Externalized memory in slime mould and the extended (non-neuronal) mind

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Abstract:

The hypothesis of extended cognition (HEC) claims that the cognitive processes that materially realise thinking are sometimes partially constituted by entities that are located external to an agent's body in its local environment. We show how proponents of HEC need not claim that an agent must have a central nervous system, or physically instantiate processes organised in such a way as to play a causal role equivalent to that of the brain if that agent is to be capable of cognition. Focusing on the case of spatial memory, we make our argument by taking a close look at the striking example of *Physarum Polycephalum* plasmodium (i.e., slime mould) which uses self-produced non-living extracellular slime trails to navigate its environment. We will argue that the use of externalized spatial memory by basal organisms like Physarum is an example of extended cognition. Moreover, it is a possible evolutionary precursor to the use of internal spatial memory and recall in animals thus demonstrating how extended cognition may have emerged early in evolutionary history.

Introduction

The hypothesis of extended cognition (HEC) claims that cognitive processing is sometimes partially constituted by entities that are located external to an agent's body in its local environment (Clark & Chalmers, 1998; Clark, 2008; Menary, 2010). HEC claims that entities located in the external environment of an agent are partially constitutive of a cognitive process when they are coupled to the cognitive agent in the right way.[1] Coupling takes the form of a two-way interaction in which an agent acts upon (or with respect to) an external entity *and* the entity, as a result, differentially affects the agent so as to provide behaviour-guiding sensory feedback. Focusing on the case of spatial memory, our aim in this paper is to argue that an agent need not have a central nervous system to make use of this kind of two-way causal coupling to cognise.

We base our argument on memory research in the biological sciences. Baluska & Levin (2016) serve as a representative example of this body of research when they define memory as follows:

> "Memory is defined as experience-dependent modification of internal structure, in a stimulus specific manner that alters the way the system will respond to a stimulus in the future as a function of its past" (Baluska & Levin, 2016, p 902).[2]

Baluska and Levin's definition of what we will call 'Generalised Biological Memory' (henceforth abbreviated as GBM) applies to a wide range of experience dependent biological structures that determine how stimulus specific behaviour unfolds. GBM requires some form of stable biological structure that persists over time, but it need not take the form of stable patterns of neural activity. In other words, memory is not confined to organisms with a central nervous system. For example, various experimental results have supported the idea that even bacteria (Macnab & Koshland, 1972; Casadesus & D'Ari, 2002; Kobayashi et al., 2004; Lambert & Kussell, 2014; Yang et al., 2020; Gosztolai et al., 2020) and plants (Gagliano et al., 2016; Trewavas, 2014; Calvo et al., 2020) exhibit some form of memory. Moreover, studies suggest that bodily cells and subcellular structures also exhibit GBM (Monod & Jacob, 1961; Alon, 2006; Burrill & Silver, 2009; Watson et al., 2010; Levin, 2019; Biswas et al., 2021).

Baluska and Levin's definition allows for a broad application of the concept of memory to biological systems. GBM does not require an agent to have a brain. However, one might think that GBM must always be realised by processes internal to the organism's body insofar as it depends on the modification of internal structures by an external stimulus. We agree the structure must be located internal to the *cognitive system* but we will argue this internal structure can also include elements located outside of the organism's body in its external environment.[3] To support this claim, we shall look at a striking example of *Physarum Polycephalum* plasmodium (i.e., acellular

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[1] There is a long-standing debate about what kind of coupling is sufficient for a cognitive process to extend into the environment. Clark & Chalmers (1998) originally proposed what have come to be called "glue and trust" conditions to specify conditions, in addition to bidirectional coupling, a system must satisfy to form an extended cognitive system. The glue-conditions require that the external resource be reliably available (i.e., easily accessible as and when required), and that the resource be typically invoked in the performance of a cognitive behaviour. The trust-conditions require that the information the external resource provides be automatically endorsed. Critics of the extended mind have argued these conditions are too easily satisfied, leading to a problem of cognitive bloat (see e.g., Rupert 2004). We suggest that what is needed to solve this problem is a principled way to individuate cognitive systems that continuously interact with their environment. Here we are in agreement with Rupert (2009), Palermos (2014) and Kiverstein (2018).

[2] To avoid any unnecessary confusion, it should be noted that "experience" in this characterization of memory does not refer to conscious experience; rather, "experience" merely refers to an event in which a system encounters a detectable stimulus.

[3] We assume here that GBM is a variety of cognition. Thus, the system that undergoes experience-dependent modifications of internal structures that alter the way the system responds to stimuli in the future as a function of the past is, we will assume, well-described as a cognitive system. We say more in defense of this assumption below.

slime mould) which uses self-produced non-living extracellular slime trails to navigate its environment (Reid et al., 2012; Reid et al., 2013; Smith-Ferguson et al., 2017; Smith-Ferguson & Beekman, 2019). If such extracellular slime qualifies as externalized spatial memory, this directly challenges the brain-centred view within HEC, while also calling for a widening of HEC's explanatory scope. We will argue that the use of externalized spatial memory by simple organisms like Physarum was an evolutionary precursor to the use of internal spatial memory and recall in animals (Chung et al., 2009; Heylighen, 2015; Hunt et al., 2020). Extended cognition as it is found in neuronal organisms may be seen as a continuation of a general evolutionarily conserved adaptive strategy. Extended cognition is not a recent evolutionary accomplishment but is commonplace in the natural world. Many defenders of HEC claim that the idea of extended cognition that takes place partly in the world is counter-intuitive because it clashes with common-sense psychology (Chalmers, 2008; Wheeler, 2019). From the perspective of the biological sciences however HEC is far from surprising. It is exactly what would be expected given the way in which primitive living systems build structures in their environment, which they recruit to guide their behaviours.

In what follows we do not attempt to defend HEC against the various arguments which have been pitched against it (see e.g., Adams & Aizawa, 2008; Rupert, 2004, 2009). We make an argument for HEC based on findings from the biological sciences. Some philosophers will no doubt question whether GBM qualifies as *bona fide* cognition (see Lyon et al., 2021 for a defence of basal cognition). Our aim in this paper is to argue for a generalised conception of biological memory that recognises how traces and modifications that organisms leave on their environment can provide feedback, such that the organism's behaviour in the future is a function of its past experience (Thierry et al., 1996; Heylighen, 2015).

