

The Psychophysical World of the Motile Diatom *Bacillaria paradoxa*

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Abstract

There are a large number of candidate hypotheses for the movement of diatoms, a taxonomic group of Algae. In particular, the genus *Bacillaria* exhibits highly interesting movement dynamics resembling a number of physical systems. None of these hypotheses account for the information processing that might result from the connection between environmental stimuli (e.g. photic, chemical, turbulence, and temperature gradients, and mechanical constraints) and motility. Even when there is no significant variation in terms of sensory input, the colonial structure is coordinated and mediated through information processing. Here, we propose a series of perspectives on how the concept of aneural cognition might explain the movement dynamics of individual colonies. More specifically, we can use analogies of neuronal mechanisms such as Collective Pattern Generators, Hebbian Learning, and predictive processing to understand and explore the potential for behavior generation. Quantitatively, these mechanisms can be summarized using psychophysical metrics, particularly the Weber-Fechner law. This analogy could be extended to out-of-equilibrium behaviors such as halting of oscillatory movement patterns, and further interpretations in terms of pseudo-intelligent behavior, which is simulated but not necessarily autonomous. Taken together, we can say that the psychophysical world can open up new avenues of exploration for understanding the regulation of diatom movement.

Introduction

In the study of organismal behavior from across the tree of life, there are traditionally two types of explanatory mechanism. The first is behavior that is generated by neuronal processes (such as a network of neurons), and is restricted to organisms with a nervous system. The second is behavior that is characterized by loosely-relevant physical, mechanical, and social metaphors and generated by biophysical processes, including at the single cell level (Schenz, 2019; Gershman, 2021; Brette, 2021). The biophysics of individual cell motility applied in parallel is assumed to be the primary explanatory paradigm. Yet there is an alternative explanatory framework that allows us to view *Bacillaria* movement as a holistic, colony-level phenomenon: aneural cognition (Drum et.al, 1971; Baluska and Levin, 2016; Boisseau et.al, 2016; Vogel and Dussutour,

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2016; Sims and Kiverstein, 2021) and the possibility of light piping between cells (Drum, 2003). While *Bacillaria paradoxa* has been divided into a few species (Jahn, 2007; Schmid, 2007), we continue to use *B. paradoxa* as including all of them. This framework ascribes information processing and decision-making capabilities to systems that lack a formal nervous system structure. Rather, the information processing function occurs in the biophysical substrate itself. One definition of cognition is as an ill-defined cluster of capacities and mental (or psychophysical) phenomena (Nosofsky, 1992; Ramsey, 2017). While aneural cognition can benefit from a representational structure in the form of neural codes (Nover et.al, 2005) and other such higher-dimensional pattern generators (Kriegeskorte and Kievit, 2013), this does not need to be a part of a cognitive system.

While the diatom genus *Bacillaria* does not have a nervous system, it nevertheless exhibits organized behaviors and collective movement. *Bacillaria* consists of a series of long, narrow cells arrayed in parallel, and the behaviors exhibited across these filaments are temporally linked in a way that results in coordinated movement (Gordon, 2016). *Bacillaria* cells can exhibit coordinated behavior by forming a colony that oscillates from one end of the colony to another. The contraction and expansion movements resemble the contractile motion of an accordion (see Figure 1). One interpretation involves using a multitude of existing mechanical and physical metaphors to interpret *Bacillaria* movement (Gordon, 2021). As an alternative view, we propose a model of minimal cognition (van Duijn et.al, 2006) defined by the relationship between stimulus intensity and adaptive movement can be used instead. This model of cognition results in the production of behaviors related to taxis (Cohn, 2001), active materials (McGivern, 2020), and even psychophysics (Reina et.al, 2018), which can be distinguished from random behavior by separating an informational signal from noise.

Aneural cognition provides a context for diatom movement behaviors, particularly in response to environmental stimuli. Taking a broader view of diatom morphology, most diatoms are single-celled organisms that live in either a solitary or colonial context. Diatoms are eukaryotic algae that have chlorophyll and silicate cell walls (Frazer, 2012). In either the solitary or colonial setting, the cell cytoplasm and extracellular components are all important for facilitating a diatom's movement and other interactions with the environment (Gordon, 2021). In general, there are three types of diatom morphology: rod, flake, and three-dimensional shape. The raphid phenotype (which includes *Bacillaria*) is around 300-500 μ m long and typically 10 μ m wide (Frazer, 2012). *Bacillaria* colonies in particular are held together by secreted polymers that enable extracellular adhesion and selective interactions with the external environment (Chen et.al, 2019). A similar kind of externalization is also observed in slime mold colonies (Sims and

Kiverstein, 2021). The morphology of a *Bacillaria* cell chain and moving colony are shown in Figures 1A and 1B, respectively.

Ecologically, *Bacillaria* is native to estuary, littoral, and riverine environments. These aquatic environments provide three main perceptual challenges to the organism. The first involves changes in water chemistry as the colony moves through the water column. Attraction or repulsion from different chemical gradients (e.g. salinity or acidity) comes in the form of chemotaxis. Movement of cells through the water column (see examples in Figure 1) also introduces them to light and chemical gradients. These gradients can affect the mode of movement, the size of individual cells, and overall colonial size (Svensson et.al, 2014). Encountering light gradients specifically leads to phototaxis, which can be positive (attractive) or negative (repulsive). In a like manner, chemical gradients lead to chemotaxis, and a combination of the two can lead to more complex movement behaviors. Cell movement over broader spatial scales introduces *Bacillaria* cells to temperature gradient exploration, which requires thermotaxis. If buried in benthic sediments, their movements may allow extrication towards sunlight. These three types of simple response allow us to move towards a model of aneural cognition that characterizes trends in these behaviors.

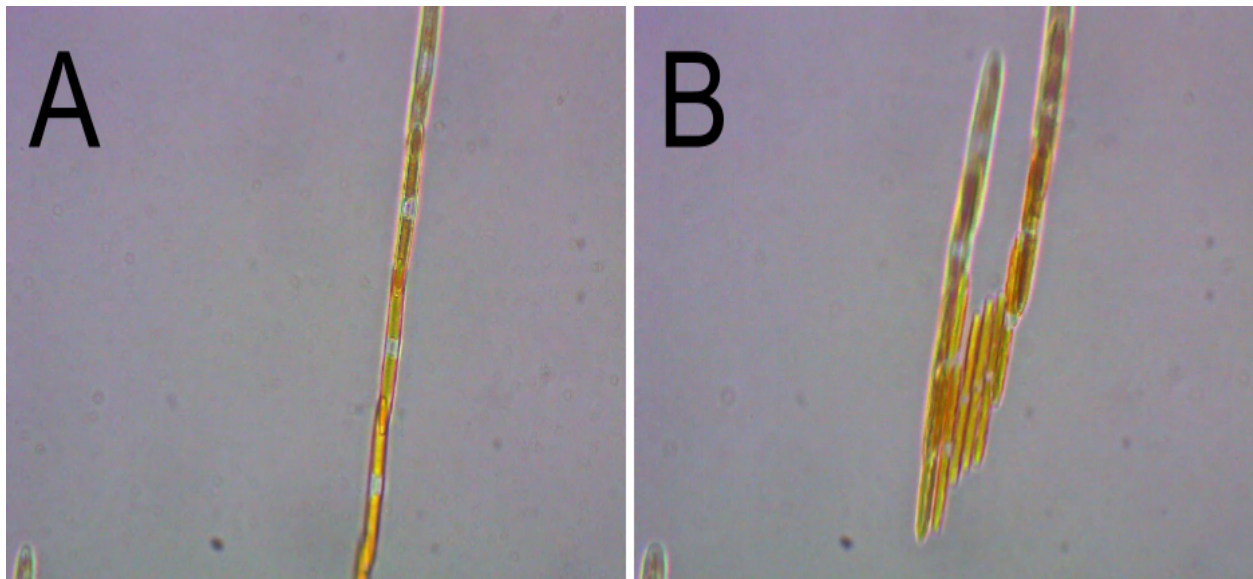


Figure 1. An image of the *Bacillaria* colony, captured in its elongated (A) and contractile (B) state. Thanks to Dr. Thomas Harbich. See also Kapinga (1987), Kapinga (1989), and Kapinga (1992). There are many online movies of *Bacillaria* movement at many magnifications.

The diatom cell and life cycles are also an important part of any adaptive behaviors and aneural cognition. Diatom cell division occurs in a manner different from

other eukaryotes, and plays a role in shaping the relationship between cell cycle checkpoint and changes in physiological processes (Huysman et.al, 2014). In general, diatom molecular processes play a key role in the perception of environmental stimuli and regulation of associated physiological processes (Falciatore and Bowler, 2002). The life cycle of a diatom (Edlund and Stoermer, 1993; Edlund and Stoermer, 1997; Amato et.al, 2005) operates at a longer time scale, but is also affected by environmental factors such as changes in the local concentrations of phosphate, iron, and dissolved silicon (Huysman et.al, 2014). Overall, variation of the life-cycle is nonlinear and high-dimensional (Sanchez et.al, 2019). Returning to the effects of environmental stimuli, light not only results in reactive taxis, but can also trigger specific acclimation-specific physiological responses. Light variation is also a feature of day-night cycles (Harbich 2021) and relative position in the water column. More generally, response to environmental conditions (sensing and signaling) are tightly linked to cell cycle checkpoint activation (Huysman et.al, 2014). This not only means that environmental factors affect simple output behaviors, but often affect organismal-level features such as transformations in shape, growth, and surface texture (Sarhou et.al, 2005; Sanchez et.al, 2019).

