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Phylogenetic origins of biological cognition: convergent patterns in the early evolution of learning

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Various forms of elementary learning have recently been discovered in organisms lacking a nervous system, such as protists, fungi and plants. This finding has fundamental implications for how we view the role of convergent evolution in biological cognition. In this article, I first review the evidence for basic forms of learning in aneural organisms, focusing particularly on habituation and classical conditioning and considering the plausibility for convergent evolution of these capacities. Next, I examine the possible role of convergent evolution regarding these basic learning abilities during the early evolution of nervous systems. The evolution of nervous systems set the stage for at least two major events relevant to convergent evolution that are central to biological cognition: (i) nervous systems evolved, perhaps more than once, because of strong selection pressures for sustaining sensorimotor strategies in increasingly larger multicellular organisms and (ii) associative learning was a subsequent adaptation that evolved multiple times within the neuralia. Although convergent evolution of basic forms of learning among distantly related organisms such as protists, plants and neuralia is highly plausible, more research is needed to verify whether these forms of learning within the neuralia arose through convergent or parallel evolution.

1. Introduction

The phylogenetic continuity between cognitive abilities found in Nature remains a controversial topic in the cognitive sciences. Most cognitive scientists by default still seem to adhere to a kind of *cerebrocentrism*: the assumption that only organisms that possess a complex brain exhibit true cognition. In practice, the behaviours of organisms that lack a central nervous system altogether, such as protists, plants and bacteria, are usually excluded from the study of cognition. In microbiology, however, there is a resurgence of attention for cognitive-like phenomena in aneural organisms, especially in microbes. Empirical evidence shows that there is no sharp, qualitative distinction between the behavioural complexities of neural and aneural organisms and that elementary cognitive behaviours are spread all throughout the phylogenetic tree, including plants, fungi, ciliates and even prokaryotes [1–5]. This research suggests that there is a much deeper phylogenetic continuity regarding the cognitive capabilities that govern the behaviour of both neural and aneural organisms, which could fundamentally change our understanding of the role of convergent evolution in biological cognition.

Recently, Frans de Waal [6, p. 282] argued that cognitive science is in dire need of a bottom-up approach to biological cognition, which plausibly explains the rich diversity of cognitive phenomena found in Nature. De Waal claims that cognitive science is preoccupied with relatively complex cognitive phenomena, such as language, self-awareness and observational learning, and that, in the process, the building blocks of these complex cognitive phenomena are ignored. Therefore, he argues for the value of a bottom-up approach to cognition that focuses on understanding the 'nuts and bolts' [7, p. 205] or the constituent elements of cognition.

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In line with Frans de Waal's view, this paper aims to contribute to such a bottom-up, mechanistic perspective for biological cognition by examining basic forms of learning that have long been regarded as the constituents for biological cognition. Specifically, given that comparative approaches to learning and biological cognition in general currently lack a perspective on convergence that extends beyond neural organisms, this paper explores evolutionary convergences between learning behaviours found in aneural organisms and neuralia[1] [8].

The approach in this article avoids a semantic discussion on the precise meaning of abstract concepts such as *cognition* and *mind* but instead attempts to construct a bottom-up perspective that focuses on the constituents of biological cognition [9]. Biological cognition is often viewed as a form of ontogenetic adaptation. That is, while phylogenetic adaptation takes place on the species level over the course of generations, the adaptive processes that we refer to as cognition are part of ontogenetic processes that take place within the lifetime of the individual. Pamela Lyon [4, p. 4] talks about a 'cognitive toolkit', in this context, by discussing a set of ontogenetic adaptive abilities displayed by bacteria that might be considered constituents of cognition, such as sensorimotor coordination in bacteria [10]. These constituents of biological cognition can be formulated in more objective terms that are easier to operationalize and directly transpose to biochemical mechanisms and behavioural processes. By focusing on these constituent processes of biological cognition, more headway can be gained in answering questions such as: 'what is *mind* or *cognition*?'