Our paper comprises four sections. In section 1 we review the classical argument for HEC. We show how previous arguments for HEC are often framed in terms that make reference to the brain. Wheeler (2010) for instance takes HEC to be the hypothesis that the material vehicles that realise thinking and thought are sometimes "spatially distributed over brain, body and world, in such a way that the external (beyond the skin) factors concerned are themselves rightly accorded fully paid-up cognitive status" (p.245). However, we will argue that although frequent references to the brain can be found in the literature, proponents of HEC need not endorse a claim we will label the neurocentric assumption. This is the claim that it is only if a creature has a brain, or is made of materials organised in such a way as to play causal roles equivalent to that of the brain, that the creature is capable of cognition. In section 2 we provide an example of extended cognition that challenges the neurocentric assumption by reviewing research on externalised spatial memory in slime mould, P. *Polycephalum*. Section 3 argues that externalised spatial memory counts as an example of what proponents of HEC call 'cognitive niche construction' - the process by which organisms build structures in their environment that aid their problem-solving (Wheeler & Clark, 2008). We introduce the notion of 'memory making' - the process of both regularly producing and using externalized biochemical cues to constrain self-organizing adaptive behaviour. Section 4 responds to the challenge that the use of externalised biochemical cues does not count as cognition. This raises the question of when a biological process should be counted as cognitive. Adopting a biogenic approach, (Lyon, 2006; Smith-Ferguson & Beekman, 2019; Lyon et al., 2021), we draw on the notion of "sensorimotor coordination" to answer this question (Van Duijn et al., 2007; Lyon & Keijzer, 2017; Calvo et al., 2020; Author's article). We use this biogenic-based account of cognition to defend the claim that the use of extracellular slime to adaptively navigate qualifies as a form of extended spatial memory.

1. HEC's neurocentric assumption

HEC has undergone various waves since it was first proposed by Clark & Chalmers (1998) but what these waves share is a focus on cognition as instantiated in humans.[4] Proponents of HEC have claimed that in certain contexts human thinking is materially constituted by resources distributed across the boundary of brains, bodies and environments (Clark & Chalmers, 1998; Rowlands, 1999; Sutton, 2010; Clark, 2008; Menary, 2007, 2010; Wheeler, 2010; Kiverstein, 2018; Kirchhoff & Kiverstein, 2019). Here, the notion of "constitution" refers to the metaphysical dependence relation that obtains between a dynamical system formed out of neural, bodily and environment elements and some cognitive process of explanatory interest (Kirchhoff & Kiverstein, 2019, ch.6). For example, the game of tug-o-war may be seen as constituted by at least two people at two of ends of a single rope, pulling in the opposite direction of their opponents. Where there is only one person and a rope, Tug-o-war cannot obtain; neither does it obtain if no one pulls in opposite directions. HEC claims that besides neural activity patterns within an individual, extra-neural bodily and environmental elements in certain conditions may be a constitutive part of cognitive processes.

HEC does not claim that human cognitive processes are always and everywhere constituted by a hybrid of neurobiological processes and environmental resources (Sutton, 2010). It suggests that a subset of cognitive processes are softly assembled out of neural, bodily and environmental elements. Nevertheless, HEC stands in opposition to internalism about the mind: the view that cognitive processes are as a matter of contingent fact wholly constituted by processes located internal to an individual (Adams & Aizawa, 2008; Rupert, 2009; Hohwy, 2016). Opponents of HEC allow that body and environment often play a necessary causal role in cognition but they hold that body and environment do not play a constitutive role in cognition. Thus, HEC's opponents retain a commitment to internalism. Methodological individualism (the view that cognition can be scientifically investigated by studying the processes that take place internal to individuals independent of their relations to their environment) has been a working assumption within cognitive science since the cognitivist revolution in the mid-twentieth century (Fodor, 1980). Insofar as HEC challenges this assumption it has been regarded by many as a challenge to the cognitivist tradition. HEC forms a part of a broader post-cognitivist 4E (Embodied, Embedded, Extended, Enactive) movement within cognitive science that conceives of cognitive processes as forming out of the coupled dynamics of biological systems (i.e., brains and bodies) and social, cultural, and technological systems (Clark, 1997, 2003, 2008; Clark & Chalmers, 1998; Sutton, 2010; Menary, 2007, 2010).

Much of the philosophical discussion of HEC has centred around the possibility of extended memory systems. Clark & Chalmers (1998) famously ask us to consider whether a person suffering from the early onset of Alzheimers could make use of a notebook to subserve the same functional role as biological memory. The notebook would of course be located outside of the boundaries of

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[4] For an exception see (Japyassú & Laland, 2017) which investigates the relationship between spiders and their webs as a possible example of the extended mind. The brain-centred view of HEC still applies to this case given that arachnids have brains.

the agent's biological body. Clark and Chalmers suggest however that the location of the notebook should not matter when it comes to considering its functional contribution to the person's memory. All that matters is the causal role of the notebook in guiding the person's behaviour. Clark and Chalmers suggest that the information stored in the notebook can make just the same functional contribution to behaviour as information stored biologically in the brain. We should not treat the two cases differently just because the notebook is located external to the person. The system the person forms with their notebook can be thought of as one among multiple possible realisers of a capacity for remembering. Just as breathing may be realized in various ways (e.g., with use of lungs, skin, gills, stomata), so also can remembering.

Critics of Clark and Chalmers have pointed out that there are important functional differences between storing information in a person-notebook system and storing information in the weighted connections of networks of neurons (Rupert, 2004; Michaelian, 2012). However, Clark and Chalmers would insist these are differences that do not matter when it comes to the question of the cognitive status of the notebook.[5] Clark and Chalmers ask us to consider what we would say if the storage and recall of information was done "wholly in the head" rather than by the notebook (p.9). They propose the following line of argument: If we would take this information storage and recall to count as a part of the memory process when it is done in the head, we should say the same when it is the notebook that is performing these functions. We should not treat the two cases differently simply because in the one case information is stored and retrieved neurobiologically, while in the notebook case this work is done partly outside of the body in the world.

