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The Principle of Dynamic Holism: Guiding Methodology for Investigating Cognition in Nonneuronal Organisms

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Abstract

Basal cognition investigates cognition working upward from nonneuronal organisms. Because basal cognition is committed to empirically testable hypotheses, a methodological challenge arises: how can experiments avoid using zoocentric assumptions that ignore the ecological contexts that might elicit cognitively driven behavior in nonneuronal organisms? To meet this challenge, I articulate the principle of dynamic holism (PDH), a methodological principle for guiding research on nonneuronal cognition. I describe PDH's relation to holistic research programs in human-focused cognitive science and psychology then present an argument from analogy based on holistic developmental biology. Last, I examine two experiments exemplifying the need for PDH.

1. Introduction

Recently, there has been a surge of interest in and empirical support for the idea that many of the cognitive capacities found in complex animals like us may be found in nonneuronal organisms, albeit in simpler form (Lyon 2015; Levin 2019; Keijzer 2021; Dussutour 2021; Gershman et al. 2021; Bechtel and Bich 2021; Levin and Dennett 2020; Lyon et al. 2021). Such capacities include associative-like learning in amoebas (de la Fuente et al. 2019), discrimination learning in paramecia (Armus, Montgomery, and Jellison 2006; Gershman et al. 2021), spatial memory in a cellular slime mold (Reid et al. 2012; Smith-Ferguson and Beekman 2019), complex avoidance behavior in *Stentor roeselii* (Dexter, Prabakaran, and Gunawardena 2019), bacterial decision-making (Shapiro 2021), and anticipatory behavior in plants (Ceccarini et al. 2021). This surge is significant for a number of reasons, one of which is that it suggests a slow but sure willingness on the part of biologists, cognitive scientists, and philosophers to abandon a long-running anthropocentric (or zoocentric) perspective on cognition. The idea of cognition in organisms like bacteria, fungi, protists, and plants directly challenges this deeply rooted anthropocentrism. Such a bias, by setting the bar for

what counts as a cognitive process at human or humanlike capacities, introduces the risk that forms of cognition that are very different from ours will continue to slip through a distinctly human-shaped net, evading identification and further study. Breaking this anthropocentric enchantment is an important step forward, for only by doing so can many of the cognitive capacities that we take to be uniquely human (or uniquely animal, for that matter) be placed in their accurate evolutionary context.

The program of basal cognition (Lyon et al. 2021; Levin et al. 2021) is an attempt to do just this. Basal cognition, as I see it, works under two basic assumptions, both of which find support in biology: first, cognition in so-called higher animals, whatever it may be, is a collection of biological processes, many of which evolved from cognitive and cognitive-like capacities and mechanisms that predate the complex forms of cognition that are often the focus of cognitive science and psychology,¹ and second, the most productive way to investigate cognition is via investigating what appear to be instances of concrete adaptive capacities belonging to the “basic cognitive toolkit” (Lyon et al. 2021) (i.e., memory, learning, decision-making, sensing and perception, anticipation, valence, and behavior). Each of these capacities has been selected for and/or maintained in various forms because of its contribution to survival and fecundity.²

Where basal cognition shines as a research program is in its commitment to housing theories that produce empirically testable hypotheses. In this sense, it is an instance of what Pradeu et al. (forthcoming) have called “philosophy in science” as opposed to “philosophy on science.” Premised on letting experimental results determine whether some system is exhibiting cognitively driven behavior (Levin 2022)—as opposed to a priori reasoning—basal cognition research proceeds methodologically by (re)interpreting results from empirical experiments so as to adjudicate the status of a given hypothesis and/or by constructing and testing newly formulated hypotheses by way of experiments at the bench. It is not only with respect to the former that philosophy plays an invaluable role; as I hope to illustrate, it also can influence aspects of the latter. It is with respect to this latter method that a formidable challenge arises: when designing experiments, how can investigators avoid using zoocentric assumptions that are insensitive to or even misrepresent how some nonneuronal model organism of interest makes its living within its *econiche*?

Investigations into the behavior of *Stentor roeselii* provide an example of this challenge and its stubborn persistence. In 1902, Herbert Spencer Jennings showed that the unicellular ciliate *S. roeselii*, after being bombarded with toxic carmine powder, engages in a complex sequence of avoidance behaviors, each behavior becoming more effective than the previous until *S. roeselii* detaches and swims away. More than one hundred years later, Dexter, Prabakaran, and Gunawardena (2019) successfully replicated Jennings’s findings using polystyrene beads in a toxic NaN_3 aqueous suspension rather than carmine powder. Although *S. roeselii*’s behavior is nothing less than striking, eliciting such behavior with either carmine powder or

¹ The first assumption does not rule out the very likely possibility that some capacities find no ancestral homologue (i.e., apomorphy) or that some capacities have arisen independently of one another in different lineages (i.e., homoplasy).

² Basal cognition is not an a priori claim that cognition is synonymous with life or that it may be found to arise at a certain level of organismal complexity.

beads in NaN_3 fails to shed light on what this behavior is a response to in *S. roeselii*'s natural freshwater habitat; because neither of these stimuli are ones that *S. roeselii* encounters outside of controlled laboratory settings, inferring exclusively from observed responses to carmine powder or polystyrene beads in NaN_3 to how *S. roeselii* might deploy the same complex sequence of behavior in its natural habitat (if at all) is anything but straightforward. Thus understanding how to complement experiments like these to obtain a more complete and accurate understanding of how (or if) nonneuronal organisms might deploy putative cognitive capacities within the context of their ecologies poses a serious challenge.³ The aim of this article is to meet this challenge head-on by articulating and arguing for what I call the *principle of dynamic holism* (PDH), a methodological principle for guiding research on nonneuronal cognition.