This article has the following structure. In the first sections, I review evidence for habituation and classical conditioning in protists, fungi and plants, and discuss evidence for convergent evolution for these abilities. Next, I focus on how the evolution of nervous systems set the stage for at least two major events of convergent evolution of adaptive behaviours that are central to biological cognition: (i) nervous systems evolved because of strong selection pressures for sustaining sensorimotor coordination in increasingly larger (i.e. on and beyond the millimetre range) multicellular organisms and (ii) associative learning evolved within the neuralia possibly several times independently, because of the adaptive benefits conferred by modifiable input–output patterns and context-sensitive behaviour. Lastly, I review evidence for convergent evolution of Pavlovian conditioning within the neuralia.

2. The phylogeny of learning

Learning has long been regarded as one of the hallmarks of cognition [11]. Regarding the simplest forms of learning, two broad categories have been distinguished: associative learning, which includes operant (or instrumental) and classical (or Pavlovian) conditioning, and non-associative learning, which includes habituation and sensitization [12]. According to Papini [13], the modern comparative psychology of learning lacks a phylogenetic perspective on homologies and homoplasies, nor does it have an accepted taxonomy of learning. Moore [14] has made an elaborate attempt to remedy this situation by reconstructing a phylogeny of learning, including the convergent and divergent patterns that characterize it. Moore provides a cladogram of 36 different learning processes, including many levels of Pavlovian, instrumental and imitative learning. He concludes that similar processes in distantly related creatures are usually analogous (i.e. based on convergent evolution) rather than homologous. For example, he claims that movement imitation evolved independently through convergent evolution in great apes, dolphins and parrots. Although his analysis is limited to learning in neural organisms, Moore [14] claims that future research should, in principle, be able to discover the hierarchical relationships linking most or all known forms of learning, including those found in protists.

However, in the comparative psychology of learning cerebrocentrism is the rule rather than the exception. Even the definition of learning itself is defined in neural terms by Dukas & Ratcliffe [15, p. 7]: 'the acquisition of neuronal representation of new information'. This definition is unnecessarily restrictive since recent empirical evidence shows that various forms of learning are present in plants, protists and bacteria. Ginsburg & Jablonka provide a more general definition that is better suited to a universal view of learning [16, p. 633]: 'a usually adaptive response to an input (an external stimulus or the organism's own behaviour) in which the input-response relation is memorized; some physical traces of the relation persist and can later be the basis of a more effective response'. This broad definition of learning also includes habituation and sensitization, the most elementary forms of learning.

2.1. Convergent patterns in habituation

Habituation is one of the most ancient forms of learning, and it is found across a wide range of taxa, from single-celled organisms to mammals. Habituation involves a temporary modification of an existing input–output relation, such as a reflex, and is characterized by a response decrement to an iterative or prolonged stimulus. This response decrement should not be due to sensory fatigue, fatigue of the motor response or sensory adaptation [17]. Habituation is an adaptive response in that it enables an organism to ignore repeating innocuous stimuli so that it does not have to waste energy in responding to them repeatedly. In contrast to habituation, sensitization involves an enhanced response to a repeated stimulus. According to Eisenstein *et al.* [18], habituation and sensitization are part of adaptive processes that regulate behavioural homeostasis by optimizing the detection and assessment of external signals, which increases an organism's chances of survival.

Kandel *et al.*'s [19] work on the model organism *Aplysia californica* provides a neuroscience textbook example of habituation. After repeated exposure to harmless tactile stimuli, the withdrawal reflex of its gill and siphon habituates, which is due to presynaptic depression of sensory neurons. This short-term habituation response involves a drastic decrease in the release of the excitatory neurotransmitter glutamate from the presynaptic terminals of the sensory neurons to the post-synaptic terminals of interneurons and motor neurons [19]. In contrast, long-term habituation involves both pre- and post-synaptic changes, in concurrence with NMDA-dependent signalling. These biochemical mechanisms that underlie habituation in invertebrates and vertebrates are highly conserved throughout evolution [20].