HEC proposes to free us from the assumption that genuine cognitive processes are only ever realised by processes taking place inside of individual agents. At the same time, Clark and Chalmers argue for this conclusion by inviting us to consider what we would say if a process taking place partly in the world were instead to take place wholly *inside of the head*. In other words, we are asked to consider what we would say of some function partly implemented in the world if it were instead the *brain* performing this function. This is in some ways an unremarkable move, since the agents in question whose behaviour we are being asked to consider are human agents that have a brain. Clark and Chalmers may however also be read as making an argument for the extended mind by asking us to first consider what brains do in evaluating the cognitive status of some external resource. This would seem to threaten to make the cognitive status of some environmental resource depend on whether it plays a role in guiding behaviour in the same sort of way that brains do (Cf. Di Paolo, 2009). In other words, it is assumed that cognitive functions are to be understood by reference to the kinds of processes that typically take place in the brains of human agents. First-wave arguments for extended cognition might therefore naturally be read as resting upon the following reasoning. First, we determine the causal contribution of some elements located in the environment external to the body of the human agent to some cognitive behaviour of interest. Second, we consider whether we would count this causal contribution as cognitive if it was carried out by the brain, or by some other system materially and causally organised to mimic the functions of the brain.[6]

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[5] We leave to one side the question of whether they are right about this, something that is questioned by Rupert and later by Michaelian (Rupert, 2004; Michaelian, 2012).

[6] This qualification is needed so as to allow for the so-called multiple realisability of cognition, a thesis that is a key premise of first-wave arguments for the extended mind (see Wheeler, 2010; Sprevak, 2009; Clark, 2008).

We will argue that there is no need to read first-wave HEC[7] as committed to the neurocentric assumption that cognition is restricted to neuronal organisms (or organisms with heads for that matter (Baluska & Levin, 2016)! A defender of HEC that makes use of the so-called parity principle could allow that non-neuronal cognition is, under certain conditions, partially constituted by information bearing structures in the environment. Crucially, the kind of sensorimotor coupling that we have seen is central to the notion of extended cognition in HEC may be understood to exemplify a general principle central to understanding cognition in non-neuronal organisms: sensorimotor coordination (Varela et al., 1991; O'Regan & Noë, 2001; van Dujin et al., 2006; van Duijn, 2017). Sensorimotor coordination may be characterized as "the process by which organisms adaptively coordinate their sensors and effectors to optimize the external conditions for their metabolism and homeostasis" (van Duijn, 2017, p.5). Sensorimotor coordination mechanisms are meta-metabolic, in the sense that they affect the environmental conditions under which metabolism functions without themselves being metabolic mechanisms. We are in agreement with van Duijn, et al., 2007; Lyon, 2006; van Duijn, 2017) in taking the engagement of such action-perception cycles to be sufficient for cognition. Through a particular process of sensorimotor coordination - sensorimotor coupling - the memory systems of some basal organisms, like those of some more complex organisms, can be located beyond the boundaries of the biological agent, within a softy assembled, extended cognitive process.

Based on this characterisation of cognition as sensorimotor coordination, we propose widening the scope of the parity principle proposed by Clark & Chalmers (1998). The parity principle asks us to evaluate the cognitive status of some process by supposing that the process were instead performed *in the head*. If we treat the process as cognitive when it is performed in the head, we should say the same of the process when it is partially implemented by elements located in the external world. We recommend instead considering what we would say about the process if it were located *in the body of an organism*, which may, but need not, include a brain and nervous system. We will call this the Generalised Parity Principle:

> **Generalised parity principle**: if a part of the world functions as a process which, were it to go on in the body of an organism, we would have no hesitation in accepting as a part of the cognitive process, then that part of the world is (for that time) part of the cognitive process.[8]

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[7] We are grateful to an anonymous reviewer for a helpful discussion of this point. They rightly reminded us Clark and Chalmers employ the so-called parity principle as a heuristic rather than a "set-in-stone law" whereby the brain fixes the details of the causal role some external structure must play if it is to have a cognitive status. Similar arguments could be made for second and third-wave arguments for the extended mind that deny that what matters for extended cognition is the functional similarity of the causal contribution of an environmental structure, and processes taking place internal to the individual (see e.g., Sutton, 2010; Menary, 2010; Kirchhoff, 2012). Proponents of these positions have suggested a shift of focus in arguments for the extended mind to the different but complementary contributions of external sociocultural systems and internal neurobiological processes to human cognition. The focus on human culture and the contribution of the central nervous system to human cognition are however best seen as contingent features of how extended cognition has typically been approached in the literature up until now. Moreover, the commitment to a neurocentric view of cognition as typically done in the head, by creatures with a brain, and occasionally leaking out into the environment is one that second and third-wave theories have already explicitly rejected.

[8] It should be stressed once more that *the body* in this wide formulation may include but is not restricted to considerations regarding bodies with nervous systems. If we are concerned with adjudicating possible cognitive extension in the case of humans, then a human brain (and body) should not be used as the basis of our intuition

The generalized parity principle provides a useful manner of not only recognizing and doing away with our internalist biases but also tracking and correcting our neurocentric presuppositions that prevent us from recognizing possible cases of extended non-neuronal cognitive systems. In the next section, we shall consider a putative case of extended memory in a non-neuronal system - plasmodial slime mould. We will argue that recent empirical studies strongly support the claim that slime mould uses a self-produced environmental information bearing structure in a manner that counts as extended spatial memory.

2. Plasmodial Slime Mould - a model organism for non-neuronal extended cognition

Physarum polycephalum, a slime mould, is a multinucleate, giant unicellular protist, the body plan of which consists of an interconnected network of protoplasm carrying tubules (Boussard, et al., 2021). It has been the subject of a number of studies of over the last twenty years, the results of which have suggested that it has the ability to process information and solve spatial optimization problems despite its lack of a nervous system. For example, studies suggest that Physarum can successfully solve the shortest path problem between nutrients in legs of a maze (Nakagaki et al., 2000). Nakagaki and colleagues introduced a starved Physarum into a plastic maze that was placed on top of agar base. The organism extended its network of protoplasm containing tubules, so as to eventually occupy all areas within the maze. Nakagaki and colleagues then placed two small oat-agar blocks (food sources) in two different areas ("exits") of the maze. Four hours after the food placement, it was observed that all of tube networks that had previously occupied dead-ends of the maze had retracted, leaving only a reduced network connecting the four available routes to the food (two routes of differing length to each of the two food sources). After another four hours, the tube networks had retracted further leaving only a thick tube connecting the two sources of food by the shortest path between the two sources.[9]

In its vegetative (plasmodium) stage, Physarum is made up of multiple individual oscillator units, the activity of which brings about the development and extension of pseudopodia, allowing for

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pumping. The generalised parity principle seems to imply a commitment to internalism that some defenders of an enactive approach to cognition have argued to be problematic. Hutto & Myin (2013) reject what they call the "Default Internal Mind (DIM) assumption (Cf. Di Paolo, 2009). They deny that minds are in their basic state unextended and brain bound (p.137). The framing of our argument in terms of the generalised parity principle seems at the same time to presuppose DIM. Instead of taking cognition to be in its basic state brain-bound, the generalised parity principle seems to presuppose that basic forms of cognition are body bound. Our thanks to Dan Hutto for pressing this objection, and to one of our anonymous reviewers. While we are sympathetic to a more thorough-going rejection of DIM, and we think the case of Physarum would provide support for such a rejection, the aim of this paper is the more restrictive one of showing that classical arguments for HEC need not be wedded to a neurocentric assumption.