We will now consider the aneural cognition and adaptive behavioral generation of *Bacillaria*. This will proceed by reviewing evidence for aneural cognition in a diverse range of species. Then, we introduce a formulation of psychophysics that is relevant to aneural cognition, particularly in the *Bacillaria* example. This will include considering the ways in which adaptive behavior can be generated in a cognitive system, including theories of neural function such as Hebbian learning and predictive processing. We will then consider whether or not aneural cognition is an epiphenomenon, followed by a review of potential measurement techniques. These include both singular equations that produce characteristic functions and networks that advance a connectionist approach to characterizing behavior (Hanson and Burr, 1990). To conclude, we discuss modeling the dynamical systems complexity of *Bacillaria* psychophysics, and further describe this model through the application of Collective Pattern Generators (CoPGs).

Aneural Architecture of *Bacillaria*

In this section, we will introduce the aneural architecture of *Bacillaria*. This architecture generates behaviors from colony physiology. This includes both intracellular microstructural elements proposed to be involved in motility and extracellular polymers (Poulsen et.al, 1999). The *Bacillaria* behavior-generation system features three architectural properties that define the coherent collective behavior of a colony. *Bacillaria* cells can respond to changes in light, water salinity, and temperature, but must regulate their response in accordance with the states of neighboring cells. This regulation and interdependence can occur in two ways. The first is that individual cells

secrete polymers that both encase the cell and act as sites of adhesion (Baluska and Levin, 2016). Secondly, an extracellular space that acts as both a site of stigmergy and a memory medium (Chen et.al, 2019). Stigmergy is an important concept that is usually applied to the collective behavior of insects (Heylighen, 2016; Oberst et.al, 2020). It is a type of collective behavior that uses various features of the environment to guide autonomous behavior. When we talk about aneural cognition, stigmergy works in concert with physiological mechanisms to produce an output that supersedes what single cells can achieve on its own (Kuyucu et.al, 2015).

From this behavior-generating architecture, there are several behavioral outcomes that provide a means for adaptive behavior. As we will see, these can take the form of potentially goal-directed or even intelligent behaviors. There are three such behaviors that can be observed among *Bacillaria*. 1) While *Bacillaria* colonies have no formal representation of space, they do exhibit limited goal-directed behavior. Behaviors are explicitly spatial in that multicellular chains move in certain directions (not simply via Brownian motion). 2) According to Graziano (2009), movement is a source of intelligence. Simple movements, even of *Bacillaria* single cells attached to a killed neighboring cell, produce a set of rounded square waves (Drum et.al, 1971). A single cell being able to identify and track the simple movements of neighboring cells and other organisms is consistent with the processing of direct perceptual information (Warren, 2005). 3) More complicated movement can result in other types of waveforms and augment the processing of direct perceptual information, and results in a basic oscillatory rhythm. For example, a colony (chain) of cells produces an oscillator lagged n degrees out-of-phase.

Viewing *Bacillaria* movement in this way provides an alternative to purely biophysical models of movement. While biophysics is the dominant mechanism for generating movement, the same can also be said for cognition in the brain. Neural cognition is generated by biophysical processes, and produces information that then translates into what is considered to be cognition. Our aneural perspective allows us to bridge the gap between purely biophysical models and analogies of cognition. Biophysical models also do not provide a means to characterize the diverse behaviors often observed across different life-history stages and environmental contexts. Furthermore, there are many interpretations of these behaviors that involve information processing and specific functional capacities. An aneural cognition model provides a potential means for understanding all of this diversity.

Aneural cognition in a broader context

Observations of so-called psychic life in single cell organisms was initially proposed by Binet (1888), while Verworn (1889) first proposed the psychophysiological

study of protists around the same time. At the time, the amoeba was thought to be an evolutionary linchpin that connected the behaviors of single-cell organisms with that of humans (Reynolds, 2008), cognitive capacity being no exception. A persistent series of studies on psychophysiology in unicellular organisms continued throughout the late 19th and early 20th centuries (Schloegel and Schmidgen, 2002). One example of such work involved studying stimulus-driven taxic responses in *Stentor* and *Paramecium* (Jennings, 1899). While this work establishes the existence of simple mechanisms for intelligent behavior, the highly metaphoric and analogical nature of this work obscures its potential to provide insight.

To establish the intentionality and intelligent nature of different behavioral and morphological functions, we can turn to examples ranging from marine invertebrates to synthetic systems. For example, the cnidarian species *Nematostella vectensis* uses a muscular hydrostatic mechanism to link morphogenesis and behavior during the larval stage (Stokkermans et.al, 2021). This requires a tight integration between two biological processes. *Physarum* (slime molds) also demonstrate a form of learning called habituation (Boisseau et.al, 2016). *Physarum* colonies exhibit response decline (weaker effect over time) and spontaneous recovery (responding after a significant period of stimulus deprivation), both of which are hallmarks of habituation. We can further observe the ability to produce intelligent behavior in minimal and non-biological systems. Simple chemical systems such as oil droplet protocells can break their symmetry when exposed to water (Hanczyc and Ikegami, 2010; Hanczyc, 2014). This facilitates movement during the aqueous phase, which may provide clues as to the origins of learned movement. In a synthetic biology context, the interactions between protocells can be characterized using the language of control, cognition, and communication (Bich, 2020).

To gain a broader perspective of what aneural cognition looks like in single-cell organisms both without brains and with simple brains, we can turn to two other model organisms: one being a single-celled organism from another taxonomic order, and the other a larval crustacean with a highly rudimentary nervous system. One such taxon is the genus *Paramecium*. *Paramecium* is able to regulate its swimming movements in an intracellular fashion (Brette, 2021). Another type of adaptive behavior is associative learning (Gershman et.al, 2021) which is controversial yet demonstrable in a single-cell context. Many coordinated collective behaviors can result from the tuning of physical parameters, which has been demonstrated in agent-based models that are analogous to organisms such as the water flea (*Daphnia* - Mach and Schweitzer, 2007). Although *Paramecium* does not have a nervous system and *Daphnia* has a simple brain While in both cases there is a lack of direct mechanisms typically associated with a nervous system, organisms in both groups nevertheless tend to minimize their free energy

resulting in relatively complex behaviors (Friston and Stephan, 2007; Friston et.al, 2021). Free energy is also more directly tied to cognition by enforcing sites of information encapsulation composed of specific networks and populations of cells and the source of cognitive function (Beni, 2022).

As the examples given here are phylogenetically disparate, the question arises as to the evolutionary origins of aneural cognitive mechanisms. The answer comes in two forms: the common ancestry of cell biochemistry and the polyphyly of specific mechanisms in different organisms. For example, both photoreceptors and mechanosensors share a deep molecular homology (Arendt et al., 2004; Fritzsche and Piatigorsky, 2005). As a result, cells that express sensory receptors appear in locations far from the organism's periphery where such cells would normally be found (Arendt et.al, 2004). Furthermore, shared developmental cascades (Fritzsche and Piatigorsky, 2005) produce a wide variety of mechanisms and systems for information processing. Yet many information processing systems involve more than conserved homologs and paralogs. Particularly in single-cell organisms, these systems are often built upon simple anatomical structures reconfigured in different ways. Thus, it is proposed that aneural cognition is of polyphyletic origin, but is built upon structures and system components with a deep shared evolutionary history.

From the perspective of adaptive value, the likelihood of observing aneural cognition in other algae depends upon their environmental context. Sensory accommodation and even rudimentary forms of decision-making are important aspects of dealing with nutrient fluctuations and environmental stresses more generally (Nayaka et al., 2017; Bondoc et al., 2018). For diatoms in general, physiological responses involve a large number of parameters that are dependent on various forms of sensation (Sarhou et al., 2005). For example, the diversity of chemical stimuli encountered in the aquatic environment requires multiple fitness imperatives to be satisfied simultaneously. Changes in *Seminavis robusta* behavior provide an optimal response to both nutrient gradients and reproductive needs (Bondoc, 2018), which implies an internal mechanism for temporal information integration (Lavoie et al., 2008). Among intertidal populations of benthic diatoms, the ability to adapt behaviorally to changes in light intensity is distinct from physiological adaptation to the same (Cartaxana et al., 2011). In *Thalassiosira pseudonana*, the divergent response among temperature-dependent responses evolved from 450 generations of experimental evolution points to a role for evolutionary constraints and tradeoffs in shaping environment-specific information processing (O'Donnell et al., 2018).

We will now revisit the basis for associative learning, habituation, and energy minimization by looking at their natural connections to more formal mathematical

representations such as psychophysics, Hebbian learning, and predictive processing. These explanatory frameworks provide a linkage to the more conventional interpretation of biophysical mechanisms. We will also make the connection between these processes and the concept of minimal cognition (van Duijn et.al, 2006). Minimal cognition that has an effect on behavioral dynamics of the individual and perhaps even natural selection (Godfrey-Smith, 2016). This will be placed in the context of diatoms, who may share a number of information processing properties with systems as diverse as *Physarum* (Boisseau, 2016), *Paramecium* (Brette, 2021), and even protocells (Hanczyc, 2014).