The PDH suggests that investigating cognition (or the possibility thereof) in nonneuronal organisms should, when it can, consider the ecological variables that make up the organism's niche—those variables that the organism's behavior is regularly responsive to and has evolved in relation to over multiple generations—and selectively incorporate those of central importance into the hypotheses being constructed and tested. By providing an ecologically based methodological principle that is aimed at improving hypothesis construction, experimental design and operationalization, and behavioral (data) interpretation for studies of nonneuronal cognition, this article contributes to the budding research program on basal cognition.⁴

The article is organized as follows. Section 2 articulates the methodological PDH. Section 3 describes how this holistic principle may be seen in relation to various research programs in cognitive science and psychology that have similarly focused on the importance of environmental context. Section 4 presents an argument from analogy that is based on how a similar form of holism in developmental biology has provided a fruitful complement to a purely bottom-up genetic approach to developmental explanation. In section 5, I make a case for the PDH by looking at two potential examples of nonneuronal cognition: the tracking of motile algae by the marine bacterium *Pseudoalteromonas haloplanktis* and the farming of red yeast by *Physarum polycephalum* (acellular slime mold). I argue that progress on empirically investigating either of these behaviors is contingent on deploying PDH (or something very much like it).

Before moving on, a few preliminary remarks are in order. My aim in this article is neither to argue for any particular conception of cognition associated with basal cognition (there are many) nor to argue for nonneuronal cognition in general; rather, my aim is to present and argue for the value of the PDH as an investigatory method and thereby impact scientific practice and/or philosophers interested in impacting scientific practice. There is a good chance, of course, if one does not find basal cognition or the more general project of investigating cognition in nonneuronal organisms to be worthy and/or compelling, then the principle that will be articulated in the pages to follow will seem unmotivated. That said, I ask the reader who does fall

³ I thank an anonymous reviewer for urging me to use an example here.

⁴ That said, the PDH, as it is developed in the following pages, may be used independently of basal cognition.

into this category to momentarily suspend his or her intuition and a priori conceptions regarding nonneuronal cognition throughout the duration of this article, for in doing so, such a reader may be situated to see why, if the reader *were* to find value in the program of basal cognition, he or she *would* or *wouldn't* find PDH and the methodological arguments supporting this principle compelling. Among those readers who do find the principle cogent after having evaluated the arguments in this manner, some, upon returning to their presuspended intuitions, may not recognize them as being as unshakable as they previously thought them to be.

2. The principle of dynamic holism

Often, cognition's expression (if it is expressed at all) in natural environments will have the features it does because of the presence of specific types of ecological variables (i.e., environmental conditions) that elicit behavior as such. Discovering which specific ecological variables elicit a certain behavior of interest in a particular taxon is paramount to designing experiments that have the potential to operationalize cognitive phenomena. This is the general, yet nontrivial, idea on which the methodological PDH is grounded. This principle may be stated as follows:

When investigating candidate cognitive capacities in nonneuronal organisms and/or attempting to investigate hypothesized aspects of empirically supported cognitive capacities in such organisms, close attention should be paid to the specific kinds of ecological variables that populate the organism's niche and how their dynamics change over time.

PDH suggests that discovering and revealing important aspects about cognition in nonneuronal organisms will often require understanding the wider environmental context in which cognitively driven behavior might be thought to occur in an organism's natural (nonlaboratory) environment; we must first inquire into the specifics of the environmental conditions to which some putative or hypothesized cognitive behavior is a response (i.e., how some capacity from the cognitive tool kit has been tuned to the specifics of the organism's echoniche). This principle is pitched specifically toward nonneuronal organisms (as opposed to neuronal organisms) because the environmental factors eliciting cognitively driven behavior in neuronal cases will presumably be easier to recognize than those eliciting behavior in nonneuronal cases. Unguided, there is a real threat that the choice of eliciting variables in experiments using nonneuronal organisms will tend toward those that have been effective in animal experiments, overlooking the fact that "due to differences in scale, niche and sensory apparatus, single cell organisms experience a totally different environment than most animals" (Dussutour 2021, 98). Although PDH is pitched specifically toward nonneuronal organisms, it can be reasonably seen as complementing holistic approaches to investigating human and nonhuman animal cognition.

PDH is a holistic principle in that it views cognitive investigation and explanation as methodologically aimed at cognitive processes in the kinds of natural

environmental circumstances that elicit such processes.⁵ To co-opt J. J. Gibson's (1979) phrase, our analysis must include *how* an organism lives, not just where it lives. This methodological principle for holistic explanation is premised on the more general idea that the behavior of an isolated biological system, whether it be a gene, a cell, an organ, or an organism, is "different from its behaviour in the context of the whole" (von Bertalanffy 1952/2014, 12). As such, explaining biological behavior requires both understanding the properties of the living system and understanding the whole that contextualizes the system's behavior. The whole with which PDH is concerned is the organism in its nesting environment. This way of delimiting the whole from its parts, however, is only one of many ways; where one draws the line between the part and the whole for explanatory purposes will depend on the phenomenon of interest (e.g., the cytoplasm of the nucleus, the tissue of the cell, the body of an organ) (Sims 2020; Levin 2019).