The simplest organisms in which habituation is experimentally verified are ciliated protists. Recently, Boisseau *et al.* [1] showed that the unicellular organism *Physarum polycephalum*, also known as the many-headed slime mould, exhibits habituation to substances, such as quinine and caffeine, which are

natural repellents to this organism because of their bitter taste. In this experiment, *Physarum* learned to ignore one of the repellents to get to a food source, over a training period of a couple of days. After 2 days of being non-exposed to these repellents, the response went back to the initial avoidance response, demonstrating the spontaneous recovery of the default behaviour, which is characteristic of habituation. Although the underlying biochemistry of the habituation response in *Physarum* is as yet unknown, the authors of this study speculate that it involves either transient epigenetic markings, which suppress the expression of the involved receptor genes, or an unknown mechanism that increases the activation threshold of the chemoreceptors, leading to a diminished response to quinine or caffeine.

Classic habituation experiments in protists reveal more about the underlying biochemistry of habituation. In these studies, habituation was observed in ciliates such as *Spirostomum ambiguum* [21,22] and *Stentor coeruleus* [23]. In several experiments, Wood [24] showed that after repeated mechanical stimulation *Stentor* ceases its all-or-none contraction response as it habituates to these stimuli. Wood [25] found that habituation in *Stentor* was accompanied by changes in the ionic conductance of its mechanoreceptors. Wood noticed a similarity between the involvement of *Stentor*'s modified voltage-dependent mechanoreceptors, with its calcium permeable channels, and the modifications of the Ca^{2+} permeability of the presynaptic membrane of sensory neurons in *Aplysia californica* during short-term habituation. The use of voltage-dependent ion channels is a shared strategy for habituation, and electrical excitability in general, from protists to metazoa [26].

Also in the plant kingdom, the habituation response of *Mimosa pudica* probably involves modified voltage-gated calcium ion channels. *Mimosa* has been subjected to habituation experiments for over 150 years (see [27] for an overview). *Mimosa* has touch-sensitive leaves, which rapidly fold as a protection measure after physical stimulation. This response, however, ceases after repeated physical stimulation. The folding response is stimulus specific in that habituation can occur in response to the physical touch of, say, a finger, but not to water droplets, or vice versa [28]. Gagliano *et al*. [3] argue that this form of plant habituation might rely on co-option of Ca^{2+}/calmodulin (a calcium-binding messenger protein) signal transduction pathways, which control a wide variety of processes, from the expression of genes in plant roots to neuronal memory process.

According to Moore [14], it is unlikely that these different forms of habituation, from protists and plants to higher vertebrates, are all homologous. Although the biochemical mechanisms that underlie habituation phenomena in protists, fungi and plants are still largely unknown, it is plausible that habituation evolved multiple times independently in these distant phyla. According to Eisenstein *et al*. [29], both convergent and divergent evolution played a major role in the evolution of habituation. Long-term habituation, for example, seems to involve many different pre- and post-synaptic changes, as well as protein synthesis [30].

Some argue that even within the neuralia there are differences in the underlying biochemistry of habituation that point to convergent evolution. Genomic analysis shows that the ion-channel gene family in animals with nervous systems has a complex evolutionary history involving patterns of convergence, divergence and loss events [31], which is likely to have had an impact on the evolution of habituation. For example, the cellular mechanisms of short-term habituation (minutes) in flatworms (*Notoplana*) are reliant on voltage-dependent changes in *post-synaptic* cells [26], whereas the cellular basis of short-term habituation in molluscs such as *Aplysia* is accompanied by *presynaptic* changes. The latter involves a decreased influx of Ca^{2+} at the presynaptic membrane of the sensory neurons, which, after a cascade of events, leads to presynaptic depression [32]. According to some authors, these structural differences possibly point to convergent evolution, although homology is not excluded. However, Glanzman [33] is highly critical of this distinction in vertebrate and invertebrate forms of synaptic plasticity. He claims that these presumed differences are misleading and that vertebrates and invertebrates share highly conserved mechanisms of synaptic plasticity. In sum, although it is plausible that convergent evolution played a major role in the evolution of habituation, clearly more evidence is needed to establish whether habituation within the neuralia emerged multiple times due to evolutionary convergence.

2.2. The ubiquity of associative learning

Associative learning is sometimes referred to as 'true learning' since unlike habituation and sensitization, which are modifications of existing responses, associative learning involves learning new relationships. Associative learning enables organisms to detect contingency relations between different stimuli, or to establish connections between a behaviour and its consequences [34]. This confers adaptive advantages for organisms by enabling value attribution, or valence, to initially neutral stimuli, the anticipation of future events and discrimination between classes of stimuli [35].