Psychophysics as Diatom Information Processing

Psychophysics is the investigation of the relationship between mental phenomena and physical stimuli, particularly the minimal differences in the variation of a stimulus detectable by a nervous system (Grondin, 2016). Various psychophysical behaviors are observed across a wide range of species, including mice, goldfish, and humans (Stebbins, 1970; Sarris, 2006). While it is hard to demonstrate the mental phenomenology of *Bacillaria* (or of diatoms more generally), the response to physical stimuli has been previously demonstrated in the form of sensitivity to light intensity (Cohn et.al, 2004; Cohn et.al, 2015; Cohn et.al, 2016). In general, diatom cells are photophobic in conditions of high light intensity (Cohn 2004; Cohn 2004b). Cross-species comparative work (Cohn et.al, 2015; Cohn, 2021) reveal multiple details about this phenomenon. In general, multiple parameters can be used to understand the psychophysical properties of diatom information processing.

Several sensory mechanisms are commonly found across diatom species. For example, all species respond to high levels of light negatively by moving away from the light. These movements are similar to phototaxis that are generated by both artificial and simple nervous systems (Rano, 2009; Gorostiza et.al, 2016). There are also characteristic response times for changes in direction due to light exposure despite differences in species-specific optimal light frequencies that can be linked to ecological adaptations (Prins et.al, 2020). There is also evidence of habituation in the duration and direction of how a cell is irradiated. Using a light spot assay, Cohn et.al (2016) exposes the end of diatom cells to a light source, which leads to accumulations of cells in particular spatial locations at a characteristic rate. This rate is species-specific, but in cases where members of different species are in close proximity, this rate can be attenuated.

This research up until now has not been interpreted using a theoretical framework. In this work, a suitable psychophysical model typically describes a systematic response in the form of a mathematical model. In the case of *Bacillaria* light response, this description is both curvilinear and multidimensional. This suggests that

psychophysical models are not a sufficient means to describe *Bacillaria* aneural cognition. Indeed, we also introduce a number of complementary models that view *Bacillaria* aneural cognition as an input-output system constituting an internal model. It is these input-output models, rather than the mental phenomenon *per se*, that characterizes the stimulus-response relationship. Viewing aneural cognition in terms of inputs and outputs also allows us to view aneural cognition in terms of broader phenomena such as biological homeostasis (Biswas and Iglesias, 2021) or active inference and perception (Bentley et.al, 2014; Ueltzhöffer, 2018; Zakirov et.al, 2020) at the behavioral level. In a generic sense, these input-output are often referred to as internal models (Orban de Xivry and Ethier, 2008; McNamee and Wolpert, 2019). Therefore, our goal will be to review suitable mathematical models that provide a reasonable description of behaviors relative to a potential stimulus. With this definition in mind, there are a number of psychophysical phenomena that are demonstrated by *Bacillaria*, and perhaps even diatoms more generally. These include, but are not limited to, flow detection, resonance detection, obstacle detection (Gordon, 2021), and phototaxis thresholding. More generally, there are four basic regularities of psychophysics as discussed in Lubashevsky (2019). The first regularity involves range effects leading to the overestimation of weak stimuli and the underestimation of strong stimuli. Secondly, a predictable response to environmental stimuli can be found in the form of the Weber-Fechner law. Related to this, the effects of sequential presentation can serve as the structure for a memory encoding mechanism. Finally, dynamic range allows for behaviors that adapt to a range of states between the lower- and upper-bound extremes of stimulus intensities or sensory magnitudes. Psychophysical models allow for dynamic range to be modeled with respect to a stimulus of variable intensities presented over time.

These regularities will apply broadly to systems both with and without a nervous system. This leads us to two assumptions when applying the cognition metaphor to *Bacillaria*. The first assumption is that movement of a *Bacillaria* colony is driven by information processing. This information processing is neuronal in scope, which means that *Bacillaria* behavior is both reactive and adaptive. A second assumption involves a distinction between the behavior of *Bacillaria* and behavior generated by a network of neurons that produce electrical potentials. However, as our multitude of models will demonstrate, this may be a distinction without a functional difference.

Information Processing and Aneural Cognition

Traditionally, information processing in nervous systems and organisms more generally has been assessed using an information theoretic approach. For our purposes, this means the production, transmission, and storage of various output processes are considered from the perspective of probabilistic channels (Wibrall et al., 2015). Information theory is particularly useful for examining multiple realizations of

random processes (Sayood, 2018). In models of the nervous system, the type of modulation determines the information-carrying capacity of specific links (MacKay and McCulloch, 1952). When extended to aneural systems, the properties of connective components within and immediate to the cells themselves determine the rate of transmission. Yet information is about more than simply transmission. Stimulus structure is of great importance, and goes well beyond activating the sensory apparatus (Garner, 1974). Part of this structure involves redundancy, and in a biological context serves to enrich interactions of the organism beyond simple reactivity (Garner, 1974).

Sensory and internal states also determine the rate of information processing. This has been characterized in terms of active inference, where organisms must minimize their free energy to retain their integrity as individuals (Kirchhoff et al., 2018). However, this also minimizes information content characterized in the form of surprise. The minimization of surprise, or unexpected information from external states (Friston et al., 2021), protects an organism's internal states from drastic changes. The relationship between surprise and organismal information processing relies upon a Bayesian formulation of information as opposed to a probabilistic one (Baldi and Itti, 2010). This type of Bayesian approach, commonly utilized in predictive processing models, also provides a dynamic perspective on causality (Aalen et al., 2012; Hipolito, 2021). Using this formulation, continually updating the internal state with information has a cost. This leads to fluctuations in information processing over time, and results in some behaviors having a higher utility than others (Zenon et al., 2019).

Hebbian Intelligence and Predictive Processing

The assumptions posed in this paper also allow us to borrow approaches from the neuroscience literature to more broadly understand how behaviors are generated among *Bacillaria* colonies. This section will review two candidates for interpreting the mechanisms responsible for a colony's information processing capacity. The first candidate approach is Hebbian learning, or more broadly Hebbian interactivity. Hebbian interactivity allows for higher-order patterns such as dynamic inhibition between processing units (O'Reilly, 2001), which in the *Bacillaria* context might be single cells or intracellular units. Hebbian associations occur when two or more units behave in a synchronized manner, thus strengthening future associations. A somewhat related approach is predictive processing, or the ability of an internal model to anticipate future environmental events. This also involves association between processing units that explicitly represents predictions of sensory inputs based on comparing prior and current observations (Bubic et.al, 2010).

We can apply a version of Hebbian learning where the site of action is cell coupling sites rather than synapses. Hebbian learning can be summarized as the causal association of activated neurons (Hebb, 1949), often summarized as "neurons that wire

together, fire together” (Shatz, 1992). In our case, cells that are adjoint also provide each other with a learning signal. This learning signal provides the basis for a coordinated, sliding motion. Once a pair of cells learn movements of their neighbors, their independent phase oscillations become entrained to each other (du Bois and Elliott, 2017). While this seems to happen as a result of mechanical constraints with the onset of movement generation, we ask a more fundamental question: how does this behavior become organized in the development of a *Bacillaria* colony? The answer is through a form of differential Hebbian learning (Cocchi et.al, 2017). Differential Hebbian learning is concerned with the temporal difference between activation and response rather than the causality of the activation itself. The synchronization of *Bacillaria* cells may indeed be due to active associative processes.

While Hebbian learning is a convenient metaphor and heuristic mechanism, this type of mechanism is not observed in diatoms. While the components can synchronize, diatoms use something more similar to aneural connectionist learning. Connectionist learning (Hinton, 1989; Hanson and Burr, 1990) involves the temporal association of two connected components. Even in neural systems, but particularly as a metaphor for aneural systems, Hebbian learning presents many drawbacks to producing a capacity for cognition. Hebbian models are typically oversimplified models of neural processing and not precise with respect to specific connected components. While this may not be important for aneural purposes, in their most general context, Hebbian mechanisms have been shown not to implement learning on their own (Rosenblatt, 1958).

In Hebbian models, feedback is captured in the form of updated weights between connected components. This can be superior to other models of simple learning, such as classic conditioning. Classic conditioning has been shown to exist experimentally in rabbits (Gormezano et al., 1962; Yeo et al., 1985), sea slugs (Glantzman, 1995; Lechner et al., 2000), and other organisms from across animal phylogeny. In this form of learning, a stimulus results in a predictable response in only a few exposures to the stimulus. Yet even in this simple form of learning, there are multiple neural processing steps (Hawkins, 1984; Glantzman, 1995). What is needed for many forms of aneural cognition is a feedback loop that provides a predictive path between interacting components, environmental stimuli, and future behavior. Therefore, a stronger mechanism that establishes more intentional behavior in a behavioral substrate is active inference and predictive processing.

Approaching aneural intelligence from a broader perspective, we can turn to predictive processing for clues as to how the proposed network is able to maintain its coordination across the colony. The mechanism behind predictive processing is active inference (Friston et.al, 2010; Nave et.al, 2020), which in turn is based on a free-energy

minimization approach to constraining behavioral outputs (Friston, 2009). The predictive processing and active inference approaches are particularly useful in cases where the colony shifts orientation and behavioral mode. This combined approach offers us a mathematical framework for action and perception (Buckley et.al, 2017) that is compatible with psychophysical laws describing a more general perception-action relationship. More specifically, active inference offers a formal feedback mechanism for the relationship between perception, action, and even learning (Bogacz, 2017). This can in turn be more fully understood using more formal tools such as a PID controller (Baltieri and Buckley, 2019) or a Bayesian model (Millidge et.al, 2021). Overall, active inference allows us to build upon *Bacillaria* aneural cognition in two ways. Active inference makes an explicit connection between our behavioral analogue and biophysical processes, particularly energy minimization. Secondly, the link between active inference and predictive processing also provides a regulatory rationale for understanding processes such as prediction and anticipation.