PDH is a dynamic principle in that it recognizes that the relationship between cognition and the environment oscillates between stability and variation; this relationship—relative to both individuals and taxa—is something that develops as niches are modified by the (often purposive) activity in which organisms engage. The dynamic element of PDH thus allows room for the lively possibility that introducing increasing heterogeneity to a previously stable habitat or relocating to a new habitat may drive the evolution of phenotypic modifications that provide ways of coping with new heterogeneity, thereby changing the manner in which a previously established cognitive phenomenon should be investigated. More generally, the fact that biological processes like cognition "to a greater or lesser extent always have the character of processes determined within a dynamic system gives them adaptability to changing circumstances and regulability following disturbances" (von Bertalanffy 1952/2014, 18). The fact that this is true of developmental processes also, as we shall see in section 4, suggests that investigating cognition and development will require a similar focus on examining such dynamic processes holistically.⁶

Three important points regarding PDH require clarification. The first is that the introduction of PDH is not meant to suggest that previous studies on nonneuronal cognitive capacities are somehow faulty, inaccurate, or have limited explanatory value. Myriad extremely well-designed and informative studies using nonneuronal organisms have taken into account how some model organism can be maintained in a controlled laboratory setting without, however, taking the ecology variables of the organism's natural habitat into account; the former conditions are not exhaustive of the latter conditions. Moreover, many of these experiments represent the foundation on which the basal cognition program has been erected. That this is the case, however, does not diminish the value of PDH. To the contrary, using PDH, if I am correct, promises to further a number of explanations supported by the many

⁵ *Holism*, as I am using the term, is a methodological-explanatory position and agnostic for the most part toward any particular ontological view of what cognition is. Importantly, this form of holism should not be confused with the now defunct and scientifically discredited position of vitalism, which has on occasion historically been referred to also as holism (Gilbert and Sarkar 2000).

⁶ Some practitioners of basal cognition see the relationship between cognition and development as being close enough to warrant treatment of developmental processes (e.g., morphogenesis) as a cognitive process occurring at the level of the cell (see Levin 2019).

important experiments that have failed to implicitly deploy PDH (or something like it).

Here is a second point: there is no sense in which PDH implies that a cognitive investigation should privilege the environmental context and the dynamic place that an organism occupies in it over the features, states, and processes that make up the organism. Rather, PDH, in the tradition of methodological holistic programs like organicism, works under the assumption that biological cognition requires that attention be paid to the organism's parts, the organism as a whole, and how the organism functions and evolves within its wider environmental niche (Gilbert and Sarkar 2000; Baedke et al. 2023). In other words, PDH emphasizes a need for an integrative methodological approach.

A third point is that PDH does not suggest that the ecological variables that one considers when formulating a specific testable hypothesis and that one incorporates into the experiment should represent the environmental context accurately in terms of the number of variables used. The more variables that are used in an experiment, the more difficult it becomes to control each variable, and thus the higher the likelihood is of introducing confounds.⁷ How, then, does one decide which variables to include? I would like to suggest the following rough, two-step procedure as one option (of many likely options): (1) observe the model organism in its natural environment, identifying roughly those variables with which that organism regularly interacts and which have a direct impact on its survival and fitness, and (2) select from these the minimum number of variables that may be relevant to eliciting the candidate cognitive capacity when constructing (or refining) a particular hypothesis and designing experiments to test that hypothesis. What the minimum number of relevant variables is and which variables they are will be based largely on an investigator's intuitions and previous observations made over the course of step 1. The outcome of this procedure should thus respect the trade-off between ecological validity and simplicity (Kominsky et al. 2020). By limiting the number of variables introduced to those which are significant to an *ecologically informed hypothesis*, the procedure helps to avoid the introduction of confounds and yet acknowledges that the expression of cognitive phenomena and various facets thereof is context sensitive (cf. Kingstone, Smilek, and Eastwood 2008).⁸

To take a toy example of how PDH might influence an experimental procedure, suppose that one would like to investigate the possibility of anticipatory behavior in a plant species, *P*. Prior to designing and running an experiment in the lab, one should observe and/or collect information about how *P* lives in its natural environment. Doing this might entail learning about local competitor plant species, the specifics of the resources being competed for (e.g., nutrient sources, pollinators), *P*'s local herbivores, the predators of *P*'s local herbivores, the timescales and ecological periodicities at which various fitness- and survival-relevant biotic and abiotic

⁷ The introduction of confounds is often argued to be a reason for preferring controllable and easily manipulable simple experimental variables over the kinds of variables that are found in the model organism's natural environment (cf. Kingstone et al. 2008). PDH, as I see it, attempts to find a middle ground, suggesting that *some* ecological variables should be introduced, but not in abundance.

⁸ Another potentially interesting option consistent with this procedure that was suggested to me by Chris Reid (pers. comm., 2023) may be to utilize mesocosm experiments that are halfway between in situ and ex situ setups.

environmental events occur for P , and any regular patterns (correlational or causal) between contiguous environmental events on which P 's survival depends. Some of these characteristics will influence the construction of the hypothesis (H), ecologically constraining it: (H) *Species P engages in an anticipatory defense response that is guided by the presence of a volatile chemical cue, C , in the soil, which is produced by nematodes that prey on P -damaging herbivores.* Moreover, some of the observed environmental characteristics will determine how the notion of anticipatory behavior is operationalized (O), and those select features which do that will be partly dependent on the kind of anticipatory response that features in the hypothesis: (O) *If P regularly produces higher amounts of defense hormones upon detection of C than without C , and if the C -elicited response occurs prior to the onset of herbivore attack, then H can be supported.* This kind of procedure that is premised on PDH does not guarantee anything in terms of results; it is only by carrying out the experiment that progress can be made with respect to the adjudicating status of a hypothesis. Moreover, it is an additional, theoretical step to justifiably interpret this kind of anticipatory behavior as being cognitively driven. What this procedure does do, however, is bring the hypothesis, its operationalization, and the chosen experimental variables closer to some of the meaningful aspects of the model organism's (P 's) *ecologic*. Interestingly, that something like H can be accepted is supported by the results of an experiment by Helms et al. (2019) on the priming of herbivory defenses in the potato plant (*Solanum tuberosum*) against the Colorado potato beetle (*Leptinotarsa decemlineata*). Such priming was shown to occur in response to volatile chemical cues given off by nearby *L. decemlineata* that had been preyed on by entomopathogenic nematodes.

