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THEMATIC ISSUE ARTICLE: LADISLAV KOVÁČ AND THE ORIGINS OF COGNITIVE BIOLOGY

Eating and Cognition in Two Animals without Neurons: Sponges and *Trichoplax*

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Abstract

Eating is a fundamental behavior in which all organisms must engage in order to procure the material and energy from their environment that they need to maintain themselves. Since controlling eating requires procuring, processing, and assessing information, it constitutes a cognitive activity that provides a productive domain for pursuing cognitive biology as proposed by Ladislav Kováč. In agreement with Kováč, we argue that cognition is fundamentally grounded in chemical signaling and processing. To support this thesis, we adopt Cisek's strategy of phylogenetic refinement, focusing on two animal phyla, Porifera and Placozoa, organisms that do not have neurons, muscles, or an alimentary canal, but nonetheless need to coordinate the activity of cells of multiple types in order to eat. We review what research has revealed so far about how these animals gather and process information to control their eating behavior.

Keywords Cognitive biology · Control mechanisms · Eating behavior · Placozoa · Porifera

> [I]n a multicellular organism, such a biologically significant goal as feeding requires substantial integration of multiple effectors: ciliated, contractile and secretory cells. Feeding also includes innate immune protection against potential pathogens (e.g. using nitric oxide and toxins) and injury-induced regenerative responses.
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> —Moroz, Romanova, and Kohn (2021)

Introduction

A basic requirement for every organism is to extract energy and matter from its environment, which it then uses to construct/reconstruct itself and to carry out the activities it must perform to maintain itself far from equilibrium, including avoiding predation. That is, every organism must eat. Eating requires procuring and taking foreign material into itself, but only some foreign substances are appropriate to provide the organism matter and energy—some are actually toxic. Consequently, organisms must be selective with respect to what substances they take in. If they take in something toxic, they must expel it. To be successful at eating, organisms must procure information and select eating behaviors based on this information. Accordingly, the centrality of eating makes it a powerful lens through which to understand the foundations of cognition.

Some may think that eating is too basic an activity to require cognition. They may associate the term *cognition* only with more esoteric human endeavors—solving abstract problems, writing novels, or designing experiments. This is misguided. The core of cognition is procuring information, processing and evaluating it, and making decisions based on it. And this is what is required for any animal to be successful at eating. Moreover, a little reflection on our own lives will reveal that eating is an activity to which we devote considerable cognitive effort—we decide when to eat, plan our meals, select strategies to procure food, choose how to prepare or cook food to make it digestible and appetizing, and decide when to stop eating. The importance of the last is evident in that failure to stop eating when it is appropriate

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to do so has given rise to the obesity epidemic that is inducing serious health effects. A further indication of the importance of eating in our cognitive lives is that cookbooks are a mainstay of the publishing world and increasingly many computer apps are designed to help us execute the activities involved in eating. Food-related activities take up a substantial portion of every person's cognitive life. Moreover, food is an important accompaniment to many other human activities. An academic conference without food will generate as many complaints as one with poor talks.

An important research strategy in biology is to investigate physiological processes and behaviors in as simple an organism as possible, especially if there is reason to expect that the means for carrying out these behaviors have been conserved. Not all questions can be answered by focusing on relatively simple organisms, but researchers can often learn the basic strategies underlying the process or behavior. This principle has not been as widely adopted with respect to cognition; instead, humans have been the primary object of study, with some attention paid to other mammals. A number of theorists, however, have argued for adopting such an approach to cognition, most especially Kováč (2000, 2006, 2008, 2023), who has characterized the approach as *cognitive biology* and to whom this issue is dedicated. He also emphasized the importance of grounding cognition in chemistry, a theme that will be developed further below. Eating is a promising behavior for developing cognitive biology as all organisms need to perform this activity. Phototropic organisms can synthesize organic molecules themselves utilizing the energy of sunlight, but even they must procure the required molecules from their environment. Other organisms are heterotropic—they must acquire material and energy from already synthesized organic molecules (specifically, carbohydrates, proteins, and lipids) found in their environment.

For many prokaryotes, these nutrients are mostly organic molecules, and the information processing required to locate, move towards, and consume them is carried out by individual cells. We have previously discussed information processing through which the bacterium *E. coli* directs activities toward procuring nutrients (Bich and Bechtel 2022). Even as they process information individually, bacteria and other single-cell organisms often act collectively in procuring nutrition. *E. coli* and other bacteria join biofilms in which they surrender some of the capacities of independent life and acquire new benefits from mutual action. After joining a biofilm, individual bacteria adapt their information processing so as to coordinate with other cells. For obligate multicellular organisms, acting as a collective is not optional, but required. One of the features of multicellular life is that cells divide the labor and specialize. The consequence is that cells in plants and animals are no longer able to perform all of the activities needed to procure and consume food and are dependent on each other. For each to carry out the activities that are required by the others for the whole to survive, it must acquire and process some information both about the status of itself and other cells within the organism and relevant conditions in the environment. It can procure this information directly or by processing signals emitted by other cells that procured that information. In the next section, we develop a framework for characterizing the role of information in controlling activity that serves to maintain the organism that we will then apply to the cognition of eating.

Most animals employ neurons for much of the communication between cells. With their extended processes along which changes in membrane polarization can be passed, neurons provide a means of rapidly communicating information over relatively long distances. But neurons are distinct cells, and electrical communication terminates at the end of the processes. Transmission between neurons, or neurons and other types of cells, is typically chemical.[1] This chemical activity, moreover, is what allows for the processing of information—of bringing together information from multiple sources and generating responses specific to the information that arrives on a given occasion (Bechtel 2022). Transmission along a membrane (or along an electrical wire) has no intrinsic informational content. Its value stems from the conditions that initiate its transmission and that make use of it—the chemical processing that occurs between and within neurons or other cells.

