberg, & Donelan 2024). If a fungus is controlling and coordinating the movements of an ant to climb the best plant for fungal reproduction and attach to it, this is likely to involve a remarkable degree of cognition.

Another, related counterargument is that the fungus could be manipulating the ant without necessarily extending its cognition to it. The fungus could only be releasing a set of chemicals in the brain and muscles of the ant that make it phototropic. Analogously, one can give excessively salty food to a person to make them thirsty and induce them to seek water. This is different from coupling one's mind to the person and controlling them until they find water. Hence, a method to rule out the two alternative hypotheses presented here needs to be employed.

To elucidate the boundaries of fungal cognition, we argue that experiments should be carried out using the MM criterion (Kaplan, 2012) and ensuring that the necessary manipulations happen in both ways. A potential route for testing this would involve covering the eyes and ocelli of ants, or damaging the brain area related to vision processing, as a manipulation of the putative element of the fungus' extended cognitive system. Without these key structures working properly, the cognitive behavior of finding a place for spore dispersion should be impaired. This would be a bottom-up manipulation (see Kaplan, 2012). Electrophysiological analyses could provide information about how light perception of the ant affects the fungus, and if there are chemical substances released by the fungus in the ant's brain in response to these stimuli, then drugs blocking this effect could be counted as a top-down manipulation (Kaplan, 2012). This is important to determine whether the sensory system of the ant is coupled with the fungus, thereby suggesting that the fungus perceives through the ant. These experiments could help to explain how these fungi could be manipulating the ants' central nervous system, despite the lack of hyphal growth into the brain, to make the ants abnormally "light seekers"—or at least making them use light cues to guide behavior (e.g., Hughes et al., 2011). Well-designed experiments can rule out alternative explanations and, if extended cognition in entomopathogenic fungi is proven, this would open a whole new avenue for research in these systems, with potential implications not only in the understanding of the biology of these systems, but also in biohybrid robotics and pest control techniques.

Naturally, what is presented here is a hypothesis that awaits rigorous testing. There are still alternative explanations, but looking at this parasitic relationship with the extended cognition framework can prove to be fruitful. To date, there is no evidence of extended cognition in fungi. What we propose here is that entomopathogenic fungi could be not only hijacking the ants' brains, neurons, and muscles to follow light, but also their sensorial apparatus (i.e., their eyes and ocelli), and using all of them to find the best spots to disperse their spores. If this is proven to be true, there could be no clearer example of fungal extended cognition.

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