Returning to our *Bacillaria* network, how is information processed in a way that not only maintains coordination over seconds to hours, but enables the network to operate under a wide range of conditions? While we address this issue later on, one way to hypothesize about this is to turn to the adaptive aspects of the network's nodes and edges. Processing occurs through a perceptual output, which then drives cell behaviors. These cell behaviors must be coordinated in a way that does not require a leader (Gao et.al, 2019). This requires a decentralized structure that must integrate information on multiple timescales.

Measurement techniques

In this section, we will discuss various measurement techniques that allow us to uncover details about how *Bacillaria* processes information and produces adaptive behavior without a centralized nervous system. We will begin by introducing the Weber-Fechner law (Mackay, 1963), then move to more complex psychophysical laws. Then we will talk about connectionist models of behavior generation, from artificial neural systems to decentralized networks that coordinate coherent and adaptive behaviors.

Weber-Fechner law

We can apply the Weber-Fechner law to demonstrate how *Bacillaria* may utilize psychophysics to process environmental information. To accomplish this, we introduce a generalized version of a psychophysical law for measuring the magnitude of stimulus intensity. The Weber-Fechner law is a mathematical function that describes the ability to distinguish between light sources of different intensities. It can be stated as shown in Equation 1

$$p = k \left(\ln \frac{s}{s_0} \right) \quad [1]$$

where the sensation (input of S) is proportional to the logarithm of the stimulus intensity. S_0 is the reference stimulus and S is the change from the reference to the target stimulus. The term $\ln \frac{s}{s_0}$ is the log difference between a model of the stimulus and the observed stimulus. This can be thought of as a predictive process, or even as a differential process that allows for more sophisticated computation.

Given that a model of the stimulus is involved, it may also be possible to modify the discrimination capacity of the colony by introducing it to a wide range of stimulus intensities. Particularly as information from the sensory gradient becomes highly unexpected or qualitatively unusual, the response itself may be able to be sharpened. This can be demonstrated through biased random walk behaviors exhibited by motile bacteria with flagella in response to chemical gradients (Thar and Kuhl, 2003). In diatoms, a similar effect may result as a consequence of greater experience with a wider range of phenomena. Alternately, feedback resulting from changes in shape memory are stored in the extracellular structure or raphe secretions, and act as a contributor to cognition.

The Weber-Fechner expression can be extended to a number of other models, including Input-Output Relationship (Lan and Tu, 2016) and active perception in cells (Zaikrov et.al, 2020). In these cases, our measurement is not simply a difference, but indicative of more sophisticated indicators such as Signal Detection Theory (SDT) and fold-change detection (Kerkhof and Enquist, 2009; Kello et.al, 2010; Kamino et.al, 2017; Adler and Alon, 2018). SDT is an important mathematical model for understanding the Weber-Fechner regularity as a signal-to-noise ratio. In particular, the ability to conduct magnitude estimation (Poulton, 1968) provides us with a route to laws and principles (Shepard, 1987; Chater and Brown, 1999; Chater and Brown, 2008). In terms of an input-output relationship, let us consider the input of a light or chemical gradient, and an output of a movement response. The movement is activated when a difference in the stimulus intensity is detected from one sampling point to the next. Movement will also increase or decrease when the intensity increases by a n -fold difference over a fixed unit of time. Fold-change of the stimulus (FC) can be described mathematically as

$$FC = \log_2 \left(\frac{t_1}{t_0} \right) \quad [2]$$

where t_0 is the initial condition and t_1 is the sensory input at the time point to be compared.

In the case of cell colonies where each unit moves in a correlated fashion, it is useful to have a measure of feedforward and feedback with regard to sensory information taken in from the environment at a single cell and propagated across the colony. While the Weber-Fechner law allows for us to make a connection between stimulus and response, this does not account for noise that might degrade or otherwise mask the environmental stimulus. We can thus turn to Signal Detection Theory (SDT) to characterize the signal-to-noise ratio. In aneural systems, SDT is conceived of in a slightly different way than that of neural systems. The mathematical formulation of SDT involves two (generally Gaussian) distributions: one representing pure signal, and the other representing pure noise. When completely separated, we have a signal in the absence of noise. As the two distributions overlap, the degree of noise interacting with the signal increases. The primary measurement of SDT is d' , which can be defined in the following form

$$d' = z(FP) - z(TP) \quad [3]$$

where d' is the difference between the z-scores of all false positives and all true positives in a series of discrete sensory observations. A true positive is the coupling between a sensory signal and an output behavior, whereas a false positive is the lack of coupling between a sensory signal and behavior. This lack of coupling is characterized by the generation of a behavior without a corresponding sensory signal. In a neural system, the causal relationship between sensory input and behavioral output is provided by an internal information processing mechanism defined by a nervous system. In aneural systems, this internal information processing mechanism can be defined much more broadly, often defined using a physicochemical dynamical system.

In Buckley et.al (2017), two different types of density models can be used to approximate both the production of internal states and the generation of output behaviors. In the case of the former, so-called recognition (or R-) density is the mechanism by which the brain encodes environmental states. R-density provides a means for which environmental information is encoded as a collection of internal states. This process can be captured through a Bayesian model that consists of a prior distribution, environmental samples (or empirical observations), and a posterior distribution that updates the prior distribution with the current observation. The Bayesian model is essentially a statistical feedback model. By contrast, generative (or G-) density uses a statistical distribution to produce behavior in a feedforward manner. In many

cases, a Gaussian model is sufficient in producing a behavioral output representing oscillatory movement.

Connectionist Network

The network formed through the cytoskeleton and extracellular components of a *Bacillaria* colony can be modeled as a special class of connectionist network. Using a network as a means to connect cells and their components of movement allows us to build an internal model with inputs, outputs, processing units, and interactions. In this way, certain behaviors should yield a linear or curvilinear output function that corresponds in a systematic way to sensory input.

Figure 2 demonstrates the presence of light and the effects of this light source on the proposed aneural internal model. This is characterized by a hypothetical connectionist network of points across the surface of each cell in the colony. Rather than representing connections between synapses, however, our network is a set of interacting cytoplasms of individual cells. Given what we know about the generalized diatom response to light intensity, this model of interactions provides us a way to find universal patterns of movement modalities over a variety of raphid diatoms that form a multicellular colony.

Algorithmic Information

To further characterize halting behavior in colonies, and to differentiate between continual movement and instances of halting, we can utilize a measure of algorithmic information. Algorithmic Information can be quantified as the length of the shortest description of a sequence of events, and in various applications allows us to capture information content in both the probabilistic (Shannon) and dynamic (Bayesian) sense (Devine, 2009). Mathematically, we can use the definition of Kolmogorov (1965), stated as

$$k(x) = \min(l(p)) \quad [4]$$

where p is the length of a description in bits, and $\min(l(p))$ is the shortest lossless description, or minimal description retaining all the information of larger descriptions. To yield a description, we want to encode the string as a conventional program, a time-series measurement, or a short equation. The use of an equation allows us to plug in our formulation of the Weber-Fechner law, but descriptions involving sensory inputs and/or behavioral outputs can also be plugged into any number of psychophysical models.

In a computational context, the description measure must run on a machine that transforms the description code into something observable. In the context of diatom morphology, we can bridge the length of a binary string and a complex phenotype by treating cell colony movement as a model that exhibits the Principle of Computational Equivalence (Wolfram, 2002; Nguyen, 2017). Let us consider the string in question as a momentum vector measured along the trajectory of a single cell moving in concert with other cells in the colony. When considered as a series of discrete states, this sequence can be evaluated both in terms of its absolute minimum length (represented in terms of a pure sinusoid with no zero or negative momentum) and halting behavior.

Collective Pattern Generator

Figure 3 takes our connectionist network a bit further by proposing a specific circuit that operates as a Collective Pattern Generator (CoPG). In general, signals between cells prompt pattern formation and other forms of intercellular coordination. This is demonstrated by Portegys (2002) using a 2-D Cellular Automata. A CoPG can be defined as a distributed network of oscillators coordinated by its periodic behavior. CoPGs are analogous to Central Pattern Generators (CPGs - Arshavsky, 2003; Marder and Bucher, 2011), which allow for periodic signals to emerge from distributed networks of excitable cells (Figure 3). Examples of CPGs can be found in the movement of insect locomotion or cardiac pacemaking (Mantzirria et.al, 2020; Dickinson, 2006).

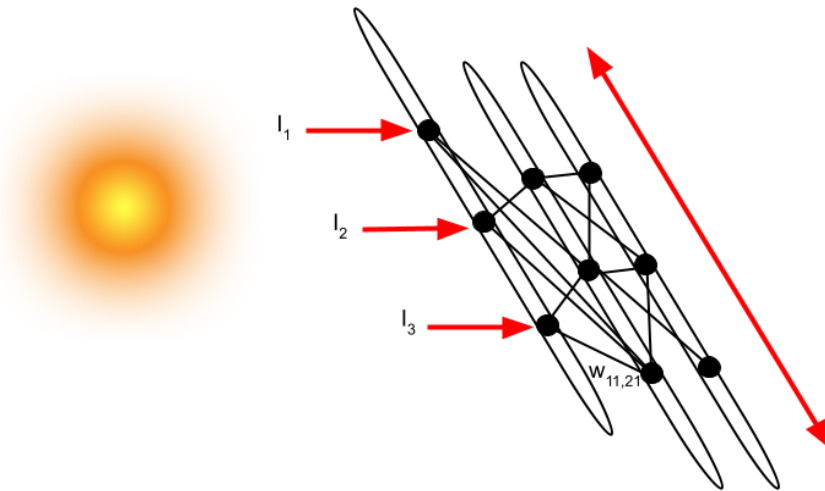


Figure 2. Sensory thresholds (just noticeable differences). Differences in light intensity measured by output movement weights ($w_{mm,nn}$). Network shown as edges and nodes that connect all cells in the colony.