With this rough procedure and PDH to hand, let us now examine some programs from primarily human-focused cognitive science and psychology that share with PDH an emphasis on methodological holism. Focusing on these programs will provide an opportunity to understand how such holism has featured specifically in efforts to investigate cognition. Moreover, the presence of such programs, I will argue, exemplifies a need that has been acknowledged on separate occasions in the mind sciences for a holistic approach that complements the analytic methodology that reductionist approaches emphasize.

3. Some holistic programs in psychology and cognitive science

The kind of methodological holism that PDH urges is not new to human-based cognitive science or psychology (cf. Hurley 2001). One instance of such a holistic program is gestalt psychology (Koffka 1935; Wertheimer 1938; Köhler 1959). Roughly, the gestalt approach to human perception and understanding viewed these as processes in which the whole configurations (*Gestalten* in German) are perceived and understood as opposed to the component parts of the whole. For instance, components “of molar perceptual units often have characteristics which they do not exhibit when separated from those units” (Köhler 1959, 729, emphasis added). Moreover, gestalt psychologists were committed to the idea that perception is a context-sensitive phenomenon in that what one perceives is often (or always) influenced by one's motivations. As such, human perception and understanding cannot be investigated in the absence of investigating the contexts (e.g., motivation) that influence perception. If motivation is thus typically related to the perceiver's

own condition and/or what kind of environmental characteristics are influencing the perceiver's motivation (i.e., object valence), then, according to this program, perception and understanding cannot be investigated without holistically considering these latter characteristics.

We may see a similar holistic approach toward investigating perception and action espoused by proponents of *ecological psychology* (Gibson 1979). A central feature of the ecological approach is the theory of affordances. These are described as perceivable relational properties that are dependent on the environmental layout in addition to the morphological and physiological characteristics of the organism and its capacities (i.e., acquired skills) (Gibson 1979; Heft 1989). Affordances are said to reflect a history of organism–environment interaction in the sense that the affordances that are available to a certain organism are dependent on its sensory system and body having been tuned to the structure of the environment over evolutionary timescales. To investigate perception, according to ecological psychology, one must investigate the role that affordances play in guiding behavior, and doing so cannot be accomplished without taking environmental structure into account. Such investigation typically involves operationalizing and measuring affordances (Warren 1984; Cornus, Montagne, and Laurent 1999; Almeida et al. 2019).⁹

A last example of another holistic program is *embedded cognitive science* (Kirsh and Maglio 1994; Hutchins 1995; Ballard, Hayhoe, and Pelz 1995; Clark 2008; Gaschler et al. 2013). This research program is based on the central tenet that cognitive processes often involve a continuous and dynamic exchange between brain, body, and environment (Clark 2008). As such, investigating cognition, it is argued, requires methods and analysis that take into account how environments are both fluidly structured and used by agents as cognitive processes unfold (Clark 2008). Understanding both how and when agents structure their environments, in addition to how the cognitive load demanded of a particular task is offloaded onto the environment as a result of such structuring, is viewed as a primary explanatory goal for embedded cognitive science. Empirical investigation prompted by this research program has typically been directed at understanding the role that environmental structuring plays in specific exercises of cognition, such as spatial navigation, problem solving, memory, and learning (see, e.g., Kirsh and Maglio 1994; Ballard, Hayhoe, and Pelz 1995; Gaschler et al. 2013). Moreover, special attention is given to how the kinds of dynamic organism–environment interactions that underwrite cognitive offloading evolve with the occurrence of such interactions. Like gestalt psychology and ecological psychology, embedded cognition takes a holistic approach in which investigating cognition is merely shorthand for investigating a cognitive process in an environmental context, the latter both constraining and contributing to the former.

PDH, like all these holistic programs, is a methodological antireductionist approach to cognition. Methodological antireductionism with respect to cognition can be understood as the general position that cognitive processes cannot be fruitfully investigated and hence adequately explained by focusing exclusively on the

⁹ Strictly speaking, although ecological psychology is an example of a holistic approach that has focused primarily on human perception and action, some notable exceptions have focused on the active perception of plants (Calvo et al. 2020).

properties of the component parts of such processes (e.g., the patterned activity of neurons and neuromodulators) and/or in settings that are far removed from the kinds of natural settings and conditions in which such processes typically arise. To be sure, ecological psychology is committed to more than a methodological antireductionist (i.e., holist) stance. It adopts a stronger *ontological antireductionist* position, holding that active perception is constitutively more than the processes and parts that are bounded by the brain or central nervous system. An *ontological antireductionist* position has also been adopted by some proponents of the embedded cognition program (e.g., Clark and Chalmers 1998). However, because ontology and methodology come apart (Gilbert and Sarkar 2000), one can be committed to PDH as a methodological antireductionist principle for cognitive explanation and remain agnostic toward the ontological status of cognitive phenomena. It is perfectly consistent, for example, for one to hold that the most fruitful manner of investigating an instance of cognition that has hitherto gone unexplored requires understanding the environmental context without committing oneself to the position that the form of cognition being investigated is ontologically constituted by the causally influencing and/or eliciting environment.