[9] Other studies, focusing upon various expressions of possible Physarum intelligence, have provided some positive evidence that Physarum possess the ability to anticipatorily respond to unfavourable periodic environmental conditions (Saigusa et al., 2008); solve the two-arm bandit problem (Reid et al., 2016); and make flexible behavioural decisions based upon comparative valuation rules rather than by absolute valuation (Latty & Beekman, 2011).

directed motility and foraging behaviour (Reid et al., 2012).[10] When a Physarum senses food or attractant gradients, the oscillation frequencies of the individual oscillator units (i.e., sections of the tubule network) that are most proximal to the food increases, resulting in protoplasmic wave propagation within the tubule network towards the direction of the food (Reid et al., 2012). Moreover, a decrease in surface tension of the outer membrane, the receptors of which bind to food molecules, also increases the protoplasmic flow towards that particular region of the membrane, causing the plasmodium to migrate towards the food. Conversely, when repellents (e.g., salt, light, caffeine) are encountered, oscillation of the units that have sensed the repellent decrease, and membrane tension increases in that region (Reid et al., 2012).

Given that slime moulds are capable of learning,[11] it must also be the case that they have some capacity to store and retrieve behaviourally relevant information. Recently, it has been suggested that intracellular oscillations underwrite Physarum's ability to learn, encoding information in the frequency, amplitude, and/or duration of the oscillations (Boussard, et al., 2021). Moreover, studies by Kramar et al. (2021) have provided suggestive evidence that Physarum directly stores information about the location of a nutrient source in its transport network morphology. Differences in the diameter of the tubules which make up its hierarchically organized transport network "encode" information via the strengthening of already existing transport connections that are closer to the encountered attractant. Contact with the nutrient source (i.e., a softening agent from the food) brings about an increase in tubule diameter, and thus an increase in protoplasmic flow in the direction of the nutrient source. Increased flow results in the development of additional tubule networks and increased network density at encountered attractant sites.[12] Both the hypotheses of Boussard et al. (2021) and Kramar et al. (2021) are important for furthering our understanding of the mechanisms underlying storage and use of memory states at the heart of Physarum's intelligent, context sensitive behaviour. We take these hypotheses to support the claim that slime moulds possess a form of general biological memory (GBM), which explains how such non-neural ameboid systems can learn about aspects of their environment and use this history-dependent information to guide their behaviour. We will argue next that Physarum also makes use of a form of externalized spatial memory.

2.1 Taking the path less travelled: the use of externalized memory by slime mould

One interesting fact about a Physarum plasmodium is that when migrating through its environment, it leaves behind a clear residue of non-living extracellular slime. This slime trail consists of the remnant cytoplasmic casing that was used during the process of locomotion (Smith-Ferguson et al., 2017). Taking this fact into consideration, Reid et al. (2012), posed the question as to whether Physarum, upon encountering extracellular slime, use it to guide its behaviour away from possibly food depleted locations that they have previously explored. In other words, is

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[10] Physarum can also enter into a dormant stage, or what is called a "sclerotium" under three joint conditions: when nutrients are scarce, when humidity is low, and when exposed to a long period of light. Physarum can revive to the plasmodium stage upon encountering better conditions again.

[11] This kind of learning is most likely non-associative (Smith-Ferguson & Beekman, 2019) but rather habituation - the simplest form of learning (Boisseau et al., 2016; Dussutour, 2021) (but see Saigusa et al., 2008). Remarkably, Physarum has also been shown to directly acquire learnt behaviour via cell fusion with an already habituated plasmodium (Vogel & Dussutour, 2016).

[12] However, see Austin (2021) for an argument that an information-processing explanation is not required, and the behaviour of slime moulds can just as well be explained in terms of physics. We return to this debate in section 4.

extracellular slime used as externalized spatial memory so as to avoid expending metabolic energy on (re)visiting areas, the nutrients of which have already been exploited?

To answer this question, Reid et al. used two experimental conditions to test how the ability to use extracellular slime affected Physarum's speed and success in reaching a food (glucose) goal. In the first (blank) condition, a non-treated layer of agar (a growth medium for Physarum) was fitted to the surface of a Petri dish, upon which a glucose solution was placed. The glucose, as it diffused through the agar, created an attractant gradient which the Physarum could follow to navigate to the glucose source. In between the source and the slime mould's starting zone, Reid and colleagues placed a dry, U-shaped acetate trap on the surface of the agar. Physarum locomote less easily over dry surfaces. This meant that although the increasing gradient in the agar flowed under the trap in the direction of the source, the trap could nevertheless act as an obstacle to the glucose source. In the second (coated) condition, the experimental set up was identical except for the fact that the agar was treated by covering it with a layer of extracellular slime. In both conditions, Reid et al., measured the amount of time Physarum took to successfully reach the glucose source goal. These researchers hypothesized that if extracellular slime was indeed used by a Physarum to avoid revisiting areas of the agar which it had already visited, then the amount of time spent reaching the goal would be significantly longer in the coated condition than in the blank condition because the slime-treated agar would mask a Physarum's own extracellular slime tracks. Strikingly, Reid et al. found that the average amount of time that Physarum spent migrating across areas of agar they previously explored was nearly 10-times greater in the coated condition than in the first blank condition. The results of this study, according to Reid et al., "provide a unique demonstration of a spatial memory system in a non-neuronal organism, supporting the theory that an externalized spatial memory may be the functional precursor to the internal memory of higher organisms" (2012, p.1).

Further studies by Reid et al. (2013), using a Y-maze set-up, have shown that the detection of increasing attractant (food) gradients on the part of Physarum can override the organism's avoidance response to extracellular slime. This is important because it provides evidence that Physarum's response to environmental cues is not reducible to a hard-wired "stimulus-response" pathway. It is more accurately described as a flexible and context sensitive sensorimotor response that balances multiple sources of sensory information (e.g., extracellular slime, food, etc.). Such flexibility allows Physarum to use extracellular slime in ways that best support its continued homeostasis. Slime trails are used to avoid nutritionally unrewarding and energy expending foraging behaviour but ignored when food is present, ensuring that Physarum does not maladaptively avoid locations with extracellular slime deposits that contain food.[13]

The question we will take up next is: can extracellular slime be thought of as an example of cognitive niche construction? Niche construction refers to the process by which organisms modify and partly create their local environmental surroundings, building nests and holes, and constructing webs and dams in ways that differentially impact on their evolutionary fitness (Laland et al., 2000).