Two of the most well-known forms of associative learning are (i) classical (or Pavlovian) conditioning, the learning of a response-independent association between a biologically significant stimulus (i.e. the unconditioned stimulus, US) and a neutral stimulus (i.e. the conditioned stimulus, CS) [36], and (ii) operant (or instrumental) conditioning, the learning of a response-dependent association between a response and a stimulus [11]. Moore [14] distinguishes between many more forms of associative learning, including at least 11 levels of Pavlovian processes, and many types of instrumental learning with varying degrees of complexity. In this paper, I will focus on classical (Pavlovian) conditioning, the most basic and widespread form of associative learning [37]. The general neurochemical mechanisms that underlie these learning behaviours are well known. Experimental work on *Aplysia* has revealed that presynaptic facilitation is the driver for Pavlovian learning, which is accompanied by changes in both the pre- and the post-synaptic cell, involving the activation of post-synaptic NMDA receptors and retrograde signalling [19]. Adaptive learning processes like Pavlovian conditioning provide selective advantages and enhance fitness of individual organisms, which promotes their evolvability.

Although biological cognition is about changes within the lifespan of organisms, it is worth noting that bacteria can 'learn' associations on a phylogenetic time scale. That is, in predictable environments microorganisms can evolve regulation strategies that anticipate contingent temporal changes between events. For example, upon entering the digestive tract, bacteria such as *E. coli* have 'learned' that a temperature increase is

always followed by a drop in oxygen levels. Their genetic regulatory circuits have adapted to dealing with both environmental changes in that particular temporal order so that the rise in temperature serves as a cue for the expression of genes that help to anticipate dealing with lower oxygen levels [38]. Similarly, Mitchell *et al*. [39] found that, during its passage through the digestive system, *E. coli* has 'learned' that the presence of lactose is a reliable predictor for maltose. *E. coli* bacteria have evolved this association into their genetic regulatory network to be able to anticipate this change by activating the genes for the digestion of maltose, upon encountering lactose. Learning associations within a single lifetime, however, is a different matter, although this distinction between phylogenetic 'learning', or evolution, and learning on an ontogenetic scale is often neglected.

Although there is no evidence for associative learning in prokaryotes on an ontogenetic time scale *in vivo*, several studies do report conditional learning in bacteria *in vitro*, after modifications in synthetic genetic networks [40]. For example, Zhang *et al*. [41] used four synthetic genetic modules that implemented a Pavlovian-like conditioning function that enabled associative learning in the *E. coli* bacterium. In their study, the bacteria learned to associate two chemical stimuli, so that in the end they produced a green fluorescence protein when detecting the CS.

The possibility of *in silico* associative learning was investigated by McGregor *et al*. [42] by simulating the evolution of chemical networks selected to perform various classical conditioning tasks. Their networks were capable of forming predetermined associations between stimuli within a single lifetime. Given the relative simplicity of these networks, McGregor *et al*. argue that there is no reason that similar modifications to genetic, metabolic or signalling networks could not have evolved in Nature to enable associative learning in bacteria. So at least it remains an empirical possibility that prokaryotes are capable of associative learning. According to Mitchell *et al*. [39], however, it is possible that, since populations of prokaryotes rapidly evolve to 'learn' contingency relationships in their environment, ontogenetic associative learning might not confer substantial additional adaptive advantages.

The evidence for *in vivo* associative learning in single-celled eukaryotes, such as protists, is more convincing. Some prior studies have reported classical conditioning in protists such as *Paramecium caudatum* (e.g. [43–45]). However, these studies remain controversial because of their questionable experimental design. Fortunately, recent experiments have provided more robust evidence for classical conditioning in *Paramecium*. For example, in a series of experiments it was found that *Paramecium* can develop a preference for illumination level (either light or dark) using a mild electric shock as a reinforcer [46,47]. In one experiment, *Paramecium* learned to avoid either the light or the dark location, whereas in the other experiment they learned to favour either the light or dark environment. So, in both studies, *Paramecium* learned to associate the illumination level with a reinforcer.