Do the cumulative results of these antireductionist programs in cognitive science and psychology suggest that a holistic approach to investigating human cognition is indeed more fruitful than a “ruthless reductionist” (Bickle 2006) approach? Perhaps. Without needing to commit to answering one way or another, one can admit this: that a number of programs and frameworks have on separate occasions seen the need for a holistic methodology in human-focused mind sciences does suggest that at least some cognitive scientists and psychologists have been dissatisfied with reductionist explanations, and this is most likely because some have seen such reductionist methods as failing to tease out and provide explanations of some very important aspects of cognitive phenomena in humans (Hurley 2001). This, as methodological holism would have it, is due to a continued practice of denying the impact that ecological variables have on whether and how cognition is expressed in behavior—something that Broadbent (1991) criticized as being “pathological” science. If there is value to these primarily human-focused holistic research programs, something that their presence, continued influence on contemporary mind science frameworks (cf. Favela 2020), and longevity reveal, then there is no reason to think that such a holistic approach is limited to human-focused (or animal-focused, for that matter) ways to investigate cognition. Thus, by the same merit, a holistic approach to investigating cognition in nonneuronal organisms should also be of value. As such, the kind of methodological holism that PDH urges should be welcome and viewed as equally valuable in attempting to tease out cognitively driven behavior in nonneuronal organisms.

In the next section, I take a different approach to arguing for the importance of using PDH. In contrast to looking to how holism has featured in the human-focused mind sciences to support the value of using PDH, I shall look at how a dynamic and holistic approach to method has led to progress in identifying and/or offering explanations for developmental phenomena in biology, phenomena that would have otherwise remained unaccounted for and/or failed to be recognized as developmental. My aim in doing this is to lay the ground for an argument from analogy.

4. From methodological reductionism to holism in developmental biology

4.1. The route to developmental holism

Around the middle of the twentieth century, the idea that genes provide complete phenotypic instructions for development became the prominent view of mainstream developmental biology (Gilbert and Sarkar 2000).¹⁰ In the 1960s, this view was couched in terms of a self-contained “genetic programme” (Minelli 2021). Accordingly, all that is required to explain development is to investigate gene sequences that encode the phenotype. The environment, on the other hand, was viewed as being a mere background (or noise) against which development unfolded according to the genetic program. This genetic reductionist view was largely influenced by foundational studies in genetics, the methods of which held both environmental and genomic conditions constant while observing the phenotypic effects of variant DNA sequences (Neumann-Held 2006). As Sultan (2015) noted, the reasoning behind this kind of method (i.e., inferring that allelic variation is the only determinate of phenotypic change by way of exclusively observing allelic variation) is circular at best. Despite this circularity, the genetic reductionist approach to development took hold and maintained its status as the prevailing model among mainstream developmental biologists up until the latter half of the twentieth century and still has a persisting influence.

Genetic (methodological) reductionism was met with and directly challenged by *developmental holism*, often referred to as *organicism*.¹¹ This approach recognized the role of genetic information as constraining development but also emphasized the need to investigate development as a dynamic regulatory process that always—at least in natural, “real-life” settings—occurs in the context of an organism embedded in an environment (von Bertalanffy 1952/2014). Building from the experimental embryology of Weiss (1955), Lederer et al. (1949), Harrison (1969), and Waddington (1956), developmental holism “was not built bottom-up from theory, it was built top-down from observation” (Gilbert and Sarkar 2000, 4). For example, by investigating exclusively how cells grow and develop in petri dish cultures that have very little to no resemblance to a cell’s cytoplasmic environment, various aspects of embryonic cell development are inaccessible because those aspects are dependent on the presence of factors in a cell’s natural environment (von Bertalanffy 1952/2014; Gilbert and Sarkar 2000). To conclude that a cell fails to engage in some behavior *at all* on the basis of its

¹⁰ This gene-centric turn was not specific to developmental biology; it was also the dominant view of evolutionary biology as the study of evolution became slowly pulled apart from developmental biology over the first half of the twentieth century, under the influence of the newly formulated modern synthesis and the efforts of Mayr from the 1940s onward. See Amundson (2014) for a detailed account of the separation of developmental biology and evolutionary biology and of the rise of the modern synthesis.

¹¹ The use of the term *organicism* is meant to both emphasize the level of the organism as the primary *explanandum* and to distance the holistic developmental (and evolutionary) approach from the “spooky” holism associated with the developmental vitalists of the nineteenth century. For purposes of consistency within this article, I use the term *developmental holism* with the understanding that it is altogether distinct from vitalist explanation.

not behaving as such in a petri dish may be premature and/or inaccurate. Moreover, using this conclusion to support a general explanation about the development of cells carries this inaccuracy over to the general explanation. Be it an intercellular, intracellular, or organismal environment, context matters to how biological systems behave. Holistic developmental biology put the environment back into methodology and explanation (Gilbert and Sarkar 2000; Baedke et al. 2023). Investigating developmental processes involves investigating “developmental systems” (Oyama 2000) that include the dynamic interactions between the genome, the epigenome, and the inducing organismal environment. It is only by taking these interactions into consideration that both robust and flexible, context-sensitive developmental phenomena can be identified as *such*, further investigated, and adequately explained (cf. Newman 2002).