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[13] Reid et al. make this clear in writing: "This makes sense if the slime mold's response to the presence of extracellular slime evolved to avoid areas that have been searched previously and stripped of resources; it would be maladaptive to then ignore definitive food cues even if this area contains extracellular slime. It is possible that the slowly renewing food sources could regrow in exploited areas still containing extracellular slime. Thus, the slime mold's behavioral response to the presence of extracellular slime is flexible" (2013, p. 817).

Cognitive niche construction refers to the same process of actively building structures in the local environment that aid learning and problem solving (Clark, 2008; Wheeler & Clark, 2008). The idea is that the constructed environment transforms computationally demanding problems that would be difficult, or perhaps even impossible to solve, into simpler perception and action tasks that allow for the solving of a problem through action on the environment. We will argue in the next section that extracellular slime is an example of what we will call 'memory making' - a variety of cognitive niche construction.

3. Memory Making

The notion of cognitive niche construction is often characterised in terms of enculturation (Menary, 2007, 2015). Informational structures are constructed in a public space which we learn to manipulate by being educated in what Menary calls 'cognitive practices'. Human children are subjected to training regimes by their epistemic peers in which they learn to factor culturally inherited tools and artefacts into their problem-solving behaviours. Children might learn for instance through instruction in a mathematics class at school how a graph can be used to represent quantitative relationships (Menary, 2015; Fabry, 2015; Dutilh-Novaes, 2013). So understood, cognitive niche construction would seem to be an evolutionarily recent accomplishment that began with the use of language, tools, artifacts, and culture. We suggest however that the notion of cognitive niche construction can be detached from the 'anthropogenic' starting point of much of the work on extended cognition; actively structuring the environment in ways that directly impacts cognition, does not depend upon culture (human or otherwise), and nor does it require a brain.[14]

External spatial memory as described in section 2 is arguably an example of cognitive niche construction that predates the evolution of internalized spatial memory. Hunt et al. express the rationale behind this idea clearly when writing:

> "Exploring an unfamiliar, changing environment in search of valuable resources such as food or potential nest sites is a challenge for many organisms. A memory of where one has already explored, to avoid revisiting unprofitable locations, would generally seem to be an advantage. Spatial memory of foraging locations, for example, is likely to be beneficial, but it would entail physiological costs. These include the metabolic overhead of a bigger

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[14] The term 'anthropogenic approach' was originally coined by Pamela Lyon (2006) who used it to refer to a particular kind of methodological starting point for cognitive science. More precisely, an anthropogenic approach uses human cognition as a starting point for the investigation of various cognitive processes and phenomena. Taking the anthropogenic approach is often – yet needn't be - accompanied by a general tendency to use human cognition as a gold standard against which all other possible forms of non-human cognition are recognized and measured. One thing that typically follows from this latter anthropocentric move is a commitment to the idea that brains and neural activity (or something very similar to them) are required for any instance of bona fide cognition given the central role that brains and neural activity play in human cognition. As such, the anthropogenic approach is often – yet need not be - accompanied by a general neurocentrism. One of the main thrusts of this current paper is that although an anthropogenic approach deplete of a general neurocentrism is a valid and fruitful approach to some forms of complex cognition, an investigation into possible forms of non-neuronal cognition requires an alternative – yet compatible - kind of starting point and it is this kind of *biology-first*-based starting point that we deploy throughout this paper (for the specifics see Section 4).

> brain (memory storage capacity) and the cost of encoding and retrieving memories (brain activity); these costs have to be traded off against the benefit of improved foraging performance. One way to circumvent the cost of carrying memories internally is to store the information externally in the environment. Indeed, such externalized information storage may have been the historical precursor to the development of internalized memory storage and retrieval" (Hunt et al., 2020, p.1).

We will call this process of storing information externally in the environment for later retrieval and use by Physarum in navigation 'memory making', which we characterise as follows:

> **Memory Making (MM)**: the joint process of regularly producing and using external biochemical cues and signals to construct temporary spatial memory systems that constrain navigational behaviour.[15]

We follow Maynard-Smith & Harper (2003) who, adopting a definition by Hasson (1994), characterises cues as "feature[s] of the world, animate or inanimate, that can be used by an animal as a guide to future action" (p.15). Cues can be contrasted with signals that are produced by a sender with the aim of modifying the behaviour of another organism - the receiver. We suggest that cues and signals can be thought of as information-bearing structures in the sense that the presence of a cue or signal raises the probability of a state of the world. This is because the cue (e.g., extracellular slime) and the state of the world (e.g. the depletion of food) stand in a relation of reliable causal covariation (Dretske, 1981).[16]

Although MM is a joint process of production (i.e., storage) and use (i.e., retrieval) of external cues/signals, it is the active *use* of a cue or signal that makes this cue/signal into a component of a temporary memory system. In the case of Physarum, a memory system is softly assembled when a Physarum interacts with deposited extracellular slime and such slime is used to direct its future behaviour (i.e. its avoidance of returning in the future to already visited areas). A cue or signal that is never used, does not count as an externalized memory, and only counts as an external memory when it forms a part of a memory system which MM temporarily brings into being. MM is thus an active process; it is something that an organism does and not something that happens to it.

Although use is primary in MM, it is not the use of any biochemical cue/signal that results in MM. For instance, when climbing an increasing food gradient, a Physarum engages in sensorimotor coupling with the gradient. This coupling however fails to qualify as MM because food gradients, despite their being used to guide chemotaxis, are not self-produced (i.e., Physarum-produced)

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[15] It should be noted that MM is distinct from *piloitage* (i.e., using landmarks for spatial orientation/ navigation). Landmarks are often natural detectible structures in the organism's niche which are not the product of the organism's own behaviour or the result of other organisms' behaviour.

[16] We remain neutral on the question of whether cues and signals as they are used in memory making must have semantic content that tell the organism something specific about the world. An argument could be made for such an interpretation of simple signalling based on the account of informational content and functional content provided by Shea, Godfrey-Smith & Cao (2018). However, a purely physical account of slime mould navigation could also be given as is noted by Austin (2021), or a dynamical (non-representational) account that takes the biochemical traces left by the organism to specify something akin to Gibsonian affordances for action (Gibson, 1979; Cf. Heylighen, 2015). This debate turns on larger questions about the nature of semantic content that are outside of the scope of this paper.

external cues/signals that are used to guide navigational behaviour. MM is a form of cognitive niche construction, but the climbing of a food gradient is not.