Chemical transmission between neurons relies on a host of chemicals that, as a result of the tendency of researchers to focus on neurons, are referred to as *neurotransmitters*. Many of these are already found in single-cell organisms or in other multicellular organisms such as plants that lack neurons. They might better be understood as signaling molecules. To understand how the release and reception of signaling molecules figures in information processing, it helps to abstract from the electrical transmission along neurons and focus just on the chemical activities through which neurons communicate. Such a perspective can be advanced by focusing on multicellular organisms that engage in information processing but don't have neurons. This is a major motivation for looking to plants for insights into how multicellular organisms process information (Baluška and Mancuso 2021; Calvo and Lawrence 2022). Another potential source of insight for the basic processes of information processing without neurons are fungi, the closest phylogenetic

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[1] Gap junctions between neurons constitute an exception as they enable both direct electrical communication and chemical communication between neurons. They are relatively rare, and, moreover, even when they enable transmission of information, the processing of that information depends on the chemistry of recipient cells.

relative of animals (Steenkamp et al. 2006; Ocaña-Pallarès et al. 2022) Although as yet fungi have not figured in research in cognitive biology, filamentous fungi such as *Neurospora crassa* engage in complex communicative activities, detecting other cells and fusing with them. If they detect that they share genes at specific loci, they commence sharing resources and collaboration; if not, they compartmentalize and begin programmed cell death (Witzany 2012; Fischer and Glass 2019). These fungi are promising candidates for research in cognitive biology.

There are also animals that lack neurons but process information in order to maintain themselves—Porifera (sponges) and Placozoa (*Trichoplax*). Since without neurons these animals could not significantly expand in size or increase the number of cell types, current members of these phyla likely still carry out the information-processing activities needed to maintain themselves in a manner that resembles their ancestors. Moreover, as these capacities are likely to have been found in the common ancestor of current members of these phyla and Eumetazoa, examining these animals can provide important understanding of the basic information processing utilized in all animals.

Neuronless animals are of interest for a second reason—they exhibit a mode of eating that is more basic than that manifest in Eumetazoa. Eumetazoa bring potential nutrients into a cavity within their body in which they digest them. In most cases, they employ a through-gut or alimentary canal that connects a point of entry, a mouth, with a point of excretion, an anus. (Some, such as Cnidarians—jellyfish and corals—have just one pore for both consumption and excretion.) Such an inner cavity is lacking in both Porifera and Placozoa. Porifera bring nutrients directly into individual cells. As a result, they are limited to taking up small food particles through endocytosis. Placozoa utilize a variety of chemicals to digest larger bacteria and algae extracellularly, but do so outside their body. In both cases these eating activities require information processing, but not the full range of information processing required to maintain and regulate an internal digestive cavity.[2]

Research on information processing in both Porifera and Placozoa is at an early stage. But in recent years investigators have not only characterized the complex behaviors that must be regulated for these animals to eat successfully but also have begun to identify some of the chemicals they use to regulate those behaviors. Enough has been learned to justify examining the behavioral decisions Porifera and Placozoa make in eating and how they carry them out. Doing so offers numerous advantages for understanding the cognition of eating. Since the animals lack an internal digestive system, researchers can focus on specific eating activities—absorption of nutrients and release of digestive proteins. And since they lack neurons, researchers can focus directly on the chemical processing of information that supports these eating activities. We focus on Porifera in the third section and Placozoa in the fourth, describing some of the recent findings. While research to date has not provided a detailed account of the full range of information processing involved in the eating activity of these animals, it has advanced sufficiently to indicate how the complex division of labor involved in eating has created demands for processing information and to provide clues as to how the information is represented in different chemicals and used in cells with receptors for these chemicals.

Theoretical Framing

To look at the role of cognitive activities involved in procuring and eating food, this article adopts a distinctive strategy of “phylogenetic refinement” (Cisek 2019). It consists in analyzing the most basic instances of cognitive activities in relatively simple organisms and describing when possible, or at least pointing to, the basic features of the underlying mechanisms responsible for them. If the mechanisms involved are conserved through evolution, the results can then prove useful for understanding what happens in more complex organisms up to humans. This strategy is part of a wider approach variously called “cognitive biology” (Kováč 2000), the “biogenic approach to cognition”(Lyon 2006), or “basal cognition” (Lyon et al. 2021). It aims to investigate cognition starting from its biological roots in organisms such as bacteria (Lyon 2015), and emphasizes the continuity of cognitive phenomena across all living organisms. The biogenic approach is usually contrasted with mainstream “anthropogenic” approaches, which start from humans as the paradigmatic cognitive organism, aim to investigate distinctively human cognitive activities, and limit its phylogenetic extension to species phylogenetically closely related to humans. The anthropogenic approach associates cognition with the brain, especially the most recently evolved regions such as the neocortex, and thereby denies the continuity of cognition with organisms lacking such structures.

To explore the biological roots of cognition this article starts from the idea that living organisms are autonomous systems that maintain themselves in far-from-equilibrium conditions (Piaget 1967; Maturana and Varela 1980; Moreno and Mossio 2015). This means that they produce, maintain,

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[2] Fungi provide an interesting comparison phylum. Most fungi are saprotrophs—they feed on decomposing organic matter such as decaying plant matter, by releasing digestive enzymes that break down components such as cellulose. The fungus absorbs the products, such as amino acids and monosaccharides, into itself and transports them to loci where they are required. A few fungi actively entice nematodes to them before releasing digestive enzymes and absorbing the released nutrients (Lin et al. 2023). Unlike Placozoa, however, they do not locomote to their food source and do not trap it in mucus.

and control their component entities and activities by using matter and energy from the environment. Living organisms cannot exist unless they interact with their environment to procure nutrients and produce energy. These interactions are made possible by an internal variability and the capacity to manage it, which enables living organisms to do different things depending on circumstances. They do so by exerting fine-tuned control upon the exchanges of matter and energy with the surroundings and by bringing forth different viable responses to a variety of environmental perturbations. On our view, cognition is rooted in this fundamental activity of living systems.[3]

By building on a framework provided in Bechtel and Bich (2021), we identify cognition with those activities of a living organism that require making and executing decisions that allow it to maintain itself in its environment. Making such decisions requires identifying or distinguishing between some features of the organism and its environment (for example, sensing its metabolic state and the availability of energy, variations in boundary conditions, presence and concentrations of nutrients in its environment, and presence of predators) and to act accordingly. In doing this, a living organism does not just register each occurrence of a feature in its internal and external environment but categorizes each, and based on the category assigned it modulates its own internal dynamics in such a way that it maintains its viability. More specifically, doing so requires (1) procuring some information about the state of the organism and the environment through sensors such as the receptors located on the membrane of a cell; (2) processing this information to categorize and evaluate internal and external conditions by transforming the information in the input into some internal conformation change or activity of its internal components; and (3) making decisions based on these evaluations and executing them so as to modify the activity of the organism in such a way as to contribute to its maintenance. Examples of these decisions are starting or stopping movement, changing the direction of movement, and synthesizing and secreting enzymes necessary to metabolize different substances.