Polyphenism is one phenomenon that both developmental biologists and ecologists have long recognized as requiring a holistic methodological approach. Polyphenism may be characterized as “the presence, in a population, of two or more kinds of individuals, the difference between which depends upon the environmental conditions in which development took place, at least in a critical or sometimes short phase” (Minelli 2021, 138).¹² Such phenomena represent an example of extreme *phenotypic plasticity*—phenotypic change in the absence of nucleotide sequence change (West-Eberhard 2003). For example, whether the migratory locust (*Locusta migratoria*) remains a solitary and inconspicuously colored individual or develops into a gregarious, brightly colored, swarming individual is determined by high locust population density (i.e., whether it encounters few or many other conspecifics within its environment) (Uvarov 1996); whether a high-ranking female goby of the species *Trimma okinawae* remains female or develops into the dominant male of the school is determined by the death of the dominant male (Sunobe et al. 2010). Moreover, whether the at one time *T. okinawae* female will revert from male to female again depends on whether a stronger dominant male is introduced to the same school, whether an American alligator (*Alligator mississippiensis*) develops into a female or a male is determined by the temperature at which the eggs are incubated (Ferguson and Joanen 1982), and whether a honeybee larva develops into a queen or a worker is determined by whether it is fed royal jelly at the larval stage (Slater, Yocum, and Bowsher 2020). Examples of polyphenism abound in the biological world and illustrate the importance of taking a holistic methodological approach. When using a purely genetic reductionist approach, polyphenism cannot be explained. Moreover, what goes for polyphenism also goes for other forms of phenotypic plasticity that contribute to development. In other words, “no phenotype is such that only genes are

¹² Evidence suggests that this form of plasticity is underwritten by epigenetic mechanisms (Sultan 2015; Yang and Pospisilik 2019). These mechanisms, some of which include DNA methylation, histone modification, and sRNA interference (Jablonka and Raz 2009), mediate phenotypic changes by acting as transcriptional regulators, either preventing or allowing the binding of transcription factors and RNA polymerase to DNA promoter regions and intergenic sites, respectively inhibiting or activating gene transcription. Because they can be environmentally induced, epigenetic effects on gene expression straightforwardly illustrate that developmental explanation requires investigating not only the role of genetic information but regulatory activity at the level of the genome and epigenome and the inducing environment.

needed for its development in the sense that they could, like Japanese flowers, be dropped into water and open up” (Bateson and Gluckman 2011, 12).

Developmental biology today is at the point where development is being approached by way of both genetic investigation and environmental investigation (Gilbert and Sarkar 2000, 7). This developmental holism, part and parcel of *evo-devo*, examines how genetic regulatory networks and the environment interact over both ontogenetic and phylogenetic timescales, in addition to the epigenetic mechanisms mediating such dynamic “bottom-up” and “top-down” interactions.

4.2. *An argument from analogy: What developmental biology teaches us*

By taking a holistic approach, developmental biologists have been able to offer explanations for phenomena that would have otherwise been difficult (if not impossible) to account for and/or identify when using genetic reductionist methods alone. Polyphenism, as we have seen, is one such example. I would like to argue that much like the explanatory progress that has accompanied deploying a holistic approach in developmental biology, a methodological holistic approach to cognitive explanation may also reveal facets of cognitive phenomena that would otherwise be difficult to explain and/or identify—particularly in the case of nonneuronal organisms. Why might a holistic approach be expected to benefit the investigation of nonneuronal cognition like it has benefited developmental biology?

Assuming that both development and cognition qua biological processes “always have the character of processes determined within a dynamic system” (von Bertalanffy 1952/2014, 18), investigating cognition, like investigating development, requires a dynamic and holistic methodological approach. To be sure, because we can infer many of the contextual factors that would drive intelligent behavior in organisms that are more similar to us than not, but because such contextual inferences are more likely to fail the further away an organism is phylogenetically from us, a holistic approach is crucial to being able to identify and access potential exhibitions of cognitively driven behavior in nonneuronal organisms on the basis of phylogenetic distance alone. Given the analogous natures of development and cognition as flexible and context-sensitive biological processes, if taking a holistic developmental approach has been crucial for revealing and explaining environmentally induced phenotypic changes like polyphenism, then we should also expect that deploying PDH (or something very much like it) can go a long way in helping to reveal facets of cognition that would otherwise be difficult to explain and/or identify in nonneuronal organisms.

5. The value PDH: Two examples from experimental studies in biology

One way of illustrating the value of deploying a methodological principle is to show what goes wrong when that principle is flouted. In this penultimate section, I proceed by looking at two biological experiments that provide an opportunity to understand two respective risks in flouting PDH, namely, the risk of an experiment failing to elicit any cognitively driven behavior *whatsoever* and the risk of eliciting a cognitively driven behavior but failing to recognize important and nuanced aspects of that behavior.

5.1. Experiment 1: Tracking motile algae with marine bacteria

Barbara and Mitchell's (2003) investigation of the ability of marine bacteria *Pseudoalteromonas haloplanktis* and *Shewanella putrefaciens* to track motile algae *Pavlova lutheri* provides a first experiment on which to elaborate for the purposes of illustrating the value of PDH. This experiment was based on the previous observation that marine bacterial chemotaxis in oligotrophic (i.e., nutrient-impoverished) environments sometimes displays features that are distinct from the form of chemotaxis found in terrestrial and/or enteric bacteria (e.g., *E. coli*). The latter form of chemotaxis is based on a bacterium differentially detecting nutrient gradients in the surrounding medium and modulating its *run-tumble* behavior accordingly; detection of a nutrient concentration increase is followed by a decrease in the frequency of swimming in random directions (i.e., "tumbling") and an increase in the frequency of swimming in a straight line (i.e., "running"); detection of a decrease in gradient concentration is followed by a higher frequency of tumbling and diminished running. In addition to being able to engage in run-tumble chemotaxis, both *P. haloplanktis* and *S. putrefaciens* appear to be able to track nutrient-providing *P. lutheri* as these golden brown algae swim through open water, something that requires a more nuanced and controlled type of chemotactic behavior.