It is crucial to stress that although MM involves cues/signals that could be produced by the same organism that uses them, a signal may be the result of activities of different organisms (conspecifics or heterospecifics) from those which use them. Cues and signals, in these cases, must be biochemically similar enough to an organism's own cues/signals that it can couple to them, and use them to navigate space in ways that are comparable to the manner in which it would use its own cues/signals. An informative example again comes from Physarum that can detect and use the extracellular of either conspecifics or heterospecifics (Reid et al., 2013).[17] As long as the organism which uses another's extracellular slime could have also produced a biochemical cue that could be used for navigation in a comparable manner, then the source of the cue is irrelevant to whether its use qualifies as MM. To return to the notion of GBM: although an organism's GBM is typically understood to be the result of its own past experience, when GBM is an externalized process, experience-dependence needn't be construed as something that is linked to the organism's own past environmental interactions. What matters for externalised GBM is sensitivity to cues/signals, it doesn't matter who made them. Such sensitivity will typically be the case when two organisms' cues/signals are biochemically similar.

With this in mind, it should be clear by now that MM may take at least two forms: (1) a single organism may produce a cue/signal and subsequently use that cue/signal to direct its navigational behaviour and; (2) an organism may use a cue/signal that a distinct (conspecific or heterospecific) organism has previously produced to guide its navigational behaviour. That is, MM may be a process that occurs between a single organism and its environment or one that occurs between multiple organisms and their shared environment. Given this account of MM the following question may naturally arise: When some cue/signal qualifies as externalized memory, to whom does this memory belong? To address this question, it is necessary to inquire into the specific structure of MM as specified by (1) and (2) above. If the cue/signal is used by the same organism that produced it, then that external memory belongs to the producer/user; it is tied to that organism's past interactions with its environment. On the other hand, if the cue/signal is used by an organism other than the one which produced it, then the external memory belongs to the *joint producer/user system*.

In each case of MM, although externalized memories are vulnerable to damage, interference or loss by environmental impact, memory storage itself is something which comes for free. External memory does not incur any storage cost because it is not something which those organisms that engage in MM must encode and carry around with them. Importantly, this kind of frugal cognitive strategy may occur in the complete absence of brains or central nervous systems. We therefore present MM as one specific manner in which extended cognition *may be* realized in non-neuronal organisms. It is a significant instantiation of extended cognition given the possibility that MM is an ancient cognitive strategy that not only predates the emergence of internalized spatial memory

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[17] Interestingly, Physarum are able to distinguish the cues produced by conspecifics from those which are produced by heterospecifics. It has been shown that Physarum of one species will respond more strongly in terms of aversion to the presence of extracellular slime produced by a Physarum of the same species (Reid et al., 2013).

(Cf. Heylighen, 2015) but also predates other putative examples of extended cognition that take the form of the coupling of neuronal organisms to external information bearing structures.

Let us now turn to two important classes of phenomena that we consider to fall under the category of MM: patch-marking and stigmergy. Such phenomena not only illustrate that MM is not something unique to organisms like Physarum but is a ubiquitous cognitive strategy in the natural world.

3.1 Patch-marking as memory making

MM as observed in Physarum *polycephalum* is an example of "patch-marking" (Reid et al., 2012; 2013). This is the process whereby an organism leaves some chemical marker whilst searching and upon subsequently encountering those markers responds aversively. Patch-marking contributes to efficient foraging, allowing the patch-marker to avoid revisiting previously exploited patches (Nakashima et al., 2002). Patch-marking has been studied and observed primarily in parasitoid insects (e.g., wasps), where areas that have been previously exploited for host larvae are marked (see van Giessen et al., 1993; Sheehan et al.,1993; Höller & Hörmann, 1993; Bernstein & Driessen, 1996). It has also been more recently suggested that patch-marking underwrites the highly efficient search behaviour of some predatory insects such as *Orius sauteri* (Nakashima et al., 2002). The behaviour that ensues from encountering the presence of such marks is believed to be a response to the potential profitability of the patch (*ibid*). Although patch-marking has not generally been considered to be a cognitive behaviour in the ethology literature, we have argued that the use of patch-markers is an example of the soft-assembly of a memory system that underwrites navigation behaviour.[18] We will offer a defence of this claim in section 4 below.

3.2 Stigmergy as memory making

In addition to patch-marking, some forms of stigmergy may also qualify as instances of MM. The concept of stigmergy (from the Greek *stigma*: sting and *ergon*: work), was first introduced by zoologists Pierre-Paul Grassé in 1959 in the context of understanding the highly coordinated behaviour of termites.[19] Stigmergy describes a kind of environment-mediated behavioural mechanism that constrains collective behaviour by way of a feedback *loop* (Theraulaz et al., 2001). More specifically, an individual's behaviour produces a trace, altering the environment in some perceivable manner; this trace in turn stimulates further behaviour by the same individual or others which results in the further production of traces and so on (Heylighen, 2015). In other words, "the colony records its activity in part in the physical environment and uses this record to organize collective behavior" (Theraulaz et al., 2001, p.111). Environmentally stored traces may take the form of pheromone gradients, chemically impregnated material structures, or distributed colony elements (Theraulaz et al., 2001). The mediating environment allows for the bringing about of sequenced and organized behaviour without the need for planning or a central controller. The complex behaviour which emerges at the level of a collective unit (e.g., a colony) results from the

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[18] Reid et al. (2013) are recent exceptions to this.