These activities do not require a nervous system. They can be performed by more basic mechanisms with sensory, processing, and effector capabilities that direct the activities of other mechanisms in the organism. Instances of such specialized control mechanisms are found in every living cell. They enable it to coordinate the activities of its parts and respond adaptively to its environment. They also allow multicellular organisms to direct and coordinate the activities of different cells. It is important here to characterize the main features of these control mechanisms and to distinguish them from the other mechanisms on which they operate. To maintain themselves; produce, repair, and replace their parts; generate behaviors; and procure matter and energy from the environment, living organisms employ a variety of mechanisms that perform the needed physiological (e.g., digestive) and behavioral (e.g., locomotive) activities. Following Winning and Bechtel (2018), we call these mechanisms "production mechanisms." Control mechanisms are not involved in these basic activities; instead they alter the behavior of production mechanisms, so as to activate them when they are needed and to coordinate their activities so that they contribute to the maintenance of the system (Bich and Bechtel 2022). When and how control mechanisms operate to modify the activity of production mechanisms depends on measurements they make of variables in the system or its surroundings, usually by integrating information from different receptors. Control mechanisms allow an organism to perform cognitive activities such as making decisions, because they procure information from different sources by making measurements, process the information, use it to make evaluations of different modes of operations, and then select among possible behaviors of production mechanisms those expected to maintain the organism's viability.

Talking about information in this context may be seen as problematic, especially since several advocates of the autonomy tradition, notably Maturana and Varela (1980), rejected it. They viewed talk of information as carrying heavy baggage since it is thought to impute intrinsic content to signals. However, information can be given a minimal naturalistic interpretation in this mechanistic framework. For a control mechanism to contribute to the maintenance of the organism, it must be responsive to conditions in which the operation of the controlled mechanism is needed. In the simplest case, it must make a measurement of a quantity that varies either in the organism or in its environment. Making a measurement means that the activity of the control mechanism is changed due to the interaction with the measured quantity. As a result of these changes, the controller operates differently on the controlled mechanisms, enabling the latter to perform the needed activity (Pattee [1973]2012). Accordingly, it can be said that control requires acquiring and using information to assess conditions and selecting among alternative activities in light of these assessments.

An important feature of this view is that the information imputed to a signal is not intrinsic to it but depends on the operation of the control mechanism. The distinctive features

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[3] Traditional work on biological autonomy—in particular, Piaget's (1967) and Maturana and Varela's (1980)—has emphasized that this interactive dimension of life is related to, or coincides with, cognition. According to their work, cognitive activities concern the interactions with the environment and the relative internal modifications that an organism can undergo without losing its identity. However, these authors have not addressed the precise requirements for cognition, the criteria to distinguish cognition from other interactions such as structural ones, and the type of mechanisms involved.

of signals in general are the capability to trigger a response in the targets without providing the material or energy for it, and without their causal power itself being sufficient to determine the response. The response instead depends to a large degree on the properties of the receiver (Wiley 2013). Different receptors would measure different variables and with degrees of sensitivity. Moreover, the operations of control mechanisms do not depend directly on the intrinsic features of the source of information as would happen with the transmission of a physical force. In this context, processing information means that measurements are translated into activities that might not be of the same nature as the variable measured. The working of a thermostat illustrates this. As a result of the temperature measurement it makes, the state of a thermostat is changed and in turn the thermostat changes the activity of the furnace it controls. This does not imply transferring a temperature gradient from the environment to the furnace but translating a measurement of temperature into activation or inhibition of a device. The same is true of cells that employ receptors to measure the presence of nutrients.

While production mechanisms operate on nutrients to transform them into building blocks or energy, control mechanisms do not do that. They sense the presence of nutrients and trigger different activities of production mechanisms, such as activating or inhibiting protein synthesis, transporting molecules across membranes, and activating specific enzymes or starting signaling cascades. In sum, control mechanisms act as bridges between different domains, transforming a physical or chemical source of information into a functional activity. There is no necessary relationship between the change in the receptor of the control mechanisms and the resulting activity of the controlled mechanism (see also Farnsworth 2023). The connection between measurement and operations of control mechanisms is not determined by the nature of the information source but is arbitrary and depends on the structure of the control mechanisms. Framing information processing in these terms has important consequences. It justifies shifting the focus of analysis of cognitive activities from the intrinsic properties of signals to how they are received and transformed, more specifically from the transmission of electric signals along a membrane to chemical interactions.

To understand the richness of the cognitive activities involved in making and executing decisions related to eating, it is important to move the focus from the reception and processing of information to the role these activities play in the context of the whole organism. This shift foregrounds three aspects that need to be considered, and that shed light on fundamental requirements for cognition and on the differences in how it is realized. The first is the integration of information. Control mechanisms do not necessarily operate on the basis of the measurement of one variable by one sensor but rather usually integrate measurements performed by multiple receptors. Receptors in cells are often organized in clusters, with the effector activity of a control mechanism depending on combining information from these sources. Moreover, integration of information is often achieved through crosstalk between different control mechanisms, each sensitive to different sets of features of the internal and external environment.

The second aspect is the distribution of information. Once measurements are made and information gathered, it needs to be made accessible to different parts of the organism. Unicellular systems mostly rely on diffusion and active transport to do this. In multicellular systems, distribution is a challenge, as information may need to reach different ensembles of cells across different distances in increasingly larger bodies with a high number of components. This cannot always be achieved through unconstrained diffusion. Different species of multicellular systems employ different strategies to reach the desired target, such as confining signals to a module or using the vasculature or a nervous system.

The third aspect is the coordination of parts to carry out the activities required by the whole organism. Controlled activities such as foraging and feeding need the coherent behavior of many cells if not of the entire body. This requires the coordinated activity of multiple control mechanisms sensitive to different sources of information and jointly operating to orchestrate the basic behaviors of individual or large ensembles of cells, often organized in modules, tissues, and organs. These control interactions are realized by adopting strategies already employed by unicellular organisms, such as the secretion of chemical signals in the extracellular milieu and the conduction of ion changes along the membrane of cells. However, multicellular systems face the additional challenge of transmitting over yet longer distances and the need to reach specific target cells that exhibit receptors for the signal molecules.

In the following sections we discuss how animals without a nervous system belonging to the phyla of Porifera and Placozoa perform the cognitive activities required for eating and respond to the integration, distribution, and coordination challenges faced by multicellular organizations. We focus on control as exerted by individual cells or groups of cells that employ chemicals to direct and coordinate the productive activities carried out by other types of cells within these multicellular organisms.