The underlying biochemistry of associative learning in *Paramecium* is largely unknown, but modifications in voltage-gated ion channels might be involved [48]. A more recent follow-up experiment [49] investigated the duration of this learned preference for illumination level in *Paramecium*. It was found that the retention interval for this information is rather short, as the memorized association is lost after less than a minute. Still, these experiments show that single-celled eukaryotes are able to learn, as has been speculated for over a century.

The evidence for associative learning in plants is extremely rare. Few studies yielded significant effects for associative learning in *Mimosa pudica*, but replications of these experiments failed to obtain significant results [27]. Recent research by Gagliano *et al*. [3], however, for the first time demonstrates that a plant, the garden pea *Pisum sativum*, is capable of associative learning using a classical conditioning learning paradigm. In this study, the plant was able to form associations between an environmental cue (US), in this case airflow from a fan that was placed at one end of a Y-shaped maze, and the location of a light source (CS). After a 3 day training period, about two-thirds of plants in the test group ($n = 26$) successfully learned either to grow towards the cue, when they were trained to positively associate the cue with light, or to grow into the other arm of the Y-shaped maze, when they were trained to negatively associate the cue with light (CR). In a second experiment, they found that this type of learning only occurred during a particular circadian phase of the plant. That is, learning only took place when the internal circadian clock of the plant suggested it was daytime. Gagliano *et al*. [3] therefore argue that associative learning in this plant is connected to its circadian rhythm and speculate that epigenetic changes might underlie this form of plant learning. They conclude that:

> Our results now show that associative learning is also an essential component of plant behaviour. We propose that the ability to construct, remember and recall new relationships established via associative learning constitutes a universal adaptive mechanism shared by all organisms. The ubiquity of associative learning across taxa, including non-animal groups, suggests that the role this learning process plays in nature is thus far underexplored and underappreciated. Our findings raise the possibility that associative learning may have played a similarly important role in the remarkable diversification of the plant kingdom and that this kind of learning emerged in plant and animal groups alike via convergent evolution. ([3], p. 5)

With this recent evidence for associative learning in plants and protists, the idea that associative learning does occur in a variety of aneural organisms becomes more plausible, although it remains difficult to estimate its pervasiveness. Given that there is only sparse evidence for associative learning in aneural taxa, it could be the case that associative learning is the exception rather than the rule. Nevertheless, these findings do seem to provide proof of existence for basic forms of associative learning in aneural organisms, which was until recently widely assumed to be precluded to neuralia. Although little is known about the underlying mechanisms that govern associative learning in species such as protists, fungi and plants, it is plausible that these abilities evolved independently from one another through convergent evolution, and that they evolved independently from basic associative learning capabilities in organisms with nervous systems.

3. Nervous systems and convergent evolution

It is unclear whether the first organisms equipped with nervous systems were able to learn. In extant neuralia, basic non-associative learning capabilities appear to be universal [50]. Habituation and sensitization are found in organisms as small as sea squirt larvae, which possess as few as 100 neurons.

Owing to the lack of fossil evidence and the extremely rapid adaptive radiation during the Cambrian explosion, it has proved exceedingly difficult to reconstruct an accurate phylogeny of early nervous system evolution. Based on fossil evidence, a conservative estimate holds that the first nervous systems evolved some time in the Ediacaran, around 600 Ma [51]. However, estimates based on molecular clock data suggest that the metazoan nervous system originated much earlier, in the Cryogenian (850–635 Ma) [52].

Using modern research techniques, the study of early nervous system evolution has made much progress over the last few years. Based on genetic data, it has become apparent that the role of convergent evolution in nervous systems is much more prominent than was widely assumed until recently [53,54]. Several authors have argued that nervous systems are not monophyletic, but that they evolved several times independently[2] [55–57] (but see [58]). Irrespective of whether nervous systems evolved once or multiple times, the emerging picture suggests that the evolution of nervous systems in general is characterized by patterns of convergence [59], loss of features [60] and duplication/divergence [61].