[19] With the notion of stigmergy, Grassé was able to provide a solution to the "coordination paradox" for social insects. This is the puzzle of how to reconcile the fact that insects at the individual level are limited in their capacities and resources, whilst at the colony level, the groups are highly coordinated and organized.

mediated patterns of indirect, trace-driven communication between individuals. Although stigmergy has been used to typically describe the behaviour mechanisms of groups composed of multiple individuals, it has also been more recently suggested that it is helpful in understanding the complex behaviour of a single individual (Heylighen, 2015).[20]

Ant foraging behaviour provides an illustrative example of stigmergy. When a foraging ant has found food, it leaves a pheromone trail as it returns to its nest. If the discovered food source is too distant from the nest, the pheromone trail will decay before other members of the colony can use it to locate the food source. However, if the food source is nearby (i.e., the rate of decay being slower than the time it takes to reach the food source) then the original pheromone trail will be reinforced with each trip from the source to the nest that each colony member makes (Wilson, 1971). In other words, as more ants *use* the trail, it will increase in strength (i.e., quantity), attracting more ants, increasing in strength, and so on.[21] Unlike extracellular slime, pheromone trails are not only susceptible to change and transformation over time due to their volatility, but can also be actively updated. The feedback loop mechanism that arises from the circular interaction of multiple users and pheromone producers results in collective MM at the level of the active colony resulting in a primitive form of *joint memory* (Thierry et al., 1996, p. 128; Beckers et al., 1990). MM will occur in such a case until the food resource is depleted, at which time the external memory is forgotten as the pheromone trail decays with lack of use and continued updating.[22]

Both patch-marking and stigmergy are examples of what we are calling MM. But should we think of MM as a cognitive strategy (Cf. Marsh & Onof, 2007)? It is common to encounter biologists describing the use of extracellular slime by Physarum in terms of external spatial memory (see e.g., Reid et al., 2012, 2013; Smith-Ferguson et al., 2017). Moreover, the term ‘memory’ as used by these biologists is not being deployed metaphorically or instrumentally.[23] However, a natural objection one might raise in response to such talk is to question whether Physarum’s use of extracellular slime really counts as cognition. We already encountered Austin’s (2021) suggestion that descriptions of Physarum as encoding memories and learning are unwarranted, and the behaviour of Physarum could just as well be explained in purely physical terms. This brings us to

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[20] Stigmergy is typically understood to take two distinct forms: *quantitative stigmergy* and *qualitative stigmergy* (Theraulaz & Bonabeau, 1999). In the former, differences in signal/cue the quantity (i.e., the concentration levels of pheromone gradients) modify the probability of a certain behaviour being executed. In qualitative stigmergy, it is differences in trace quality (i.e., type or absolute presence) that brings about different forms of behavioural response.

[21] Stigemery is not limited to using cue/signals as positive feedback. Harvester ants (*Pogonomyrmex*) leave chemical traces when foraging for new food resources they later avoid, a behaviour which has been interpreted as a means of avoiding search redundancy (Holldobler, & Wilson, 1970). More recently, Hunt et al. (2020) have found evidence that ant *Temnothorax albipennis* avoids the footprints of nest-mates when foraging unfamiliar spaces, which these researchers suggest is a form of externalized memory (also see Robinson et al., 2005). In all of these latter cases cues/signals are used as negative feedback.

[22] Although stigmergy as it occurs in an ant colony is best thought of as an instance of collective MM, one can easily imagine a case in which a single ant uses its own pheromone trail to return to a food source it has previously discovered. In such a case, the ant’s production and use of its own pheromone trails to return to the source is a case of MM at the level of the individual.

[23] See Figdor (2017, 2018) for independent philosophical reasons for taking such biologists at their word in using psychological predicates. It should be noted however that in the original (2012) paper Reid et al. place quotation marks around the word memory in the paper’s title. However, we suggest their use of their term ‘memory’ is in line with what we have called GBM above as defined by Baluska & Levin (2017). Moreover, in both the follow up studies Reid et al. (2013) and Smith-Ferguson et al. (2017), quotation marks with the term memory are completely omitted.

a larger question, with which we will close our paper: when should a process that guides an organism's behaviour be counted as a cognitive process?

4. Evaluating externalized memory in the case of slime mould

We saw in Section 1 how much of the debate surrounding HEC has been concerned with understanding the contribution of the environment to human cognition and hence represents an example of an anthropogenic approach to the investigation of cognition (Lyon, 2006). The argument of our paper has taken a different, yet equally valid, starting point. Our argument has been premised upon what Lyon (2006) has called a 'biogenic approach' to cognitive science that starts from the facts of biology and works 'upwards' from there to human cognition. This kind of methodological approach to cognition views cognition as a toolbox of various capacities (e.g., memory, learning, anticipation, sensing, behaviour, etc.) that have evolved – perhaps many times independently (i.e., convergent strategies) over evolutionary timescales. We have been arguing that extended cognition may be an ancient strategy that has evolved many times and takes various forms in much the same way as processes such as vision and breathing. The fact that vision in humans and in microalgae (Cf. Hegemann, 1997) differs greatly in its implementation details does not mean that applying the term vision to what microalgae do is somehow stretching the term beyond its conceptual limits. Nor does the fact that vision in humans may have been investigated prior to vision in microalgae present itself a challenge to the status of the latter as a form of vision. It is just not the case that the historical order in which a phenomenon has been investigated with respect to a particular model system determines the scope of systems that such a phenomenon can be fruitfully applied to (Figdor, 2018).

The biogenic approach recognises a difference between cognitive explanations and molecular and mechanical levels of explanation. The subset of biological processes that count as cognitive are those implicated in sensorimotor coordination that play out at the scale of "whole organisms acting as a unity on its environment by physical displacements of this unity with respect to the environment" (Lyon & Keijzer, 2017: p.158). What is distinctive of cognition is "whole-organism motility" (*Ibid.*).[24] An obvious objection to such a biogenic approach is to question whether sensorimotor coordination is sufficient for cognition (see e.g., Adams, 2018). To deal with this objection, we devote this section to justifying our claim that memory making of the kind found in slime moulds should be thought of as cognitive. With this aim in mind consider again the generalised parity principle we proposed at the end of section 1.

> **Generalised parity principle**: if a part of the world functions as a process which, were it to go on in the body of an organism, we would have no hesitation in accepting as a part of the cognitive process, then that part of the world is (for that time) part of the cognitive process.

Importantly, the generalised parity principle, in order to guide our intuitions without being either overly permissive or overly demanding, must be based upon functional analysis with the appropriate fineness of grain (Wheeler, 2010). Identifying an appropriate fineness of grain (not too

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[24] It should be noted that other researchers taking the biogenic approach do not restrict sensorimotor behaviour on the part of the whole organism to motility. See for example Calvo et al. (2020), who approach their investigation of plant cognition biogenically.

restricted, nor too relaxed) means identifying a functional role for spatial memory. Following Michaelian (2012), we would like to suggest the following features as providing a functional sketch of the causal role of *spatial memory*: (1) survival relevant storage; (2) instability over time; and (3) metamemory. Let us look at each of these characteristics in turn.[25]

One uncontroversial feature of any form of memory is that information used for the guidance of behaviour is stored in internal structures. This much is clear from Baluska and Levin's characterization of GBM as a modification of a system's structure. Importantly, however, what information gets stored is determined (largely) by the relevance of that information for survival. This feature should be recognized as having some intuitive plausibility given that memory storage is expensive (Hunt et al., 2020) and as such, that which gets stored must be worth its weight in terms of long-term fitness benefits. Crucially, as long as storage is determined by information's survival relevance such survival-relevant information needn't be stored internally in the body (or brain).