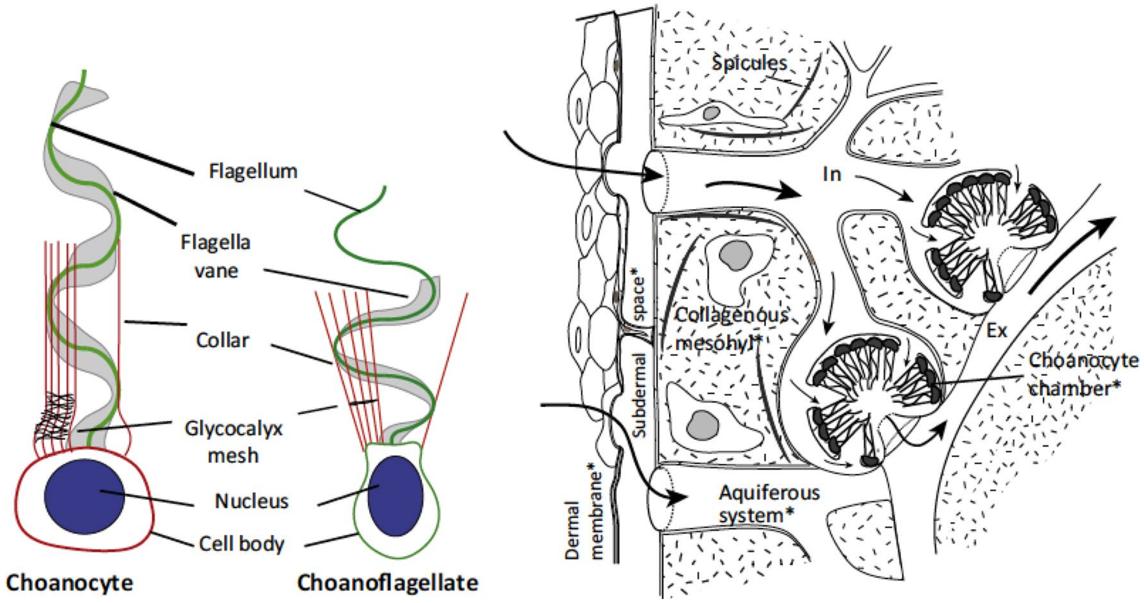

Fig. 1 *Left* Comparison of choanocytes in sponges and choanoflagellates. *Right* Situating choanocytes within the multicellular environment in sponges. From Dunn et al. (2015)

Information Processing to Regulate Eating in Porifera

Porifera is a diverse phylum with nearly 9000 identified species. These are classified in four groups: demosponges, calcareous sponges, glass sponges, and homoscleromorph sponges (Godefroy et al. 2019). Demosponges are the most numerous and most studied. Although there are important differences in eating behavior between sponge species, we abstract from these and focus on the common mode of eating employed by sponges and the information processing they employ to regulate this activity.

Sponges are distinctive among animals in relying exclusively on intracellular digestion. This limits the size of food that they can eat. Although some sponges are carnivorous, feeding on somewhat larger prey by phagocytosis (Vacelet and Duport 2004; Martinand-Mari et al. 2012), most sponges rely on filtering small food particles, including bacteria, from water that flows through them. The task of collecting and taking up these particles is performed by specialized cells in their interior, choanocytes. Choanocytes resemble *choanoflagellates* (Fig. 1, left), single-cell eukaryotes that constitute the sister group to animals. Choanoflagellates feed by generating an undulatory wave with their flagellum that pumps water away from the cell. This creates a pressure drop around the base of the flagellum that results in food particles present in the water collecting on the collar of microvilli surrounding the flagellum. Those particles that are small enough are taken up into the cell by pinocytosis and metabolized internally. While choanocytes resemble choanoflagellates both in their morphology and their way of capturing food,[4] there is a major difference—choanocytes are just one of multiple cell types forming a sponge. Its other cells are dependent on the choanocytes for their nutrition. Choanocytes are also dependent on these other cells as they constitute the ecosystem creating the flow of water from which choanocytes can extract food. The core of this ecosystem is the choanocyte chamber in which typically 80–100 choanocytes reside with their flagella oriented

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[4] For many decades these similarities led researchers to assume that choanocytes and choanoflagellates were homologous (Brunet and King 2017), with the rest of the sponge developing around the inherited cell type. Recently more detailed examination of cell structure, operation, and development has challenged this assumption (Mah et al. 2014). Laundon et al. (2019) have reconstructed both choanocytes and choanoflagellates from serial electron micrographs, and identified both many similarities but also differences—choanocytes devote more of their cell volume to food vacuoles and less to glycogen reserves and mitochondria. Choanoflagellates are genetically more similar to sponge archeocyte cells, stem-like cells which are thought by many to be the ancestral metazoan cell type (Sogabe et al. 2016; for discussion, see Steinmetz 2019). There has been active debate as to whether sponges represent the earliest multicellular animals; an alternative view argues that ctenophores, which have neurons, arose earlier. We do not address that debate. We do note one attractive proposal, articulated in particular by Nielsen (2008, 2019), according to which the first metazoan, a choanoblastaea, consisted of a colony of choanocytes, cells that resemble choanoflagellates but are derived from division of a common cell, with individual cells adhering to each other surrounding a hollow sphere with their flagella directed outwards. This arrangement facilitates sharing of nutrients and provides a context for differentiation of cell types, both between choanocytes and in the hollow sphere. The major change in sponges is the inversion of the choanocytes so that their flagella are directed inwards, not outwards.

inwards (Fig. 1, right).[5] The only water to which they have access is that which enters the choanocyte chamber from the aquifer system that fills much of the interior of the sponge. Water enters the sponge through small pores, ostia, in the layer of epithelial cells that constitute the outer layer of cells, and then passes through a branched canal system to the choanocyte chamber. Water leaving the chamber passes through more canals until it is forced out through a large pore, the osculum. A large volume of water is pumped through a sponge and filtered each day—up to 1000 times the volume of the sponge's body. The pumping is produced by the coordinated beating of the flagella of the choanocytes constituting the chamber. Coordinating this beating is itself an information-processing challenge. Musser et al. (2021) propose that it is regulated by neuroid or center cells that they identified as situated among the choanocytes (typically, one at the center or in the lining of each choanocyte chamber), with extensions contacting the microvilli collars and cilia of individual choanocytes. These cells create and release secretory vesicles that could, for example, signal to the choanocytes to arrest their cilia. Arrest enables a sponge to engage in larger-scale activities such as the contraction of part or all of the sponge's body. We focus on this behavior and its control below, but first it will be helpful to introduce some of the other cell types which figure in it and other eating-related behaviors of sponges.

