Introduction

Liquid brains, solid brains

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Cognitive networks have evolved a broad range of solutions to the problem of gathering, storing and responding to information. Some of these networks are describable as static sets of neurons linked in an adaptive web of connections. These are 'solid' networks, with a well-defined and physically persistent architecture. Other systems are formed by sets of agents that exchange, store and process information but without persistent connections or move relative to each other in physical space. We refer to these networks that lack stable connections and static elements as 'liquid' brains, a category that includes ant and termite colonies, immune systems and some microbiomes and slime moulds. What are the key differences between solid and liquid brains, particularly in their cognitive potential, ability to solve particular problems and environments, and information-processing strategies? To answer this question requires a new, integrative framework.

This article is part of the theme issue 'Liquid brains, solid brains: How distributed cognitive architectures process information'.

1. Introduction

As complex living forms emerged around the time of the Cambrian explosion, cognition and the networks sustaining it became a major enabler of multicellularity. The scale and complexity of multicellular organisms led to specialization of cell types and function, goal-directed movement, and other coordinated behaviours, requiring improved perception and memory of the environment. Although behavioural patterns were already present before the advent of neurons [1], the appearance and rapid expansion of neural components facilitated new complex behaviours. These evolutionary achievements would have been impossible without neurons, their precursors and the circuits that emerged after them; they transformed the living landscape in profound ways. Information became an essential part of how complex organisms adapted to new conditions within their life spans, allowing much faster and more flexible responses than those allowed by genetic information. One path in the tree of life that emerged from the Cambrian era included bilaterians—animals with a well-defined lateral symmetry. Within this group, nervous systems appeared that spread their neurons in a symmetric configuration. These networks ultimately evolved into segregated masses of neurons that are organized in a distinct central control system. The 'first' brains were formed [2] and became powerful prediction machines [3].

The *moving hypothesis* posits that active exploration of an organism's spatial environment was a key step in the evolutionary trajectory that produced brains [4]. From this viewpoint, prediction is both a cause and a consequence of animal movement, and its implementation required learning networks to emerge [5]. Predation was likely the most important selective pressure to create learning networks [6]. This powerful evolutionary innovation was not limited to neural networks, and we suggest here that the many kinds of networks of interacting agents that evolved to process information have characteristic similarities and differences.

Information processing networks can be found in microbial communities, inside cells (as gene regulatory webs), and in immune systems. The diversity of architectures and information-processing strategies of these networks is stunning. Fluid webs of information exchanges among thousands or even millions of ants or

termites unfold in most of the biosphere [7,8]. Simple life forms known as slime moulds, made of a single macroscopic (multinucleated) cell, can solve complex problems. Plants seem to occupy a very different region of the space of cognitive networks, lacking neural-like structures and physical movement, yet defining a tremendously successful and ecologically important group. Liquid computers and chemical reactions provide a rather different set of case studies, where computation and informational processes are not clearly defined. In this context, developmental programmes and pattern formation are also considered to be forms of cognition [9].

What is common among all of these disparate examples? Are there well-defined classes based on organizational structure, mechanism, or function? Is the physical state associated with each system a major constraint on the types pf computations that can be achieved? Are there basic design principles and constraints that would allow us to predict systems that have not yet been discovered by evolution? Are there strategies that have been discovered by natural evolution that could lead to new forms of computation, perhaps using synthetic biology? Answering these and other fundamental questions was the goal of a small workshop held at the Santa Fe Institute in December 2017. The meeting convened a group of researchers from diverse fields of science and engineering, including social insect behaviour, microbiology, synthetic biology, developmental and systems biology, neuroscience, computer science and statistical physics. Over several days, the participants took the initial steps towards formulating a theory of liquid versus solid brains with the long-term goal of establishing the basis of a general theory of cognitive networks.

2. Liquid or solid, neurons or no neurons

The starting point of this ambitious programme was a high-level review of the space of cognitive networks: small and large, distributed and centralized, modular and hierarchical, alive and artificial. All of them are composed of multiple components that exchange and react to both environmental and internal signals to gather, store and process information. Their nonlinear character requires (in most cases) an appeal to extended views of computation beyond standard definitions [10]. In addition, the collective dynamics exhibited by large populations of agents interacting nonlinearly depends critically on whether or not the basic network components are mobile. We identified two key dimensions to characterize different categories of cognitive networks (figure 1): the physical characteristics of the system, and the presence or absence of neurons.