Dynamical States of the CoPG

One alternative to thinking about CoPGs as a connectionist model is to contrast them with CPGs. While CPGs are generally consistent across the lifespan, being disrupted only in times of injury or neurodegeneration, there are not a lot of good models for understanding their dissolution. In *Bacillaria* and their associated CoPGs, however, we consistently see degeneration of oscillatory behavior. We propose that this halting behavior is driven by a dynamical state transition occurring at points where the colony is fully elongated (Figure 1A) and/or fully contracted (Figure 1B). At either point in the oscillation, we observe either a gradual contraction at a characteristic rate, or halting behavior that freezes the colony in this position for a random interval of time (Figure 4).

CPGs vs. CoPGs

We now return to the notion of CoPGs as an analogy with generators of cyclical electrical activity. While it has been established that electrophysiology plays a role in diatom cellular biology, it is unknown to what extent significant electrophysiological activity plays a role in *Bacillaria* rhythmic movement. In the diatom species *Coscinodiscus wailesii*, electrophysiological activity is enhanced after nitrogen starvation (Boyd and Gradmann, 1999). Unlike the case with coordinated CPGs, *Bacillaria* does not utilize action potentials. An example of how CoPGs might work comes from the pennate diatom *Pseudo-nitzschia fraudulenta* (Rocha et.al, 2018). In this species, single cells use paracrine signaling to coordinate Ca^{2+} dynamics between cells. More generally, ion channel flux is driven by exposure to light, chemicals, motility, and temperature (Bondoc et.al, 2016; Trewavas et.al, 1997). This is similar to what we observe in a broader group of diatoms in terms of behavioral response to stimulus gradients.

Now that we have considered the potential role of electrophysiology in *Bacillaria* movement, as well as its connection to collective behavior and psychophysics, we can find the right level of analysis of this oscillatory behavior. While ion channel activity does not lead to action potentials, there are nonetheless relationships between electrophysiology and forms of a neural cognition in a variety of organisms and life-history contexts (Bonzanni et.al, 2020; Rutenberg et.al, 2020). Rather than including physiological detail in our model, we will proceed through the use of sine waves, sinusoidals, and hybrid sinusoidal-tangent functions. This maps to various features of the cell phenotype such as bounding boxes that define the edges of each cell and cell centroids that move in space relative to one another (Alicea et.al, 2021). This provides a framework we call the Digital *Bacillaria* that provides a quantitative framework for a dynamic model.

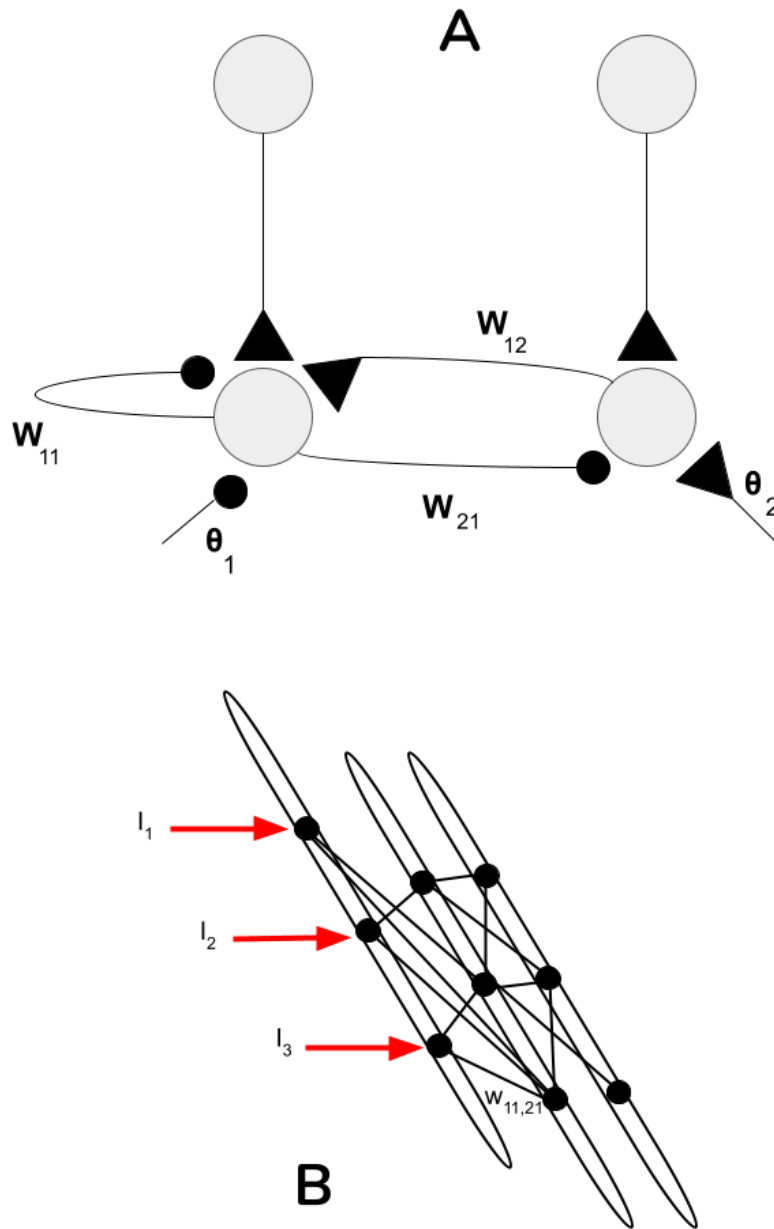


Figure 3. Deviations from the Collective Pattern Generator (CoPG). Difference between a Central Pattern Generator (CPG), characterizing a neural circuit (A), and Collective Pattern Generator (CoPG), characterizing collective behavior (B). In Panel A, black circles denote inhibitory synapses and black triangles denote excitatory synapses.

Each pair of digital *Bacillaria* cells acts as an oscillatory unit in a CoPG, in which a single cell oscillates. Oscillatory units overlap, so that a colony of three cells consists of two oscillatory units as shown in Figure 3B. While these oscillatory units (or pairs of

cells) generally produce a sine wave, they can also stretch to a maximal value and stay there for long periods of time. Initially, we introduce chains of x interconnected oscillatory units. At subsequent time steps, we model the modes of movement behavior using a sinusoidal function as the baseline condition. We can also introduce an offset of phase in movement between neighboring oscillatory units, so that any two units move at different rates. Noise in the form of higher-order changes in velocity and acceleration can also be introduced, particularly at the extent of the oscillation.

How does this compare with models of CPGs and collective biological locomotion? We can look to stick insects (Daun et.al, 2019) to understand synergistic CPGs (Delcomyn, 2004; Buschges, 2012; Ayali, 2015; Emanuel, 2020). In this case of the genus *Phasmatodea*, the movement of multiple legs are integrated into a neuronal network. The activity of this network is generated by nerves in each leg, and the bilateral symmetry of the insect body results in an oscillatory electrical signal. The measurement of nerve activity is electrical activity exhibiting significant complexity. Not only is there information at multiple time scales, but noise can be both introduced through the regulatory capacity of peripheral sensory information (Bidaye et.al, 2018) and dampened by ion channel activity (Goldammer et.al, 2018). Yet it is essentially oscillatory, and allows for movement to be coordinated for each pair of legs. In this sense, we can return to *Bacillaria* and our connectionist model of collective movement. In the CoPG case, we also see pairwise coordination between units of analysis. However, the oscillations can be much simpler, and the regulatory mechanisms less complex. Nevertheless, we can use an aneural model and psychophysical estimation to understand how this integration between oscillatory elements is coordinated over time, particularly in the face of environmental stimuli.

To demonstrate how we can model *Bacillaria* psychophysics, we introduce a series of characterizations of cell movement in a pairwise, nearest-neighbor cell comparison. The movement of two cells oscillating against one another is characterized by two overlapping sine waves. Yet before we discuss the overlapping case, let us look at the case of a single oscillator that halts after $\frac{1}{4}$ and $\frac{3}{4}$ phase of a single cycle (Figure 4). This halting behavior results in a tangent representing the cessation of anterior-posterior movement. Figure 5 features overlapping sine waves without halting between two neighboring cells for the $\frac{1}{4}$ and $\frac{3}{4}$ phase cases. We can add random noise to the sine wave to approximate noisy movement (Figure 6, top). The addition of noise (in this case Gaussian) represents changes in acceleration, orientation, and colonial integration over time. The non-halting pairwise case can be mapped to an attractor map. Figure 6 (bottom) shows the signal for an idealized movement trace (sine wave), which does not fully represent biological movement. Nevertheless, we can use such a comparison to understand the pairwise relationships that define a CoPG.

The non-halting case provides us with a full cycle that characterizes the information processing potential of a CoPG. While the full cycle is modeled using a pure sine wave, prior analysis of these cell tracking signatures shows instabilities and higher-order noise at both minimal and maximal amplitudes (Alicea et.al, 2021). This may represent a regulatory role for noise in the stretch dynamics of each cell. From an information processing perspective, the interaction between cells results in an offset between the trace of neighboring cells. Changes in the strength of an environmental stimulus should change aspects of these traces. In some cases, the offset might be reduced either over time or sporadically. Alternatively, instability at the amplitude extremes with an additive effect of environmental signal might lead to halting in subsequent movement cycles.