One of the fundamental questions in the research field that studies the early evolution of nervous systems is: 'What was the selective pressure that drove what is an exceedingly complex and energetically expensive trait?' [55, p. 501]. In the next section, I will argue that the answer to this question has to do with convergent evolution. The evolution of nervous systems set the stage for at least two major events of convergent evolution of adaptive behaviours that are central to biological cognition: sensorimotor coordination and associative learning. In the next sections, I examine both events in more depth.

3.1. Size constraints on sensorimotor coordination

Sensorimotor coordination is the process by which organisms adaptively coordinate their sensors and effectors to optimize the external conditions for their metabolism and homeostasis [9]. It is a phylogenetically ancient adaptive strategy that is used, for example, by bacteria and protists to perform fast-paced coordinated locomotion strategies, such as chemotaxis [10]. The evolution of sensorimotor strategies was the high road to complex forms of intelligence. It enabled organisms to seek out and select more favourable habitats, to hunt down and capture prey, to avoid predators and to spread the risks of extinction. Sensorimotor coordination is regarded as a central principle for understanding cognition in general [62,63]. In the cognitive neurosciences, the coordination of perception and action is also shown to be fundamental to the development of human cognition [64].

While it is clear that modern nervous systems have many functions, including the regulation of vital housekeeping functions, it is a popular view that sensorimotor coordination is one of the main reasons why nervous systems evolved. There are many different hypotheses on this matter. Various intermediate stages have been proposed (e.g. feeding movements) that ultimately lead up to the functionality of nervous systems as control systems for coordinated locomotion (e.g. [65–68]). One view suggests that the evolution of nervous systems is best understood in the context of the evolutionary transition from a motile lifestyle driven by cilia to contraction-based motility governed by a neuromuscular organization, involving the coordination of increasingly larger multicellular bodies [69]. This is supported by the finding that the evolutionary origin of nervous systems is closely coupled with that of muscle tissue [70].

Size is a key factor in the transition from cilia-based to neuromuscular-based motility. The fossil record reveals two major transitions in evolution regarding the maximum size and complexity of organisms. The first one marks the transition from prokaryotes to eukaryotes, and the second one occurred during the Late Neoproterozoic and Early Paleozoic eras 600–450 Ma [71]. According to Liebeskind *et al*. [55], the first complex macroscopic organisms exceeding the millimetre range in size appear in the fossil record in the Middle Ediacaran, some time around 580 Ma,[3] which coincides with the early stages of nervous system evolution. Coordinated locomotion using cilia imposes strong limitations on the size of the organisms involved. In large multicellular organisms, ciliary swimming systems are ineffective for generating movement because of physical constraints, such as higher Reynolds numbers. At the level of single-celled organisms viscous forces are dominant, whereas at the level of large animals, such as whales, inertial forces are dominant, the latter of which has profound implications for body morphology and locomotion strategies. At low Reynolds numbers, ciliated swimmers have to overcome friction drag, and generally do not exceed sizes beyond the millimetre range [72], whereas lift-based and jet-based forms of locomotion are only practical at higher Reynolds numbers where inertial forces and pressure drag predominate [73]. So on the scale of relatively large organisms, nervous systems are necessary to generate the complex and coordinated actions that support muscle-based locomotion strategies, such as hydrostatic propulsion, head–tail undulations and locomotor limb movements.

A modern example of how such an ancient nervous system might have worked can be found in the jellyfish *Aglantha digitale*, a small (about 1–2 cm) thimble-shaped hydromedusa. It has a distributed nerve net that consists of two marginal nerve rings that generate oscillating patterns, which cause the semi-arched subumbrellar muscle sheet inside the margin of the bell to rhythmically contract and expand, forcing water out of the bell so as to provide a kind of jet propulsion [74].

The evolution of nervous systems was an event of convergent evolution, in the sense that it enabled fast forms of coordinated locomotion, such as the ones we find in prokaryotes and protists, but now in macroscopic animals at size scales that are up to six orders of magnitude larger than their single-celled precursors. The evolutionary arms races between increasingly large motile species and a more heterogeneous environment [75] must have provided strong selective pressures, promoting fast-paced and increasingly complex sensorimotor behaviours. This led to increased morphological diversity and a marked increase in the size of organisms beyond the millimetre range [52,68]. So whether or not sensorimotor coordination was the primal reason why nervous systems evolved, nervous systems became an evolutionary success because they lifted some of the size-dependent biophysical constraints on sensorimotor coordination.