The second dimension immediately raises the question of how to define a 'brain', a question rarely addressed (with few exceptions, see [11]) in neuroscience textbooks. The standard picture is that a brain is an organ composed of a (usually very large) number of neurons whose functionality is grounded in changing connectivity patterns based on environmental interactions, usually mediated by sensory interfaces. Connectivity patterns are described by synaptic weights, determined over time by patterns of interactions with the environment. An early discussion of the nature of brains and how to define them [12] considered only vertebrate brains. Pagán [13] and Turner [14] extend the question to consider the wider picture, from the smallest brain to very different (solid and liquid) cognitive systems.

The study of brains has flourished over the past few decades, leading to a science of brains where the network perspective has become central [15]. The concept of the *connectome*, defined as the different levels of complexity associated with both anatomical and functional neuronal networks, is today a dominant view in the neurosciences. The reason is obvious on multiple scales. Small neural circuits of single cells connected through their synaptic terminals have been a key element in most classical approaches to learning and conditioning.

Even before complex neuronal networks evolved, microorganisms discovered collective structures that could respond to stressful environments, especially those that posed threats to individual cells. Survival was thus tied to cooperation, and cooperation required novel forms of communication within collectives. To quote James Shapiro: 'bacteria are small but not stupid' [16]. A well-known example of this level of collective behaviour is quorum sensing (QS), a process that involves populations of cells working cooperatively [17]. QS allows groups of bacteria to monitor the presence of other bacteria at a population-wide scale, leading in some cases to the emergence of colony-level coordinated responses. This illustrates how microbial colonies can make collective decisions. In another vein, the collective behaviour of biofilms is illustrated by recent work on long-range electrical communication in bacterial communities [18]. Martinez-Corral *et al.* [19] investigate how similar chemical signalling might exist in both cortical brain activity and biofilm dynamics.

Slime moulds *Physarum polycephalum* are a particularly fascinating example of collective behaviour by aggregates of single cells. Although the organism is single-celled (but including multiple nuclei), in groups it displays highly complex spatial morphological patterns as it explores its environment. *Physarum* moves and spreads in a coherent fashion, coordinated by rhythmic pulses of its cytoplasm. This pulsatile activity occurs within a complex network of connected plasmodial tubes. A rich dynamic involving both chemical and bioelectrical components pervades the behavioural responses and allows the network to arrange and self-modify in the presence of exogenous signals, both activating and inhibitory [20]. The tubes can experience thinning or thickening under low and high nutrient availability, and this has been leveraged by scientists to use them as a biological computer capable of solving optimization tasks, from finding short paths or even solving a maze to computational geometry problems. In all of these cases, the 'output' is encoded in the morphology of the slime mould, arising from the spatial arrangement of repellent or attracting gradients. *Physarum* can also navigate through complex environments using an external memory [21], and they have been observed to make optimal decisions associated with nutritional requirements [22]. As discussed in [23], they also display habituation, i.e. a common adaptive response (displayed by neural organisms) to an unpleasant persistent stimulus. This finding supports the idea that brainless systems can under the right conditions learn from experience to discriminate diverse sources of information.