Halting behavior and its variants can be captured through the application of Algorithmic Information Theory. Likewise AIT can be used to better understand the relationship between out-of-phase behavior and halting, particularly in cases where pairs of cells begin to oscillate at different phases and desynchronize (Nanjundiah, 1986). *Bacillaria paxillifer* colonies demonstrate a very specific halting behavior related to a photokinetic response: during light periods, the colony is motile, while during dark periods, cells in the colony are arrhythmic and align in a stacked formation (Kapinga and Gordon, 1992). In some diatom species, it has been found that a chemical signal from predators can lead to a reduction in colony size (number of cells in colony) measured as chain length (Rigby and Selander, 2021). In solving this conundrum, AIT is helpful in two ways. First, AIT can describe the length of the colony in terms of optimal information given specific environmental conditions. Second, suppose that each cell in a colony has a set of instructions that guide behavior. When these instructions match (either in length or in type), cells are synchronized. When these instruction sets become mismatched, then desynchronization may occur. Reductions in colony size might become either a runaway or dampened process under the right environmental conditions, and one that is best explained by information processing dynamics.

In a case where pairs of cells begin to lag out-of-phase, this can have one of two outcomes. Either the instability continues and the colony becomes incoherent, or the instability is overcome, and the oscillations return to a stable state. A question for future research is whether colonial movement must be tightly synchronized or whether it can exist in a stable and persistent lagged state. If the former is true, excessive lag might provide a so-called tipping point for colony dissolution, perhaps based on immediate or temporally-integrated environmental cues. AIT might also help us understand this by understanding the set of behavioral instructions shared between cells that leads to stability.

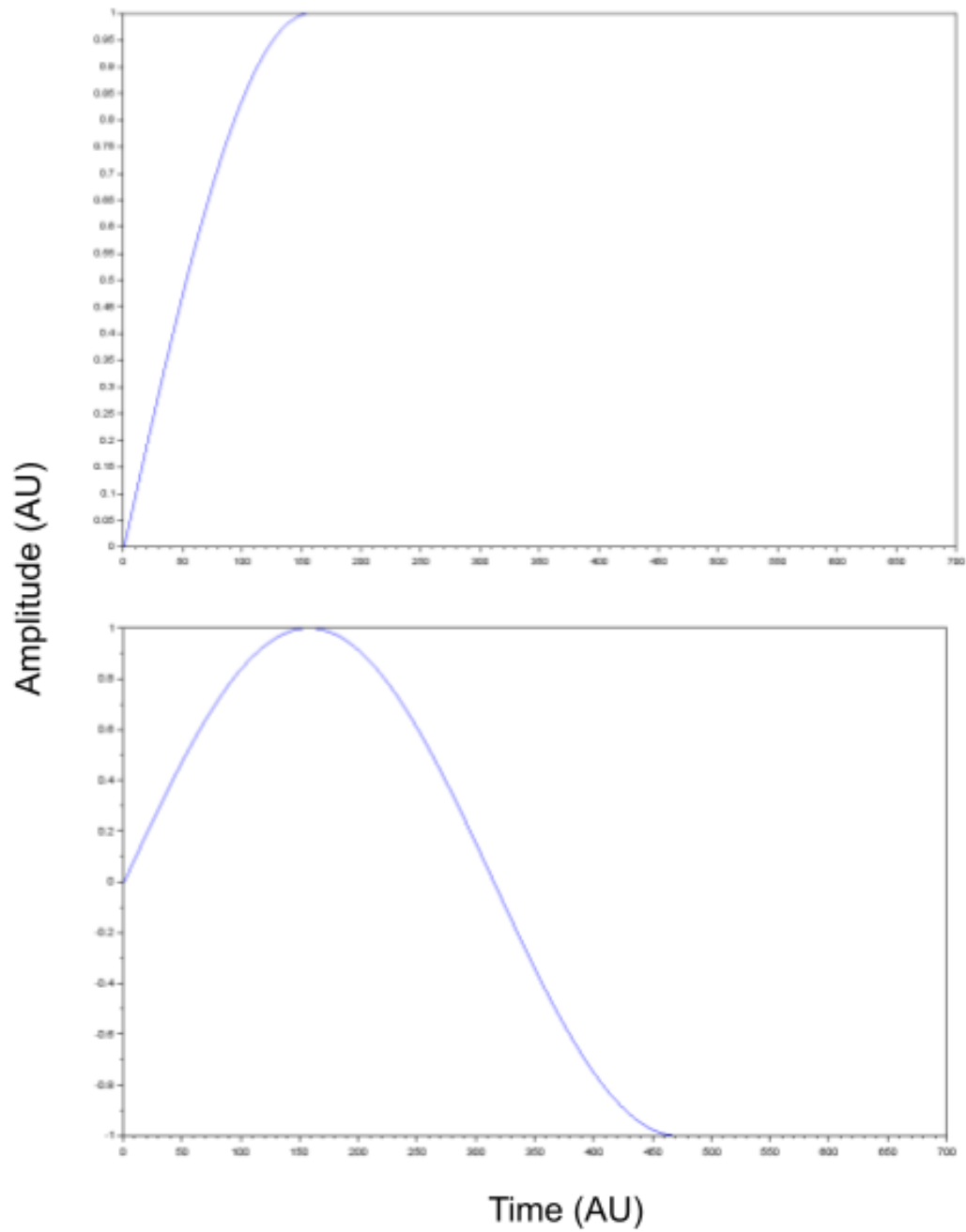


Figure 4. Movement trace of a single cell that halts at different points in a single oscillation. Top: Sine wave with tangent at quarter-phase, Bottom: Sine wave with tangent at three-quarter phase.

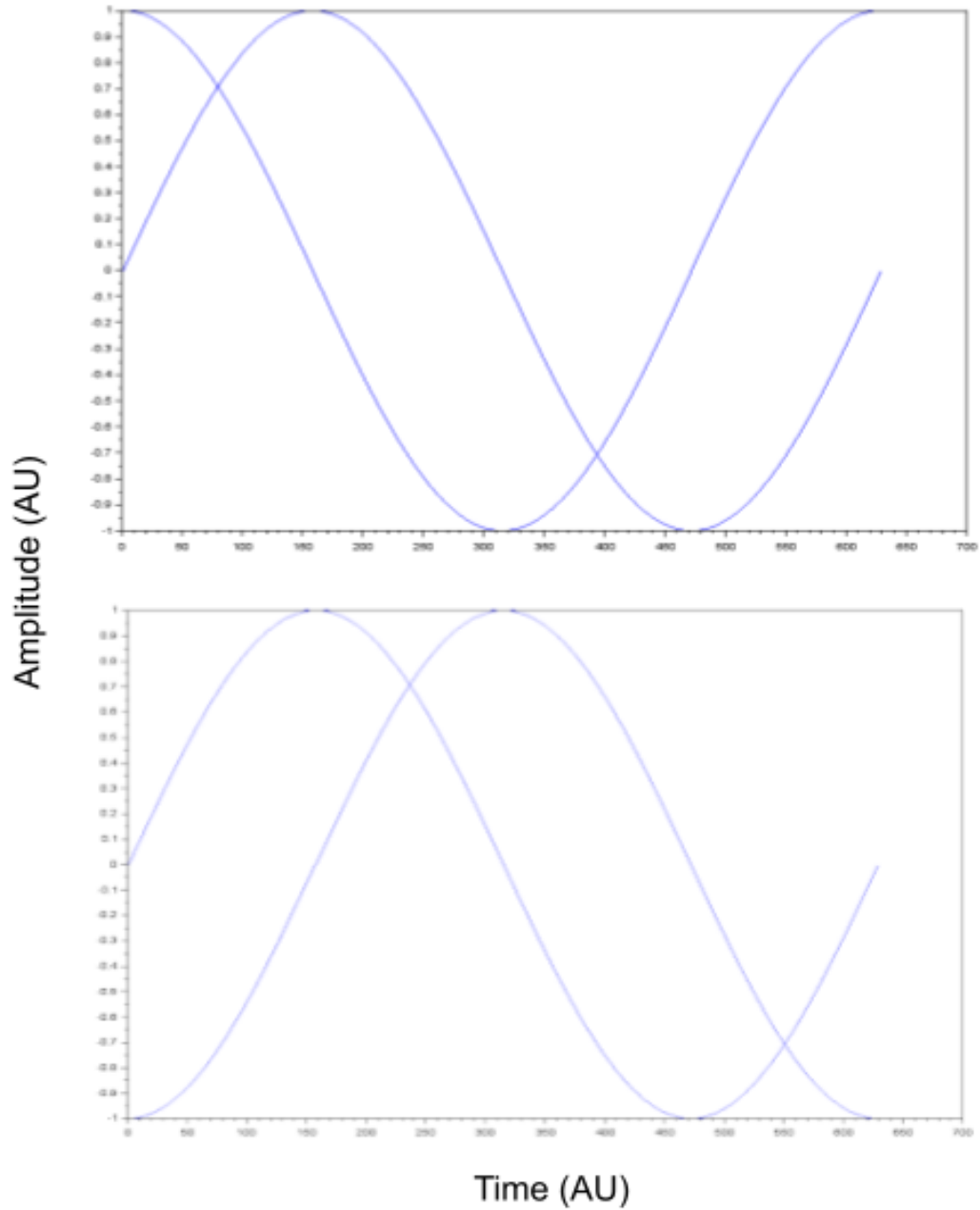


Figure 5. Movement trace of a single cell that halts at different points in a single oscillation. Top: Two adjacent and overlapping pairs of oscillatory cell movements (sine waves, three-quarter phase), Bottom: Two adjacent and overlapping pairs of oscillatory cell movements (sine waves, quarter-phase).