Musser et al. (2021) identified 18 different cell types in sponges that are organized into three tissue types. In addition to choanocyte chambers there are epithelial tissues (lining the outer covering, the canals of the aquiferous system, and a basal attachment layer) and mesophyll tissues (stem, skeletogenic, and other mesenchymal cells).[6] As the choanocytes are the primary digestive cells, cells in the other tissues must procure their nutrition from them. Choanocyte chambers are immediately surrounded by the mesophyll, a gelatinous matrix that contains various types of cells including motile amebocytes—so named because they move like amoeba. These cells contain spicules, protein structures that, among other things, provide the canal structure. Of particular relevance to feeding behavior, they transport nutrients from choanocytes to other cells. They take up nutrient vacuoles created by the choanocytes and ferry them to other cell types.[7] They move through the sponge by temporarily extending projections known as pseudopodia (generated by polymerizing actin) in the direction of movement. Little is known at present about the information that is processed to regulate these movements.

The mesohyl is in turn surrounded by an epithelium-like structure consisting of various types of flat cells referred to as *pinacocyte*. Exopinacocytes serve to seal the sponge from the environment and secrete substances that enable sponges to adhere to surfaces (Adams et al. 2010). Basopinacocytes secrete an adhesive extracellular matrix. Endopinacocytes line the internal canals and are thought in some cases to contribute to eating by taking up large particles by phagocytosis. These various epithelial cells perform important regulatory functions in sponges, sensing features of the environment, initiating contractions, and generating signals (Ca^{2+}) that act on metabotropic receptors in other cells. They also regulate the canal diameter (Leys 2015).

Adult sponges spend their lives attached to objects in the ocean or in fresh water. Many do move short distances as adults, but by far the most apparent movements are large-scale contractions involving much or all of the sponge's body. It is thought that a major function of these contractions is to eject inedible debris that collects through the feeding process. Contraction takes place over a period of minutes,[8] with each species doing so in its own stereotypical fashion. When contraction is limited to the inner canals and the osculum, it may appear as a twitch. When extended to larger parts of its body, it generates a ripple (sequential contractions of different parts of the sponge) or a cringe (a contraction occurring simultaneously across the whole body). One form of contraction, known as sneezing, is especially complex. It involves inflating and then contracting the whole body over several minutes. The process is initiated by contraction of the osculum, which prevents water from escaping. Using time-lapse video imaging, Kornder et al. (2022) showed that, as it sneezes, *Aplysina archeri* pushes mucus towards the inlet pores (ostia), creating a "mucus highway" that traps particles as it moves. The mucus is then forced out through the ostia and clumps on the surface of the sponge before being shed into the water.

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[5] The choanocyte chambers are the center of a modular design that differs from that of animals that are divided into organs (Kumala et al. 2023). Instead of a common set of organs meeting the metabolic needs of the entire organism, each module is essentially self-sufficient and the whole sponge can increase in volume by adding additional modules with their own complement of different cell types.

[6] A distinctive feature of mesophyll cells is that cells are highly plastic, able to switch structure and function as needed by the organism (Ereskovsky and Lavrov 2021).

[7] In addition, amebocytes also produce eggs for sexual reproduction and deliver sperm produced in choanocytes to eggs (sponges also reproduce asexually by budding or fragmentation). Finally, these cells also act like stem cells, differentiating into cells with more restricted functions, such as collencytes and lophocytes, which synthesize a collagen-like protein that maintains the mesohyl; sclerocytes, which secrete silica spicules; and spongocytes, which synthesize spongin that also constitutes mesohyl.

[8] An exception is glass sponges in which contraction is much quicker, a capacity attributed to the fact that these sponges employ electrical as well as chemical signaling. The electrical signal is transmitted along a syncytial tissue that connects the whole body and propagates a signal via Ca^{2+} channels that causes a flagellum pump to stop.

Sponges do not have a dedicated type of cell, muscle, to produce these movements. They nonetheless make use of the same intracellular actomyosin machinery used in muscle cells in other animals. In sponges this machinery is found in other types of cells. As in muscle cells, this machinery generates movement as the head of myosin filaments binds to actin and exerts force to pull actin filaments along it.[9] We focus on the actomyosin mechanism found in pinacocytes as these cells are principally responsible for the contractility manifest in whole body contractions.[10] Colgren and Nichols (2022) presented evidence from immunofluorescence that, as in other animals, Ca^{2+} serves as the signal for actomyosin contraction. It acts on a regulatory light chain on myosin that, as in vertebrate smooth muscle, functions as a switch as it is reversibly phosphorylated and dephosphorylated. (Musser et al. 2021 also found that pinacocytes also express other molecules that figure in control of smooth muscle in vertebrates, including tropomyosin, calmodulin, calponin, and transgelin.)

Having identified one locus at which control of contractions is localized, we turn now to what kind of information processing occurs at this locus to initiate contraction. Whereas in higher animals, researchers often stimulate neurons to elicit responses, this is not possible in organisms without neurons. But researchers have searched in sponges for molecules and receptors that figure in neurotransmission in Eumetazoa and found that a number of these are present. In particular, the two most widely employed neurotransmitters in the vertebrate central nervous system, glutamate and GABA, are present. In higher animals these transmitters often act on ionotropic receptors that directly initiate action potentials in the recipient neuron, but sponges do not appear to have ionotropic receptors. But both glutamate and GABA are also known to act on metabotropic receptors that initiate metabolic responses in the target nerve or muscle. Elliott and Leys (2010; see also Ludeman et al. 2014) showed that sponges have metabotropic receptors for both glutamate and GABA as well as nitric oxide (NO). Much as in vertebrates, they found that application of glutamate triggered contractions while GABA inhibited the response. They further demonstrated that NO initiates contraction of the osculum. In a recent study, Fabian et al. (2023) present evidence that sponges contract by relaxing a default tensional state mediated by actomyosin, proposing that the behavior should be called deflation, not contraction. They found that this process is directly initiated by the convergence of nitric oxide or cAMP on the PKG/PKA pathway.[11]