The boundaries of cognition space can be delineated by considering the simplest 'solid' brains and asking how they do their jobs compared with similarly simple liquid examples [24]. Planarians (flatworms) are a candidate for the first true (i.e. centralized) brains [2,13]. Of particular interest is the tight integration of developmental and cognitive phenomena. As pointed out in [25], remarkable information processing tasks were evolved long before solid brains emerged. Planarians can regenerate every part of their
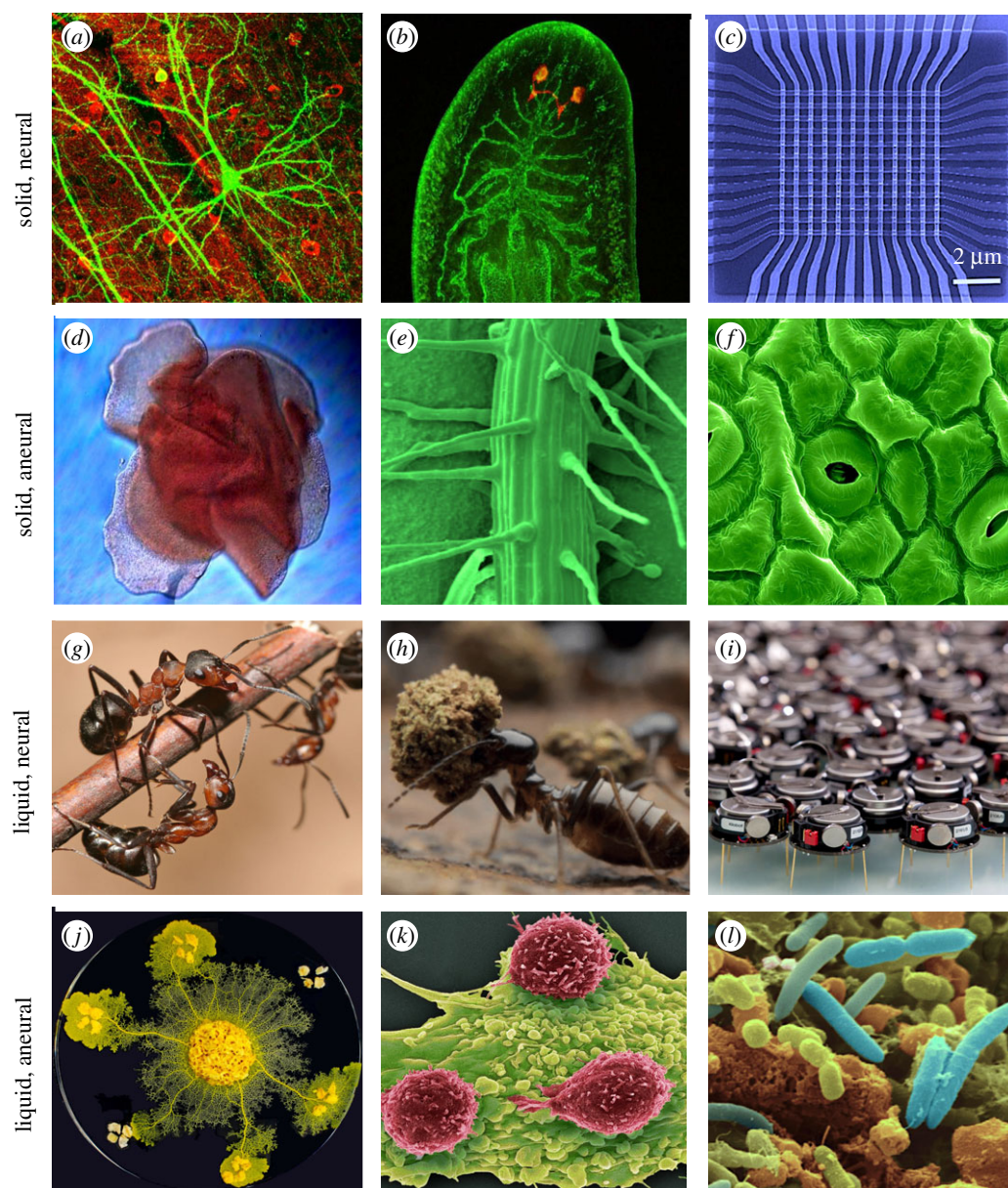
Figure 1. Example cognitive networks. The figure illustrates four classes of cognitive networks, based on whether or not actual neurons are present or absent and on the physical organization of the network. Standard neuronal networks (*a*) involve specialized, spatially localized cells connected through synaptic weights. Simpler organisms, such as planarians (flatworms, *b*) contain neural structures that differ from the more complex brains in panel (*a*). Inspired by real neurons, artificial arrays of *in silico* units (*c*) imitate some of the generic features of their biological counterparts by sensing and responding to environmental signals, but these rigid spatial structures lack neural units. Placozoans (*d*) lack neurons altogether and have very simple anatomical complexity, but exhibit active behaviours. Using a different architecture, plants also lack neurons but some of their modular parts, including roots (*e*) and stomata in leaves (*f*), belong to the 'solid' sub-class. Liquid brains include those formed by agents equipped with their own neural or neural-like components such as (*g*) ant or (*h*) termite societies and their artificial counterparts in robot swarms (*i*). In these liquid brains, each component has its own solid brain. A second major class of liquid brains includes mobile components that lack an internal brain such as (*j*) *Physarum*, (*k*) immune networks and (*l*) microbiome communities. Here there are no neural-like elements and yet in many ways these systems solve complex problems, exhibit learning and memory, and make decisions in response to enivronmental conditions. Finally, there is evidence that both the immune system and the microbiome interact at some level with the brain of the host organism.