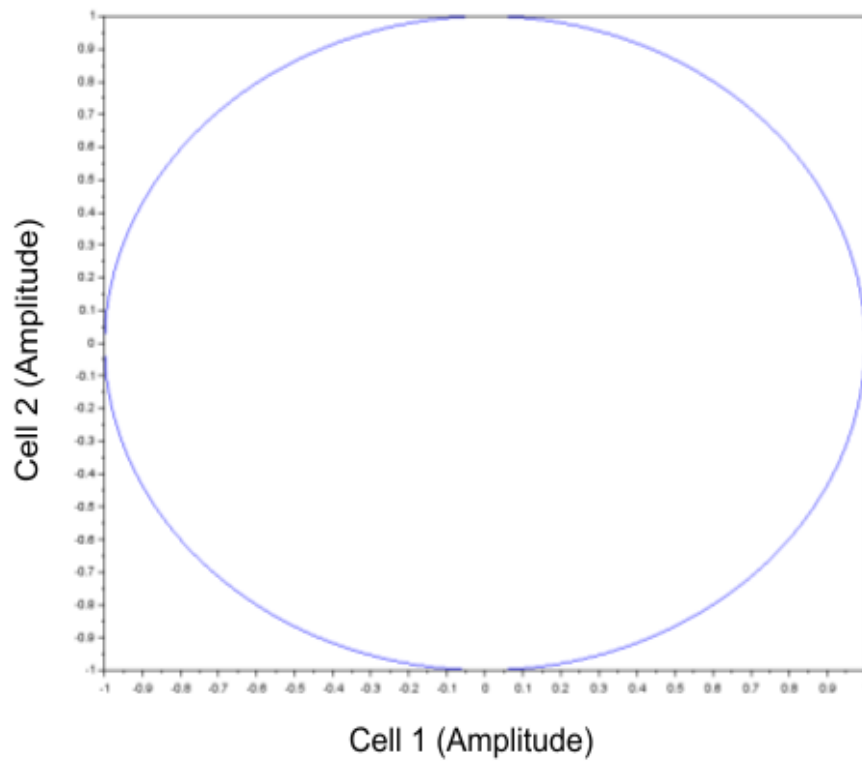
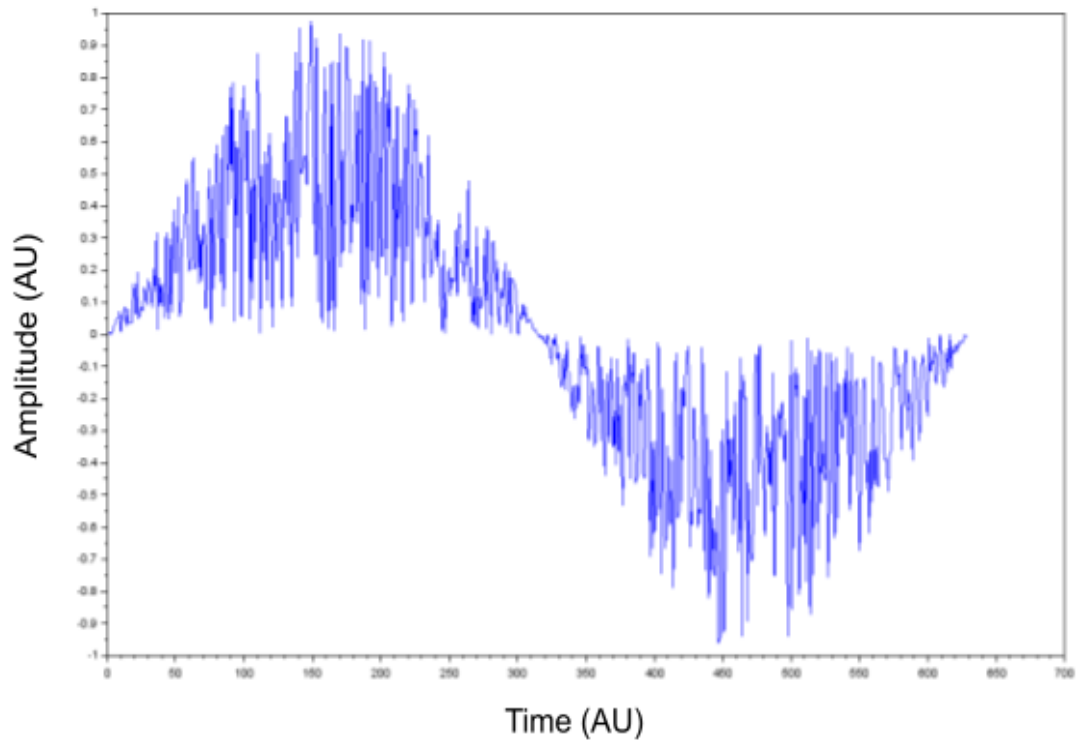


Figure 6. Single oscillations with noise and compared with another cell. Top: Sine wave with random (white) noise, Bottom: Attractor map (based on sine waves, quarter-phase).

Potential of Predictive Processing

Predictive processing provides us with more than a quantitative framework to analyze the relationship between brain and cognition. Theoretical frameworks such as the Free Energy Principle (FEP - Friston and Kiebel, 2009) may also provide a means to understand aneural systems. The connections between Markov Blankets, energy minimization, and the processing of information by a morphological system that minimizes its energetic expenditures with respect to movement, are particularly interesting. This connects psychophysics and biological physics in a unique and informative manner.

For example, a Markov Blanket can be defined as all variables which exclusively and conditionally predict a random variable of interest. This subset of variables is independent of all other variables in the system (Friston, 2009). In the case of *Bacillaria* motility, the group of variables that predict oscillatory motion might include photic inputs, water chemistry, mechanical forces, predation, orientation to light (McFarland, 2020), and resonance from other cells. Moreover, these variables act as conditional probabilities to predict the likelihood of movement in response to a stimulus at any given time. Formulating *Bacillaria* motility in this way also allows us to see how some variables are not at all predictive of coherent movement. This is connected to energy minimization in the sense that movement patterns will be optimized according to the strongest informational signal available. In other words, if the driving strength of resonance is stronger than that of the photic signal, then this should affect the phase, smoothness, and continuity of the movement output.

Phase Transitions in Bacillaria Movement

In the course of considering aneural cognition in diatoms (*Bacillaria*), we have considered not only the role of psychophysics, but the nature of colonial movement and intentionality of movements as well. We have proposed that *Bacillaria* movement can be characterized as a CoPG, which is the aneural analogue to a CPG. Like the CPG, the CoPG can be represented using a connectionist network. Unlike the CPG, the CoPG can undergo phase transitions (Kelso, 2010) that enable halting behaviors without associated dissolution or separation phenotypes (Bentley et.al, 2012). In the underlying representation, this is enabled by the structure of our connectionist network: the weights between connective components represent both intracellular microstructure and the extracellular milieu rather than synaptic connectivity driven by changes in the coupled ion channel activity. As such, CoPGs and their associated connectionist networks can represent non-equilibrium phenomena such as the decoupling of neighboring cells, damping of forward acceleration, and even halting of the entire colony at certain phases of movement.

The analogy between CPG and CoPG suggests that simple oscillators can provide a means for intelligent behavior, or at the very least adaptive information processing. In the case of CoPGs, the oscillatory behavior provides a deterministic signal that entrains behavior and thus is not directly associated with information content. On the other hand, phase transitions such as the switch from oscillation at a characteristic speed and halting at random intervals may provide information content to individual cell and colony-wide behaviors. Moreover, different modes of dynamic and static behavior have different types of information content. While stretching and halting is part of a colony-wide phase transition, this behavior also enables symmetry breaking at the level of coupled cells, where the bonds between cells dissolve and irrevocably shape the future dynamics of a colony.

One alternative means to explore the rhythmicity of collective behavior is to understand cell movement at the colony level as an array of Kuramoto oscillators (Acebron et.al, 2005; Breakspear, 2010). While we will not explore this hypothesis in detail, a system of coupled oscillators (Winfree, 1967) is an alternative to the connectionist models as introduced here, and allows us to model synchronized activity in a way that is consistent with the neurocognitive metaphor. This type of model stands in parallel to our CoPG approach, and describes synchronization rather than the rhythmicity of a cell colony. In our more generic connectionist model, nodes (neuronal units) act as aneural oscillators, but such oscillatory behavior is not the only type of coherent behavioral output.

Our aneural model of movement behavior has only one requirement: as the intensity of a sensory input varies by intensity, a corresponding intensity of behavioral response must also occur. We can also return to the concept of stigmergy to understand the relationship between extracellular components and internal physiological mechanisms. The connectionist model in particular also reveals how extracellular components adjacent to different parts of the colony can serve a heterogeneous role in aneural cognition. This is an important feature that allows for a coherent psychophysical response that is regulated depending on the environmental context. Taken together, this provides a means to extrapolate even further, from aneural cognition to the regulation of aneural cognition.

Aneural regulation

Now that we have considered the potential for aneural information processing in *Bacillaria* and demonstrated how we might understand and measure this phenomenon, we are ready to propose a potential path towards the regulation of aneural cognition. The first step involves Hebbian learning involving environmental (sensory) inputs. In aneural Hebbian learning, units that are active simultaneously couple their behavior.