To understand the nature of this tracking chemotaxis, Barbara and Mitchell (2003) placed *P. lutheri* together with either *P. haloplanktis* or *S. putrefaciens* in the same one-millimeter-deep microscope slide chamber and recorded the swimming trajectories that ensued. Analyses across two spatial (x,y) dimensions in addition to analyses of running speed changes showed that both types of marine bacteria track the motile algae by using a "run-reverse strategy which enables them to reverse direction after each stop instead of randomly tumbling, allowing them to react faster to chemical gradients" (83). The results of this carefully designed experiment uncovered the striking ability of both types of marine bacteria to track moving *P. lutheri* by sampling algal exudate gradients and using these gradient values as cues to modulate their swimming speed and steering direction accordingly.¹³

Although the authors of this study did not consider the cognitive status of the kind of complex bacterial behavior that they reported (and nor was it the aim of their study to do so), the tracking ability of both *P. haloplanktis* and *S. putrefaciens* as identified by Barbara and Mitchell (2003) seems to rely on capacities of sensing, learning, memory, and the influence of a context-sensitive behavioral control mechanism. On the basis of these capacities and characteristics, if we assume that this kind of run-reverse chemotactic tracking represents a behavior worth investigating as a form of cognition—something that some researchers might easily concede, given their chosen minimum requirements on cognition (see van Duijn, Keijzer, and Franken 2006; Bechtel and Bich 2021; Keijzer 2021)—we may reason as follows to a potential risk of flouting PDH: if the behavior of either *P. haloplanktis* or *S. putrefaciens* is experimentally investigated in the absence of *P. lutheri*, then their complex run-reverse behavior will not be elicited; given that *P. lutheri* is a regular part of the

¹³ Simulations, however, have suggested that this tracking may not be the result of active steering behavior but can also be explained by hydrodynamic effects due to the algal cell's velocity, vorticity, and strain rate fields (Locsei and Pedley 2008). Further investigation is needed to rule out the latter explanation.

oligotrophic environment in which both marine bacteria live and thus represents a survival-relevant ecological variable, if this ecological variable is absent from the experiment, then the complex run-reverse behavior will fail to be elicited. Hence, without incorporating this particular ecological variable into the experiment, a latent cognitively driven behavior would fail to be elicited. Without considering the ecological variables of the organism's environment and incorporating the most relevant of them (in this case, the motile algae) into the hypothesis and related experiment, there is a risk of failing to elicit a latent cognitive behavior and thus moving too quickly to the conclusion that such a cognitive behavior is altogether absent.

To be sure, not being able to elicit a cognitive behavior could mean that a type of organism fails to possess any such capacity. PDH, however, reminds us that it would be premature to draw such a conclusion without observing the organism interacting within its established niche and identifying possible ecological variables that might elicit cognitively driven behavior (cf. Kingstone, Smilek, and Eastwood 2008). Despite that Barbara and Mitchell's (2003) experiment was not aimed at uncovering cognitively driven behavior, its design nonetheless provides a clear example of how the same core methodological considerations that PDH emphasizes can be used to constrain empirical investigation and successfully tease out behavior that might otherwise remain suppressed.

5.2. Experiment 2: Navigational decision-making and yeast farming in acellular slime mold

Comparing the methods and results of experiments by Reid et al. (2012) and Epstein et al. (2021) on acellular slime mold *Physarum polycephalum* provides a further opportunity to illustrate the value of deploying PDH. Although the results of Reid et al. (2012) provide insights into *P. polycephalum*'s behavior that are in and of themselves valuable, the holistic approach Epstein et al.'s experiment deployed sheds light on a very important complementary dimension of this non-neuronal organism's decision-making capacities—capacities that would have otherwise gone unnoticed had a holistic approach not been used.

Deploying the auxiliary hypothesis that *P. polycephalum* tends to avoid its own (and others') extracellular slime trails, Reid et al. (2012) devised an experiment to test whether such extracellular slime avoidance might allow *P. polycephalum* to avoid revisiting previously forged locations. To test this, the researchers placed this unicellular multinucleate amoeboid on plated agar petri dishes. Experimental dishes were covered with extracellular slime (a nonliving mucus lining that is produced as *P. polycephalum* migrates across surfaces), whereas control dishes were not. Each dish also contained a U-shaped barrier that separated the *P. polycephalum* and a nutrient source (i.e., a defusing glucose solution). Reid et al. reasoned that the slime layer covering the agar surface of the experimental plates would hamper *P. polycephalum*'s ability to use its own extracellular slime to navigate out of the U-shaped barrier toward the glucose source. Measuring the length of time that *P. polycephalum* took to escape the barrier and reach the source, these researchers found that the *P. polycephalum* on the experimental plates took a considerably longer amount of time to reach the glucose source than did the *P. polycephalum* on the control plates. These

striking results provide compelling evidence in support of the hypothesis that *P. polycephalum* uses its extracellular slime as external navigational memory to avoid revisiting previously forged locations.