This research reveals that even before the evolution of neurons, information processing affecting eating behavior employed molecular signals and receptors. To further understand the process, one needs to examine the generation of these chemical signals. Some contractions occur spontaneously in a rhythmic manner (in some cases, daily) while others occur in response to stimulation, especially when particles block its water filtering system.[12] Identifying the control mechanism for spontaneous rhythmic contractions is challenging as it requires finding an oscillating pattern generator. For cases in which the contraction occurs daily, Jindrich et al. (2017) provided a suggestive lead when they showed that sponges possess several of the genes that figure in the circadian clock in other animals. Since they don't possess the complete clock mechanism found in other animals, further research is needed to determine how these genes might figure in generating rhythmic daily contractions in sponges. It is generally easier to supply stimuli to see if they initiate a response. Following this approach, researchers are beginning to identify the signals that initiate contractions. Sneezes, for example, can be triggered by mechanical or chemical stimuli, such as application of glutamate, glycine, acetylcholine, serotonin, dopamine, cyclic AMP, caffeine, and nicotine. The results with GABA are more complex: applying it in *Tethya wilhelma* stimulates sneezes, while doing so in the freshwater sponge *Ephydatia muelleri* inhibits them. Researchers have also made progress in identifying the mechanisms that respond to mechanical stimuli. Sponges possess sensory cilia along the osculum, sporadically along the canal system, and at specific locations on the epithelium. These cilia are short (4–6 μm) and, like primary cilia in other animals, manifest the typical nine sets of microtubules but lack central microtubules that are typically present in motor cilia. They are thought to initiate a Ca^{2+} wave when the cilium is moved. Transmission between cilia and pinacocytes is largely thought to rely on classical amino acid transmitters such as glutamate and GABA (Leys 2015).

There are other features of their behavior that sponges clearly regulate, although the mechanisms are not yet known. One is the speed of flow of water through them. Initially this

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[9] While actin is found as in prokaryotes, where it forms a dynamic cytoskeleton, myosin has been found only in eukaryotes. Within the lineage of single cell eukaryotes, two families of myosin are differentiated—one that acts relatively slowly and is the ancestor of myosin found in smooth muscles in vertebrates while the other acts much faster and is the ancestor of that found in skeletal muscles. Both families are found in sponges.

[10] Musser et al. (2021) also found actin filaments in irregularly shaped deep mesenchymal cells that are located around choanocyte chambers, which they refer to as *myopeptidocytes*. In addition to actin itself, they express tropomyosin and the actin binding protein coactosin. The function of actin in these cells is not yet known—they may figure in the amoeboid motility discussed above or the large-scale contractions of the sponge. These cells also exhibit markers of lytic vacuoles, suggesting they may be involved in phagocytosis.

[11] They found that the response resembled the inflammatory response of the innate immune system in higher organisms.

[12] Leys et al. (2019) for a description of how cameras have been used to document sponge behavior in the wild.

was thought to be unregulated, determined by the flow in the environment. But Ludeman et al. (2017) showed that many sponges act to reduce the rate of flow, which they proposed to be due to the need to reduce the energetic costs of operating the flagellum that generates flow. Kumala et al. (2017) showed, through an examination of osculum explants, that filtration rate is responsive to the dynamics of the osculum opening or closing—specifically, varying the osculum cross-sectional area accounted for more than 90% of the variability in filtration rates. The authors could not identify any environmental triggers for the osculum dynamics and proposed that it is governed by stimuli generated within the sponge. They further proposed that it might be partly regulated by the bacteria the sponge hosts—the bacteria may require reduced oxygen, which the sponge host provides by temporarily ceasing pumping action. A clue to how bacteria can do this was offered by Xiang et al. (2023), who showed that at least one sponge species, *Amphimedon queenslandica*, has genes for receptors for dopamine, a chemical it does not produce. The researchers traced dopamine to two bacterial symbionts and showed that, at least in the larval stage, the sponge is responsive to externally applied dopamine.

In this section we have focused on the feeding behavior of sponges, a behavior in which choanocytes play a central role but must rely on multiple other cell types, especially those that determine the flow of water through to the choanocyte chamber. Of particular importance are periodic contractions, especially sneezes, that serve, among other ends, to remove debris and clean the system. Coordinating this behavior requires that different cells in the sponge acquire information and use it effectively to determine their behaviors. That is, the sponge must engage in cognition. Given the multiple modes of control exercised in sponges, a natural question is how are sneezing and other behaviors coordinated. One might think that centralized control would be required to prevent conflict between different behaviors by different parts of the sponge. But there does not appear to be any central control. As noted by Leys et al. (2019, p. 761), "Massive effects on one osculum have no effect on a neighboring osculum. Global responses are most likely cumulative responses to the same stimulus." Accordingly, sponge cognition appears to be distributed—different information processing is carried out by different cells.

Information Processing to Regulate Eating in Placozoa

Placozoa is the other phylum without neurons (or specialized muscle cells). Until recently, *Trichoplax adhaerens* was the only known species in the phylum and it is by far the most studied.[13] *Trichoplax* are small, flat discs, about 1 mm in diameter and 15 µm in height; the shape of the disc is irregular and changes frequently. *Trichoplax* means "hair plate," an apt description of their body, while *adhaerens* means "sticking," characterizing their behavior of sticking to surfaces. Although *Trichoplax* and other species of Placozoa are found in tidal zones of all the world's oceans from south of New Zealand to north of Scotland, there are no systematic studies of *Trichoplax* or other Placozoa in their native habitats. In laboratories they are maintained on dishes. They glide over the surface, stopping to feed where food (mostly green algae and cyanobacteria) are most abundant.[14] As noted in the introduction, their feeding pattern is distinctive—they release digestive enzymes onto the algae beneath them and then take the digested products up into their bodies.[15] Accordingly, Kaelberer and Bohórquez (2018) speak of *Trichoplax* as a "wandering gut."

Before turning to how they execute and regulate this feeding behavior, we offer a brief description of the cellular composition of *Trichoplax*. It consists of three layers of cells, an upper (dorsal) water-facing protective epithelial layer, a middle layer, and a lower (ventral) surface-contacting epithelial layer (Fig. 2). In recent years researchers have identified as many as nine different cell types (Schierwater et al. 2021). The primary cells in both the dorsal and ventral epithelia are ciliated epithelial cells (together they make up 72% of the cells in *Trichoplax*).[16] These cells are joined together by adhaerens junctions that fix the relative position of each cell but allow diffusion of molecules smaller than 10 kDa (Smith and Reese 2016). Epithelial cells have cilia that generate coordinated beating movement.[17] Those on the ventral side contact the surface beneath the Trichoplax and exert force that enables *Trichoplax* to crawl. There does not seem to be any communication between ventral

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[13] Three additional species have been identified very recently: *Hoilungia hongkongensis* in 2018, *Cladtertia collaboinventa* in 2022, and *Polyplacotoma mediterranea* in 2019. There are estimates that there are more than 100 species yet to be identified.