The second central feature in our functional analysis of memory is that stored information is unstable across time. Whether during the storage process or retrieval process, memory is susceptible to change, reconstruction and/or reconsolidation (Koriat, Goldsmith & Pansky, 2000; Sutton, 2008, 2010; Vosgerau, 2010; Storm, 2011; Michaelian, 2012). In other words, memories on any account should be susceptible to the process of being forgotten or overwritten. Important for HEC is that this requirement is not interpreted as placing any restriction upon where information is stored and in which biological systems memories are found.

Our third feature is that memory systems require the presence of something like a 'metamemory' process that influences whether memory states are acted upon or ignored in favour of guiding behaviour with currently detected information (Cf. Koriat, Goldsmith & Pansky, 2000). For example, it can happen that stored information fails to be relevant given detected changes in the environment that have occurred subsequent to memory storage. Again, the fact that memory use is in this way flexible does not place any requirement upon where information is stored. Thus, it does not, on the face of it, rule out softly assembled extended memory systems.

With this uncontroversial sketch of the functional role of spatial memory, we can now apply the generalised parity principle: would we have any hesitation in counting the function of extracellular slime (and Physarum's interaction with it) as spatial memory if this function were instead to be realised within a plasmodial slime mould's body?

Let us consider first survival-relevant storage. The information which is stored by extracellular slime is indeed relevant to a Physarum's continued homeostasis. Extracellular slime may be considered as a biochemical cue or signal that reliably correlates with spatial location that have

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[25] Michaelian (2012) argues there are important dissimilarities between the way that actual biological memory functions and the way that Clark & Chalmers (1998) characterize memory as functioning. When taking these dissimilarities into consideration, the parity principle according to him returns the result that the notebook fails to qualify as externalized memory (Cf. Rupert, 2004). In what follows, we will use some of the features which Michaelian takes to be necessary for a process to count as memory. We will argue these features are satisfied by Physarum's use of extracellular slime. While Michaelian may be correct in his claim that Clark & Chalmers' characterization of the functional role of memory is oversimplified, his overarching rejection of extended cognitive memory is mistaken.

previously been explored and/or exploited. This information is relevant for survival in the sense that it allows Physarum to avoid spending its metabolic resources in foraging regions that have been depleted of nutrients prior to its arrival. As Reid et al.'s (2012) study has shown, the ability to use extracellular slime decreases the amount of time a Physarum spends navigating its way out of U mazes towards food goals. Avoiding unproductive expenditure of metabolic energy expenditure on revisiting nutrient-depleted locations, is undoubtedly relevant to a Physarum's continued survival. It seems that Physarum's extracellular slime meets the first of our conditions: it preserves survival relevant information used to guide the organism's future behaviour.

Does extracellular slime store information in a way that is subject to change across time? Extracellular slime consists mostly of sulfated galactose polymers (McCormick et al., 1970) and does not evaporate allowing for its usage by a Physarum for up to 6 days (at least) after the initial depositing (Reid et al., 2013). That being said, slime trails do slowly decompose. As such, extracellular slime, like internally stored memories, is subject to transformation over time; the decreased strength of slime trails is analogous to memory loss or forgetting. In the case of Physarum's use of extracellular slime, forgetting is dependent upon the various environmental conditions extracellular slime is exposed to, the general rate of chemical decomposition of the extracellular slime, and the organism's sensory threshold for detecting the particular biochemical (memory) medium. Once the slime trails have decomposed to the extent that they are undetectable, they can no longer be used to guide spatial navigation and hence, the past resource characteristics of the environmental patch that extracellular slime specifies are forgotten.

Turning to the third feature, we can now ask whether there are metamemory processes involved in the case of Physarum's use of extracellular slime? When Physarum detects food in the presence of extracellular slime it doesn't engage in a stereotyped sense-response behaviour. Physarum's response to extracellular slime is not driven by a stimulus-response pathway but involves the weighing of various kinds of sensory information. This overriding of response to extracellular slime is akin to a metamemory process. Physarum is able to evaluate the relevance of the presence of extracellular slime in the current foraging context. Detecting the presence of food, for instance, may be seen as causing an internal modification that brings about a *down weighting* of the relevance of extracellular slime. Physarum is able to down-weight biochemical cues/signals correlated with the absence of food, when those cues/signals conflict with other cues indicating the presence of food.

We conclude then that applying the generalised parity principle yields the result that Physarum's use of extracellular slime does indeed count as cognitive. One might still resist the claim that spatial memory as instantiated in slime moulds is a cognitive process. We have attempted to block such an objection by providing a sketch of the functional profile of spatial memory that should be agreeable to both proponents of anthropogenic and biogenic approaches to cognitive science. We therefore conclude that memory making as it occurs in Physarum does indeed qualify as an example of extended cognition (and, in particular, cognitive niche construction).

Conclusion

We've argued that memory making as it occurs in Physarum is an example of extended cognition. How one responds to this result will likely depend on the larger question with which we began this section concerning the mark of the cognitive. Given the various studies which have provide evidence that Physarum exhibits cognitive capacities such as learning that require some form of memory, ascribing spatial memory to Physarum strikes us as uncontroversial.[26] We ask any reader who may be particularly sceptical about basal cognition in general, or of Physarum cognition more specifically, to suspend their scepticism, and recognise that Physarum does possess some form of spatial memory. The generalised parity principle is deployed to unmask possible biases concerning the location of cognition. With this in mind, we may ask the following question: we have shown how the process of using extracellular slime in spatial navigation satisfies the functional role of spatial memory. If this functional role were occupied by processes located on the inside of a Physarum's body, would we thereby be willing to recognize these processes as implementations of spatial memory? Surely, we would! Defenders of HEC have argued that cognition can occur, in part, outside the brain. We've argued that cognition can occur entirely without a brain. Proponents of extended cognition would do well to give up on their residual commitment to a neurocentric view of the mind.

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[26] It has been recently emphasized that the findings of some of the learning experiments that we rely upon in our paper are inconclusive because the experiments have yet to be repeated (see Loy et al., 2021). Upon repeating these experiments, failure to replicate the same findings would of course count as evidence against ascribing certain forms of learning and memory to Physarum.

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