bodies [26] and experimental studies show that memories survive decapitation (see Shomrat & Levin [27] and references therein). These results point to a deep connection between neural-based phenomena and somatic memory. Importantly, many developmental responses to perturbations can be mapped into an attractor diagram that represents morphological end states as attractors. The dynamics leading to these attractor-based responses can be implemented in very different types of non-neural hardware, although we still lack a common theoretical framework for describing these systems, as discussed in [9].

The solid, aneural region of cognitive space is shared with other groups of living organisms with different organizations, life styles, and life cycles. Plants, in particular, define a limiting case [28,29]. The cognitive potential of plants was recognized as early as Darwin in a monograph [30], where he pointed to the interesting responses displayed by plants to external signals and environmental cues. Plants exhibit responses that suggest interesting computational abilities [28], and the concept of 'plant intelligence' [31] has also been developed (with some degree of controversy) in recent decades. Communication at multiple scales, in particular, has
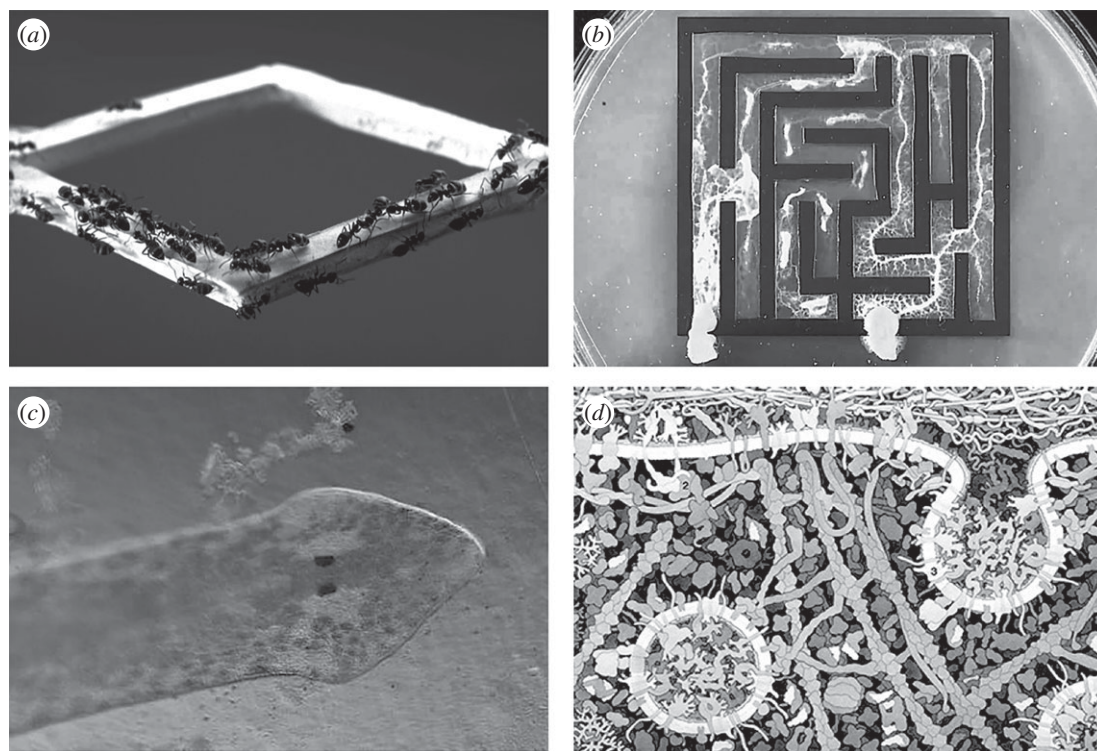
Figure 2. The diversity of computations in liquid and solid networks. Ant colonies (*a*, courtesy of Guy Theraulaz) can be understood as solving a least-action problem where the shortest path is discovered through preferential choice of paths with the highest pheromone concentration. The single-celled plasmodium of *Physarum polycephalum* (*b*) also uses least-action dynamics to solve logic, geometrical, and graph theory problems, including finding the shortest path through a maze. It is less clear how to classify problems solved by planarians (*c*), a class of flatworms whose nervous system is organized bilaterally with a solid 'brain' and two eyes. Planarians feature distributed (versus brain-centric) memory of past events: their morphology is reprogrammable through bioelectric signals which may play a central role in both cognition and development. Finally, single cells contain diverse information-processing phenomena, including complex cascades, genetic–metabolic interactions, and vesicle-associated computations, such as the machinery for storing insulin displayed in (*d*).