Over time, this synchronization is reinforced. In *Bacillaria*, each cell in the colony exhibits sliding motion. This sliding motion is coupled to neighboring oscillatory units, and establishes Hebbian learning. This can be demonstrated computationally using our connectionist model. This coupling results in a rhythmic oscillation occurring at multiple timescales, and can be approximated by our CoPG model. The last step in our path is how feedback is regulated. In diatom sensory systems, feedback comes in a number of forms: from shape memories of gradient position to physical resonance between oscillating cells. Yet regulation often comes in more universal forms, that are well-represented in models such as CoPGs, forms of Hebbian interactivity such as learning, and the free energy principle. The role of direct sensory information and feedback can be summarized by the concept of direct perception (Gibson, 1979). While direct perception has not typically been applied to aneural systems, the concept allows us to think of the relationship between cells, organisms, and their environment. The notion that the environment provides dynamic structure for goal-directed behaviors and information processing is attractive for describing behavior of organisms that do not have a nervous system.

Our approach describes only one mode of *Bacillaria* behavior, and only briefly draws from potential physiological mechanisms. In the initial step of the above model, neuronal behavior is generated by an analogy to a decentralized nervous system with electrical activity. This involves both intra- and extracellular mechanisms that leverage internal information processing and is augmented by stigmergy. We can explain a variety of behavioral modes using this model, including colony halting. This halting mode of behavior can be approximated using Algorithmic Information Theory. Eventually, this might lead to the development of a behavioral Turing test (French, 2000; Saygin et.al, 2003) for distinguishing neuronal-generated from aneural-generated behavior. Yet such a definitive standard for distinguishing neural behaviors from simulated ones requires us to address what exactly demarcates real behavior from simulated (but real-life looking behavior). We can generate realistic simulated behaviors using physics engines (Palyanov et.al, 2018; Larson et.al, 2018) and a class of agents called Animats (Watts, 1998; Boden, 2006). But the connection between the underlying mechanisms of such behaviors has not been properly established. Therefore, to better understand what kinds of behaviors are possible with aneural architectures and their relative complexity, we will discuss the phenomenon of pseudo-intelligence.

Broader Picture of Intelligence and Emergence

Pseudo-intelligence

To place the contemporary concepts in neuroscience presented here in perspective, we return to the fact that some seemingly neuronal behaviors are generated by cellular motors along with other components of the colonial cellular matrix.

The question might be asked: Is the synchronization of movements across cells in the colony simply the result of mechanical interactions, or is there a greater degree of autonomous behavior at work? If the former is the predominant explanation, then aneural cognition is merely a form of pseudo-intelligence. Yet if the latter holds true, then we face a dilemma of whether or not our output is cognitively realistic. Drawing this distinction relies on a definition of intelligence as a nonlinear and interactive process that is difficult to control using standard methodologies. *Bacillaria* colonies fall into the category of highly interactive, nonlinear systems (Pagliarini, 2008). But how do we understand the distinction between intelligent behavior and mimicry? In another context, Li (2018) defines strong Artificial Life as simulated life that exhibits characteristics of real life. This description provides a standard for interpreting the generation of realistic neural behaviors using aneural systems. In investigating realistic vs. fake-looking Artificial Life (Witkowski, 2020), contestants used methods to distinguish between movement trajectories from living organisms (Sharks, Ants, Spiders, and Jaguars) and non-living agents (simulated bird flocks and insect swarms, Artificial Chemical Compounds). Among the examples listed above, living organisms generate their movement behaviors through biologically neuronal systems. This can be contrasted with the latter examples, which utilize either non-biological neural or biologically aneural systems. The general relation between neuronal and aneural systems can be partitioned as is done in Table 1.

Table 1 demonstrates that any single instance of behavior (feeding, taxis movements, quiescence) can be classified as a neural or aneural behavior, which can be generated by neural or aneural processes. This provides us with a classification problem that can be fit into an SDT model. For example, if a neural behavior is generated by a neural process, then it is a true positive. The true positive is produced entirely through the intentional component. *Bacillaria* occupy a unique position in this typology: a neuronal instance of behavior generated by aneural processes. This is considered a false positive, as the behavior is generated through both an intentional signal and an unintentional component (which roughly maps to the signal and noise components of the SDT model). Both neural and aneural behaviors can be simulated using deep learning and/or reinforcement learning techniques. This will also allow us to propose different neuronal-like cooperative behavioral states generated in our aneural context. Such behavioral states might include feedforward movement generation, density-dependent feedback, light-responsive feedback, and resonant feedback.

To further understand the role of halting and persistence of movement in *Bacillaria* colonies, it is worth expanding beyond the cognition metaphor and consider the connection between Turing Machines and more formal mathematical formulations of algorithmic information. Specifically, algorithmic information theory (Chaitin, 2012) may

allow us to approximate whether these patterns are random or something that approximates perceptual information (Gauvrit et.al, 2016). If the entire sequence of behaviors observed is random, then the behaviors captured by the CoPG model might be due to exogenous forces such as colonial aging or hydrodynamics. If it is not random, then there is some endogenous control that might be due to connectionist network dynamics or a consequence of sensory inputs captured using a Weber-Fechner law analogue.

Table 1. A demonstration of how autonomy can be partitioned into generated and observed components.

		Generated by	
		Neural	Aneural
Instance of Behavior	Neural	Brain	<i>Bacillaria</i> chains
	Aneural	Jellyfish	Steam Engine

Discussion

We suggest that the motion of *Bacillaria* colonies is neuronal behavior generated by aneural processes. Some have suggested that physical principles can be used to understand how complex spatial information is integrated among slime molds and ciliates (Schenz et.al, 2019). Here, we not only suggest that formal information processing mechanisms are important for understanding the generative outputs of internal processing, but also provide a series of formal approaches for modeling and analysis. While we begin with a reliance on simple psychophysical models such as the Weber-Fechner law and models that make a distinction between signal and noise (e.g. SDT), generative mechanisms such as Hebbian Learning and predictive processing provide a more formal means to describe the production of a large number of degrees of freedom that enable adaptive behaviors (Hart et.al, 2018). Connectionist models also allow us to bridge between cells, and the effects of sensory stimuli on the interactions between cells as they each respond internally to a stimulus from their own point of view. As a connectionist model allows for Hebbian interactivity and extracellular information processing, the adaptive behaviors that result represent alternate paths to the same problem. Ultimately, externalized network behavior (e.g. CoPG) unfolds over time in terms of the adjacent possible (Tria et.al, 2014; Monechi et.al, 2017), and the output of such models as emergent phenomena (Fernandez-Leon, 2012; Rosas et.al, 2020). We also consider oscillatory halting behaviors through the lens of algorithmic information, and consider how aneural information processing is a form of pseudo-intelligence.

Bacillaria colonies form by cells dividing as a clone in which cells adhere to one

another, forming an accordion-like structure. As they age, *Bacillaria* colonies break. These colonies also undergo periods of extended elongation and/or quiescence in other positions. Despite periods of colonial breakage, we might be able to nonetheless utilize an aneural cognitive approach to understand if coherent behavior breaks down during this process. In particular, the uncoupling of predictive processing and the corresponding lack of tight feedback between cells in a colony may predict aperiodic oscillations by the proposed connectionist CoPG model. This leads us to an understanding of halting and dissolution behaviors using other techniques such as AIT. But in fact, colonies may simply break due to turbulence (as with a blender, Harbich, 2020, personal communication). Additional experimental validation and modeling may provide a definitive answer.

Now that we have posited a form of aneural cognition for diatoms and walked through a series of models demonstrating a collection of information processing mechanisms, we can return to our original motivation. What does the psychophysical milieu of diatoms look like? *Bacillaria* psychophysics results from a light dependent input/output curve for a single cell. This quantitative regularity determines how much input results in a corresponding degree of output. An alternate way to approach this is to apply one of our candidate psychophysical models to a behaving diatom colony, which yields predictable movement and even shape behaviors. One example of this is to build a receiver operator characteristics (ROC) curve from our SDT model, which yields the colony's ability to detect signal from noise. This might allow us to assess whether or not an aneural behavior is similar to neural processing. Yet a third way to answer this question is to consider the psychophysical milieu for different modes of colony (or collective cell) movement. This can be measured using an approach such as AIT, which enables us to measure halting behaviors and understand discrete temporal transitions in the internal state.

An alternate way to approach this is to utilize computational agents of simple neural systems as an analogue for what might be possible in aneural systems. We can base this on work involving developmental Braitenberg Vehicles (dBVs - Dvoretiskii et.al, 2020). dBVs are computational agents where the brain is gradually constructed over the course of development. During this progression, behaviors come online as neurons and their connections emerge. This in turn provides an indicator as to what constitutes the minimal components of a small nervous system (Herrera-Rincon and Levin, 2018; Alicea, 2020) as well what might be controllable with an aneural analogue. Using the dBV as a comparison also allows us to leverage the power of Braitenberg Vehicles as they emerge in development in order to determine the complexity threshold between goal-directed neurally-produced behaviors (Busseniers et.al, 2021) and incoherent behaviors.

In this paper, we have taken the position that organisms in the genus *Bacillaria* exhibit information processing capabilities that resemble cognition, despite the lack of a formal nervous system. The evidence for this rests on two aspects of *Bacillaria* lifestyle: the ability to adaptively respond to sensory stimuli, and the collective coordination of behavioral output across cells constituting a colony. We bring several paradigms for adaptive information processing to bear on this problem. These include the application of psychophysical laws, Hebbian interactivity, Connectionist models, and predictive processing. Taken together, these models, mathematical tools, and novel conceptual models provide us with new ways to understand the world of diatoms.

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