Observations by Briard et al. (2020) have, however, suggested that *P. polycephalum*'s behavioral interaction with extracellular slime is not as simple as the auxiliary hypothesis would have it seem. These researchers demonstrated that *P. polycephalum* in fact avoids biochemical cues diffuse in the substrate and presumably present in extracellular slime that has been produced by other conspecifics when those conspecifics have undergone stress (starvation); slime trails, on the other hand, left by nonstressed (well-nourished) *P. polycephalum* are not avoided but, instead, can act as attractants given the cues they contain. Taking both Reid et al.'s (2012) and Briard et al.'s (2020) results into consideration, Epstein et al. (2021) formulated a novel hypothesis based on the following observations and considerations: *P. polycephalum*, as it migrates across surfaces in the wild, regularly preys on red yeast (and other microorganisms); the extracellular slime deposited at those sites at which it has consumed more red yeast tends to be more attractive to it than the slime at other sites where it or its conspecifics consumed no nutrients—the condition of the extracellular slime at the former sites chemically reflecting the well-nourished state of the *P. polycephalum* that produced it. If the deposited extracellular slime also provides a source of nutrients for a subsequent colony of growing red yeast, and if they do not consume all the slime, then the site of slime deposition might attract the *P. polycephalum* back to the newly grown yeast. As such, Epstein et al. hypothesized that “*P. polycephalum* is capable of exhibiting a sustainable feeding strategy by depositing a nutritive slime trail, allowing yeast to serve as a periodic food source” (1). In other words, the ecological relationship between *P. polycephalum* and red yeast may represent an example of oscillatory successional dynamics.

Using advanced image technology to capture the population dynamics between *P. polycephalum* and red yeast that were introduced to the same dishes, Epstein et al. (2021) were able to detect an inverse growth relationship between the two organisms, suggesting a predator–prey relationship and, indeed, oscillatory successional dynamics.¹⁴ At first blush, this result may not strike one as relevant to the expression of any cognitive capacity. However, I argue that this would be too fast. First, it should be noted that these results are consistent with Reid et al.'s (2012) hypothesis that *P. polycephalum* uses its extracellular slime trails as a form of external navigational memory. These results and those of Briard et al. (2020), however, complicate the picture in showing that slime trails are not merely cues for avoidance navigation; depending on the condition of the *P. polycephalum* that deposited the trail and hence the chemical makeup of the trail, they can also be attractants. Epstein et al.'s (2021) results may suggest that what makes the extracellular slime an attractant *later* may be the presence of microorganisms that are more likely to grow

¹⁴ It should be noted that Epstein et al.'s (2021) statistical analysis was based on growth patterns in only five dishes (ecosystems) and that each of the five dishes was exposed to different (blue) light treatments. Because each of the five conditions was not replicated, it is impossible to infer whether the oscillatory successional dynamics observed is a generalizable and robust feature of such ecosystems. Future replication of this experimental paradigm with a significantly larger sample size of each ecosystem condition is required.

on slime that was produced by a less-stressed *P. polycephalum*.¹⁵ The question arises, however, as to where and when a *P. polycephalum* should migrate in a given area to optimize the number of consumable microorganisms that grow on its extracellular slime later. This is a decision-making problem, and some support as to what kind of decision *P. polycephalum* is making can be gleaned from Epstein et al. (2021, 9):

We speculate that as *P. polycephalum* navigates its environment it occupies specific regions of a morphospace so that it may build a spatiotemporally optimal slime sheath to farm the most microorganisms.

If Epstein et al. are correct, *P. polycephalum* exercises control over where and when it migrates, allowing the most microorganisms to grow on the extracellular slime prior to continued feeding. This kind of navigational control is underwritten by making choices regarding behavior that (nonexhaustively) balance potential metabolic costs and benefits with current physiological costs and benefits. Epstein et al.'s interpretation of *P. polycephalum*'s behavior as farming rests on the idea of the cell making spatiotemporally based decisions that allow for an “optimal” yield—waiting for the red yeast to grow to a cover a sizable area as opposed to consuming any and all yeast despite how few they are.¹⁶ However, from the perspective of Reid et al.'s (2012) results and the hypothesis that their results support, navigational decisions for optimal foraging are made primarily on the basis of the spatial distribution of extracellular slime. When considered in light of the results of Epstein and colleagues' (2021) experiment—results they obtained, I suggest, by implicitly deploying something like PDH—Reid et al.'s (2012) explanation is accurate but may be also incomplete: it stops short of capturing important aspects of the kind of nuanced decision-making that drives *P. polycephalum*'s navigational behavior. The importance of using PDH-guided investigation to complement experiments from which the kind of ecological variables found in an organism's niche are abstracted away is made explicit when considering the difficulty of inferring the complex kind of navigational decision-making that occurs in Epstein et al.'s (2021) experiment strictly from the kind of externalized navigational memory use that is supported by Reid et al.'s (2012) experiment.

6. Conclusion

In this article, I have presented and argued for the methodological PDH. This principle serves the function to steer the investigation of nonneuronal cognition in a way that is aimed at circumventing anthropocentric (or zoocentric) assumptions. Empirically investigating potential cognitive capacities in nonneuronal organisms, however, will ultimately be very different than investigating cognition in brained animals, if only because the forms of environmental heterogeneity to which nonneuronal organisms

¹⁵ This is consistent with the results of a follow-up study by Reid et al. (2013) that showed that *Physarum polycephalum* can override their aversion to extracellular slime if traversing slime allows them to reach a high-quality food source.

¹⁶ The oscillatory growth dynamics captured more prominently in the experimental ecosystems 3a and 3b (and less so in 3c–3e) reflect some delay in eating red yeast while yeasts are repopulating and may possibly represent a delayed reward strategy.

are sensitive and which they must accommodate may be very different from our own. Be that as it may, such differences do not rule out the possibility of fruitfully investigating cognitively driven behavior in basal organisms. This much should be made clear by at least a century of groundbreaking experiments in biology that have edged us closer to understanding some of the various forms that cognition takes and their underlying mechanisms. However, to advance our understanding of non-neuronal cognition and its evolution even further, the role of ecological variables in eliciting potential cognitively driven behavior must be not only acknowledged but rather incorporated into the foundations of a (basal) methodology.

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