been of interest, ranging from networks of stomata in leaves to signals sent through root systems. These examples point to the need for better understanding of information processing in plants [28], including genetic switches and analogue computations that take place within the process of seed dispersal and germination [32]. Intriguingly, these processes involve the 'movable' part of the plant's life cycle.

3. Discussion

The examples described above provide a glimpse of the diverse repertoire of cognitive distributed systems that are naturally described by some sort of nonlinear network of interacting agents [33]. Beyond the specific functional roles they play, such networks will surely share some fundamental properties. Some of the potential commonalities were suggested nearly three decades ago [34], including two key properties shared by most connectionist models: (1) The interactions between the variables at any given time are explicitly constrained to a finite list of connections. (2) The connections can change, in that their strength and/or pattern of connectivity can change with time. Farmer's discussion [34] pointed to these commonalities as the 'Rosetta Stone' for a unified picture (see also [35]). Within the context of liquid brains, these ideas are particularly relevant. Common (perhaps universal) phenomena associated with attractor-like dynamics suggest a statistical physics approach to liquid brains [36,37]. Novel models, general enough to include several case studies (even if in abstract terms) will be needed. These might not necessarily be based

on living systems, as illustrated by the richness of computational phenomena associated with chemical computers (see [38]). Moreover, the liquid–solid term, which we have used here with no rigorous definition, might become rigorously incorporated using mathematical approaches to collective motion that explicitly account for mobile (self-propelled) entities (see [39], and references therein).

Beyond statistical physics, information and computation are central concepts as well, and we lack rigorous models that characterize which computational problems are solved well by liquid brains and which are not [40]. As summarized in figure 2, it is often not clear what kind of formal approach is appropriate. Wood [41] suggests that understanding capabilities of different kinds of brains requires a more formal distinction between information processing and computation, terms that are often used interchangeably. Other powerful computational paradigms, such as Reservoir Computing might be more appropriate when dealing with biological information processing, as discussed in [42].

Vining *et al.* [43] develop liquid cellular automata to demonstrate how liquid systems compute without sophisticated physical network structures. Mobility is shown to increase information flow among moving agents, which encounter and communicate with new agents over time. Calovi *et al.* [44] show that liquid systems, in this case termites, use the physical structure of the surrounding environment as an essential component of computation. Kao *et al.* [45] describe a different sort of hybrid system in which the modular structure of moving animal populations implies that some communication is more persistent and local (as in a solid

brain) even in a larger liquid system, and that this can lead to better collective decision-making in complex environments.

In both ant colonies and *Physarum* networks we can find similar ways of solving problems using the least-action principle. The computation performed is a consequence of a pattern-forming structure. But, it is also important to recognize that there is a human-made set of boundary conditions that allow the slime mould to actually compute the shortest path. How much is this prepared set of conditions defining the richness of computations performed by this unicellular system? In planarians, as discussed above, memory is far from completely centralized, suggesting a totally different form of regeneration-related computation.

At the smaller scale, when dealing with the complex computations performed by a network of molecules within cells, we find a wide array of possibilities, from Boolean-like switches, finite-automaton machines and membrane computations. All of these alternatives operate under highly noisy conditions. Although computational models at this level are usually described in terms of gene regulatory networks, they also take place on different networks [46–48], Silva-Rocha *et al.* 2011. A unified picture of all these types of biological computation would require the proper formulation of a 'computational morphospace' [49].

The contributions to this theme issue collectively provide a first roadmap for the development of an integrative view of network cognition. Understanding the relative computational advantages of liquid versus solid systems is important scientifically, and in the future these understandings are likely to suggest important new ways of thinking about and configuring traditional computations. As computation continues to move off the desktop and into the physical world, we expect that liquid systems characterized by networks of distributed, mobile, and largely autonomous components will become even more important than they are today.

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6

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