[14] In addition to feeding behavior, researchers have also investigated how *Trichoplax* adjusts its activities in response to detecting temperature (Zhong et al. 2023).

[15] The extinct organism, *Dickinsonia* (Sperling and Vinther 2010), lacks any mouth, gut, or anus and is hypothesized to have fed in a similar manner.

[16] These cells in *Trichoplax* lack a basal lamina separating them from the organism's interior that is characteristic of epithelial cells in Eumetazoa. Accordingly, these cells are sometimes referred to as *epitheloid*. The nuclei of epithelial cells on the dorsal side protrude into the animal, assuming a T-shape. They are also contractile (Armon et al. 2018).

[17] The movement of cilia is produces by axonemes, structures involving nine pairs of microtubules surrounding two central ones. Movement is generated by dynein arms that generate opposing motions on the two sides of the axoneme, causing it to bend back and forth.

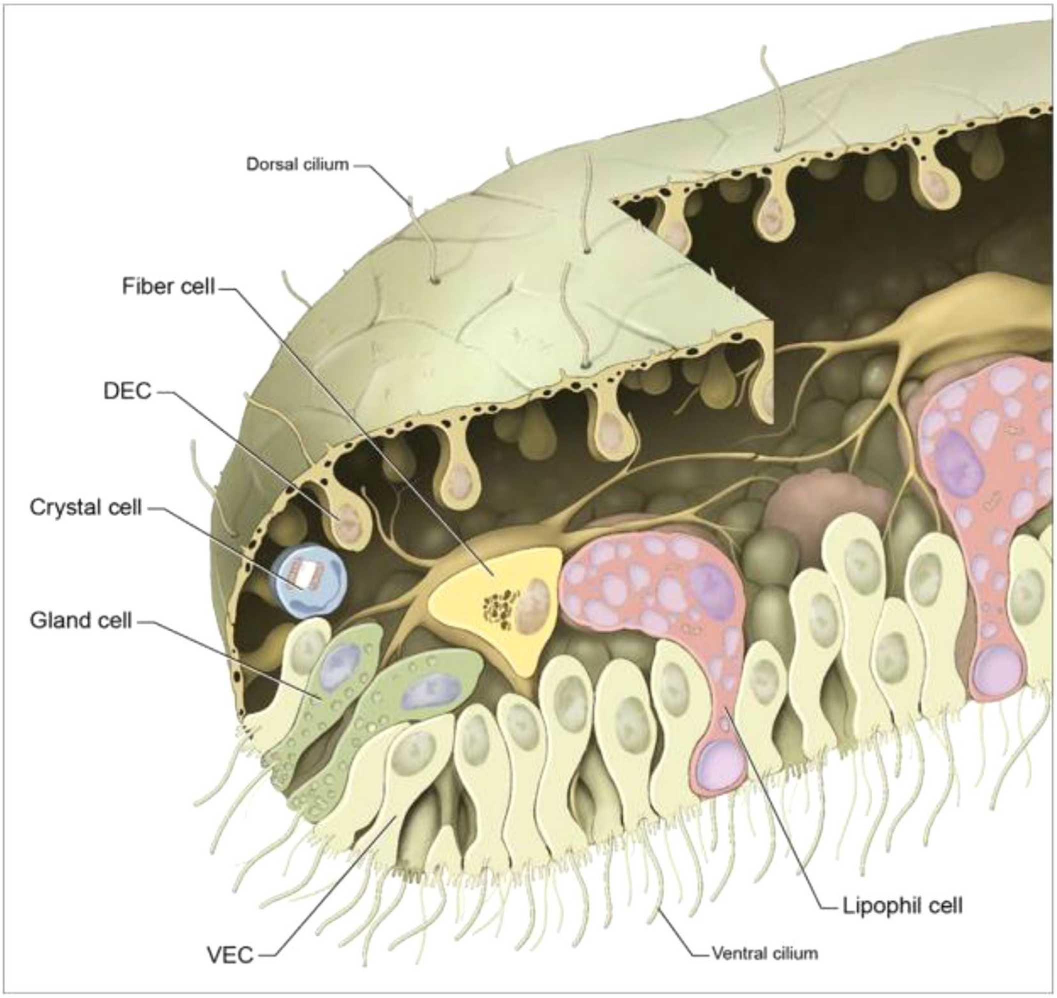

Fig. 2 Major cell types in *Trichoplax adhaerens*. From Smith et al. (2014)

epithelial cells to coordinate the beating; rather, coherent behavior results from physical forces transmitted through the junctions between the epithelial cells. Surrounding the cilia are microvilli through which the epithelial cells take up digested material, which is then shared with other cells by transcytosis. Interspersed among the epithelial cells on the ventral surface are lipophil cells and gland cells. Lipophil cells synthesize digestive enzymes and release them in large granules. These enzymes act on the algae beneath them. Mayorova et al. (2019) distinguish at least three types of gland cells. They found that those of the most numerous type secrete mucus that then coats the outside of the *Trichoplax* as well as the surfaces over which it moves. The different types of gland cells also synthesize and release a number of peptides that function to coordinate the behavior of different cells. We return to these signaling peptides below.

Fiber cells constitute the primary cell type in the intermediate layer. They form a multiply branched syncytium, a network of shared cytoplasm with numerous nuclei that, as a result of containing actin and myosin, are able to modify their shape (Smith et al. 2014). Because this network is in contact with both the ventral and dorsal epithelial cells and extends processes that contact multiple epithelial cells as well as lipophil cells, when they change shape, they produce dynamical change in the whole body. Among other things, these shape changes can modify the direction in which *Trichoplax* moves. Fiber cells also perform other tasks. When *Trichoplax* are wounded, fiber cells appear in the wound area, suggesting they figure in wound healing (Mayorova et al. 2021). Often endosymbiont bacteria are phagocytized by fiber cells and live within their endoplasmic reticulum (Schierwater et al. 2021). At the periphery, fiber cells interact with crystal cells that contain calcium carbonate and are thought to be gravity sensors (Mayorova et al. 2018).

We turn now to *Trichoplax* feeding behavior. When they are crawling over a surface and detect food, they stop for several minutes and hover over the site. Lipophil cells closest to the detected food release large (up to 3 μm) granules of digestive enzymes (trypsin, chymotrypsin, and phospholipase 2, a homolog of the human pancreatic enzyme). These rapidly begin to lyse the algae or bacterium into consumable particles. At the same time gland cells release additional mucus that generates pockets that prevent diffusion of the particles until they are taken up by endocytosis into the microvilli of epithelial cells. The mucus may also serve to protect the ventral epithelial surface from the digestive enzymes. When they have stalled for a sustained period or the food is consumed, *Trichoplax* dissociate from the substrate and fold up, with their ventral surface inside the fold. They then rotate before upfolding and reestablishing contact with the substrate. After they do so, they begin to move, leaving a mass of mucus at the site of attachment (Mayorova et al. 2019).