But the costs were significant as well. At the size scale of macroscopic animals, the metabolic costs of sustaining a motile lifestyle increase allometrically. Motility at this level demands specialized tissues, such as muscles dedicated to pattern generation, support structures, such as a hydrostatic skeleton or a rigid exo- or endoskeleton, and neurons that enable fast coordinated electrical signalling across relatively large distances.

Energy consumption levels of neural tissue per unit of mass are almost an order of magnitude greater than most other somatic tissues. At least in extant organisms, a large fraction of those costs are due to the generation of action potentials and synaptic transmission [76]. The propagation of electrical signals and the maintenance of the resting potential require the continuous activity of the $3Na^+/2\,K^+$ pump, which consumes vast amounts of ATP. For example, modelling studies suggest that the squid giant axon consumes 2.3×10^{12} ATP molecules per action potential [77]. Although these metabolic costs vary substantially between species, and are dependent on neuronal types and size, ion-channel types, synapse complexity, neuronal wiring efficiency and other biophysical properties, nervous systems must have required a considerable metabolic investment for the first neuralia. These high metabolic costs of nervous systems are balanced out by the important adaptive benefits conferred by sensorimotor coordination.

3.2. Nervous systems and associative learning

The evolution of associative learning is often viewed as another major event in the early evolution of nervous systems. Ginsburg & Jablonka [35] even argue that associative learning was one of the drivers for the Cambrian explosion, which started around 540 Ma. Not all extant organisms equipped with nervous systems are capable of associative learning. For example, according to Ginsburg & Jablonka [78], there is only sporadic evidence for associative learning in Ctenophora (comb jellies) and Cnidaria. One of the exceptions is the Cnidarian sea anemone, *Cribrina xanthogrammica*, a sessile organism with a relatively simple nerve net. One study reports classical conditioning in *Cribrina*, involving a learned association between a light stimulus and an electrical shock [79]. This example demonstrates that a nerve net may suffice for conditional learning.

A classic view on the evolution of associative learning is that there was a step-wise evolutionary sequence of adaptations in nervous systems that gradually led from non-associative to associative learning. Based on comparative analysis, Moore [14] suggests that long-term sensitization was the evolutionary precursor of associative learning, as they share many highly conserved molecular mechanisms [19,80]. Others claim that habituation diverged into associative learning [81]. The shared assumption in these views is that pre-existing learning mechanisms were co-opted to enable associative learning. These views, therefore, presuppose continuity from non-associative to associative learning. Other authors suggest an evolutionary discontinuity. That is, associative learning in nervous systems may have evolved independently from habituation and sensitization. For example, Hollis & Guillette [82] hypothesize that associative learning is an emergent property of nervous systems that evolved along with them. From this perspective, associative learning is an inherent property of the information-processing capabilities of nervous systems. However, this claim is solely based on indirect evidence of insect learning, so the gradual evolutionary scenario seems to be better supported by neurobiological evidence.

According to Sara Shettleworth [37], current evidence indicates that the neurobiological and molecular mechanisms that subserve conditional learning evolved multiple times independently. The mechanisms that underlie Pavlovian conditioning may differ across and even within species. For example, studies in mice show that Pavlovian fear conditioning, which is mediated by the amygdala, and eyeblink response conditioning, which is mediated by the cerebellum, are governed by 'almost completely nonoverlapping circuits' [83, p. 208]. That is, although these different conditioning responses share some organizational similarities in that both require negative feedback circuits, and neuronal mechanisms capable of coincidence detection, there are also some important differences in the biochemistry of synaptic plasticity and mechanisms of gene expression.

Determining whether a particular learning behaviour in two different species is the result of convergent or parallel evolution can be quite difficult. One reason for this is that the distinction between convergent and parallel evolution is not always clear-cut [84]. This is especially true for phenotypic traits that depend on some underlying 'deep homology' [85,86]. Papini [87] distinguishes four hierarchical levels of mechanistic analysis that can be used to determine whether a learning behaviour observed in two different species is the result of convergent evolution: (i) the psychological level, (ii) the neurobiological level, (iii) the neurochemical level, and (iv) the cell-molecular level. According to Papini, convergence of a particular learning behaviour (i.e. the psychological level) would require independently evolved mechanisms at all underlying levels.

Although I found no unequivocal evidence for convergent evolution of associative learning within the neuralia, the most plausible cases come from neurobiological studies in cephalopods, such as the nautilus, the octopus and the cuttlefish. Cephalopods belong to the Mollusca phylum, but they diverged from other molluscs around 550 Ma [88]. Research has shown that the brains of the octopus and the cuttlefish show analogous features on many levels of neuronal organization. According to Katz [89], the vertical lobe of the octopus, which mediates associative memory, exhibits a 'fan-out/fan-in' organization, which is analogous to the organization of the insect mushroom body and the mammalian hippocampus [90]. Hochner *et al*. [91] found that the octopus brain shows evidence for convergent evolution not only in brain organization but also in the biochemistry of long-term synaptic plasticity that is crucial for memory and learning (i.e. the neurochemical level; see also [92]). According to Brown & Piscopo [93], the neurochemical mechanisms that underlie synaptic plasticity in cephalopods are quite different from those studied in mammals and insects. For example, Shomrat *et al*. [90] state that, unlike vertebrates, the octopus seems to exhibit a form of long-term potentiation that is not mediated by NMDA receptors, and depends exclusively on presynaptic modifications. Although both vertebrates and invertebrates make use of cAMP-dependent genes in long-term potentiation, there are also marked differences at the cell-molecular level that underlie associative learning. Katz [89] argues that while vertebrates and invertebrates share a conserved genetic toolkit, which includes developmental patterning genes such as Hox, many of these homologous genes have been co-opted differently in the cephalopod nervous system (see also [90]). This research suggests that there are different ways to construct the cell-molecular processes that give rise to associative learning. In sum, the mechanisms that underlie associative learning in some cephalopods may depend on independently evolved features on different organizational levels (i.e. the neurobiological, the neurochemical and the cell-molecular level), which could be indicative of convergent evolution.

4. Conclusion

Recent empirical evidence shows that basic learning abilities are much more widespread than was long presumed. Habituation and Pavlovian conditioning are found in most neuralia, and also in some protists and plants, although it is still unknown how common these capabilities are in aneural organisms. The available molecular evidence suggests that habituation and conditional learning evolved independently in phylogenetically distant species, such as protists, plants and neuralia, which appear to have converged towards the same adaptive solution, because of the important adaptive benefits conferred by flexible within-generation behaviours. The evolution of nervous systems was an event of convergent evolution in that it enabled fast forms of sensorimotor coordination, such as the ones we find in prokaryotes and protists, but now in macroscopic animals at size scales that are up to six orders of magnitude larger than their single-celled precursors. Classical conditioning was a subsequent convergent adaptation in the neuralia that allowed these organisms to detect contingency relations between stimuli, which enabled context-sensitive behaviour and a more ontogenetically flexible sensorimotor repertoire. More research is needed to verify whether associative learning evolved through convergent or parallel evolution within the neuralia, although cephalopods provide a promising research avenue for establishing evolutionary convergences. Many of the biochemical processes that underlie primitive forms of learning in protists, fungi, plants and neuralia are still unknown. Further research needs to integrate molecular, physiological, neurobiological and psychological data to establish the evolutionary connections between these elementary forms of learning.

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Endnotes

[1]The term *neuralia* is used by Claus Nielsen [8] to refer to the collection of organisms that possess a central nervous system or a nerve net, including Bilateria, Ctenophora and Cnidaria.

[2]According to Liebeskind *et al*. [55] most extant nervous systems are derived from ectodermal tissue. In organisms such as hydrozoan Cnidaria and Echinodermata, however, non-ectodermally derived neurons are found, which have different morphologies and alternative functional properties, such as bi-directional signalling, which is suggestive of convergent evolution of neural tissue.

[3]I thank Graham Budd for pointing this out to me.

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