Much of the investigation of control of feeding behavior has focused on the how *Trichoplax* pauses in response to detected food. Senatore et al. (2017) show that the process is regulated by the release by gland cells of two peptides, FMRFamide and an endomorphin-2-like peptide (ELP), YPFFamide. These diffuse to epithelial cells where they act to stop cilia from beating.[18] These gland cells are relatively sparse and not likely to generate a signal that can reach distant epithelial cells. Senatore et al. hypothesize that these cells employ positive feedback to enhance their signal—the gland cells have ELP receptors and release additional peptides when they detect ELP released by other cells. This response is nonetheless typically limited to cells nearest to the food source.[19] The movement of *Trichoplax* when not feeding appears to be random. But Smith et al. (2019) determined *Trichoplax* engage in chemotaxis, navigating up a chemoattractant gradient towards food. The process is not centrally controlled; rather, each epithelial cell detects the gradient and initiates its own motion. The physical connectedness of the cells and elastic forces in their mechanical response constrain the cells to move as a group. The ability of individual cells to respond on their own is evident in the individual movements of cells in the interior of the ventral surface where these constraints are relaxed.

The catalog of chemicals that have been identified as involved in the information processing controlling eating behavior continues to expand. Recently, Nikitin et al. (2023) tested *Trichoplax's* response to several known signaling molecules. They found that glutamate and ATP initiate feeding behaviors even in the absence of food whereas GABA and glycine suppress them. They also investigated the receptors in *Trichoplax*. They identified 14 ionotropic glutamate receptors,[20] 34 metabotropic glutamate receptors, and 37 metabotropic GABA receptors and described this as "the richest repertoire of amino acid receptors among all analyzed animals, from sponges to humans" (2023, p. 8).

The use of peptides and other chemicals to regulate behavior extends beyond feeding. One way researchers have identified chemical signals used by *Trichoplax* has been to expose the animals to them and record their responses. Varoqueaux et al. (2018) did this for eleven peptides and found that several elicit whole body movements: PWN and SIFGamide cause Trichoplax to crinkle (the response to SIFGamide was significantly stronger), while LF and LFNE cause it to rotate, assuming a different shape with each peptide. Other gland cells release different peptides—one type expresses an insulin-like peptide (Ins3) that has been implemented in metabolism as well as growth and development. Fiber cells release peptides, glycine, nitric oxide, and other low-molecular weight neurotransmitters whose role is not well understood.

Although mostly studied as solitary organisms in the laboratory, *Trichoplax* have been observed to feed socially, joining into groups over algae. Doing so enables them to increase the digestive enzymes released, making more nutrients available for consumption (Smith et al. 2015). In an aquarium with rocks covered with algae, Fortunato and Aktipis (2019, p. 2) described how "aggregated animals formed a 'moving front' which consumed the algae as it moved along the surface of the aquarium... digesting the algae as they passed." They observed that, when algae were plentiful, the number of *Trichoplax* increased to several hundred in multiple groups, many containing only three animals, but some over 100. Notably, animals in a group tend to stop together when food is detected. This behavior likely results from the same peptides that act to stop cilia in a single animal—the peptides diffuse into the media and act on receptors in individual epithelial cells in nearby animals. As within the animal, other animals that detect the ELP release their own, resulting in a spreading signal (Senatore et al. 2017).

Conclusion

Eating is a fundamental activity for organisms and in multicellular organisms requires coordination of different cell types. For cells to coordinate to achieve this goal, they must procure information, both about conditions in the organism

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[18] As in sponges, the cilia response to peptides is mediated within cells by Ca^{2+} signaling.

[19] Much about this process remains to be understood. Smith and Mayorova (2019, p. 357) refer to the "yet to be identified cell type [that] detects algae and triggers secretion from nearby lipophil cells, while the temporal coordination of secretory events in different parts of the animal would seem to require a mechanism for long-range communication."

[20] Ionotropic receptors modulate membrane currents, including action potentials. Although little is known about how they are employed, Romanova et al. (2020) found evidence of action potentials in four species of Placozoa.

and in its environment, process that information to decide on activities, and alter conditions in the cells that will carry out the required activities. We have identified this as a foundational cognitive activity. To identify basic cognitive processes involved in controlling eating, we have turned to two phyla of early evolved animals that lack neurons, Porifera and Placozoa. Their information processing involves releasing chemicals from specific cells, with other cells possessing receptors appropriate to these chemicals responding. Unlike Eumetazoa, these animals lack an internal canal in which they digest food. In both phyla, food is directly taken up by one cell type. In sponges, other cell types direct sea water to chambers of these cells and then disseminate the food that is acquired to other cells. These are activities that must be controlled on the basis of information processed. Placozoa carry out the additional activity of digesting food, which they do in a mucous medium they create outside their body. This too requires specific cells to acquire information and direct activities in themselves and other cells. Neither Porifera nor Placazoa have to regulate an internal digestive tract. This enables researchers to limit their focus to the eating activities in which these animals do engage and to investigate how they control these activities. We have reviewed what they have learned in these investigations about how the generation and processing of chemical signals enables these animals to procure the nutrients they require to maintain themselves. This analysis supports the thesis that cognition is first and foremost a chemical phenomenon, common to all living organisms regardless of the presence of a nervous system. When a nervous system is present, it enables rapid transmission of information over longer distances, but the processing still involves the chemical processes occurring within and between neurons (including those that produce ionic differences across neural membranes that can be transmitted).

One theme that emerged with both sponges and *Trichoplax* is that different cells in the organism perform different acts of information processing. This may seem like an important difference between their cognitive activities and those in us that depend on a centralized brain. But that is mistaken on two counts. First, brains themselves are composed of large numbers of neurons (as well as other cell types such as glia), organized into different brain structures. Neurons in one structure operate differently from those in other structures, and overall activities are determined by the interaction of different neural populations. Second, the information processing in us is not restricted to the brain—it involves neurons and other cell types located in diverse tissues of the body.

Clearly much remains to be understood in terms of how Porifera and Placozoa carry out the information processing that controls their feeding behavior. What has been discovered, and what we have described in this article, suffices to show how research on these animals can provide foundational insights into the cognition of eating.

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Declarations

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