Predation and the Origin of Neurones

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Abstract

The core design of spiking neurones is remarkably similar throughout the animal kingdom. Their basic function as fast-signalling thresholding cells might have been established very early in their evolutionary history. Identifying the selection pressures that drove animals to evolve spiking neurones could help us interpret their design and function today. We review fossil, ecological and molecular evidence to investigate when and why animals evolved spiking neurones. Fossils suggest that animals evolved nervous systems soon after the advent of animal-on-animal predation, 550 million years ago (MYa). Between 550 and 525 MYa, we see the first fossil appearances of many animal innovations, including eyes. Animal behavioural complexity increased during this period as well, as evidenced by their traces, suggesting that nervous systems were an innovation of that time. Fossils further suggest that, before 550 MYa, animals were either filter feeders or microbial mat grazers. Extant sponges and *Trichoplax* perform these tasks using energetically cheaper alternatives than spiking neurones. Genetic evidence testifies that ner-

vous systems evolved before the protostome-deuterostome split. It is less clear whether nervous systems evolved before the cnidarian-bilaterian split, so cnidarians and bilaterians might have evolved their nervous systems independently. The fossil record indicates that the advent of predation could fit into the window of time between those two splits, though molecular clock studies dispute this claim. Collectively, these lines of evidence indicate that animals evolved spiking neurones soon after they started eating each other. The first sensory neurones could have been threshold detectors that spiked in response to other animals in their proximity, alerting them to perform precisely timed actions, such as striking or fleeing.

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Introduction

If neurones are the answer, then what was the question? The neurones of millions of species, from dozens of phyla that are quite disparate in other respects, use similar protein channels to create similar action potentials and communicate with other neurones using similar chemicals [Sakarya et al., 2007; Renard et al., 2009; Tompkins-MacDonald et al., 2009; Galliot and Quiquand, 2011;

Liebeskind et al., 2011]. These core functional features might have been established very early in their evolutionary history. Whatever the question was, ancient animals might have quickly found spiking neurones to be an effective answer. Understanding why they first evolved could help us interpret their function in complex modern nervous systems.

Fossil evidence can reveal much about the timing and circumstances surrounding the evolutionary appearance of spiking neurones. Fossils can reveal not only the morphology of ancient organisms and when they lived, but also their ecology and their behaviour. Fossil evidence indicates that animals started experiencing profound morphological and behavioural changes just before the Cambrian explosion. Within 20 million years, simple and defenseless animals had developed weapons and armour. The earliest direct and indirect fossil evidence for nervous systems is dated to about this time, suggesting that spiking neurones were another such development.

Fossil evidence also informs us about the ecological conditions of the distant past. Evolutionary change takes place in a context of contingent climatic, geochemical and biotic affordances, in which it is difficult to assign causality [Gibson, 1979; Chemero, 2003]. Affordances are conditions that allow, but do not require, organisms to undergo evolutionary change. For example, animals cannot evolve spiking neurones if their genomes do not allow them to do so (i.e. if the genetic affordance is absent). However, even if the genetic affordance for spiking neurones is present, animals may still not evolve them if ecological affordances remain absent. Animals would not evolve spiking neurones, even if they could, unless there was an ecological benefit to compensate the cost of developing and operating them. Establishing when an ecological affordance for spiking neurones appeared is central to identifying when they evolved.

Modern molecular genetics has revolutionised our understanding of the relatedness of animals, their nervous systems and when lineages diverged. Molecular evidence indicates that all nervous systems share a degree of genetic conservation [Ghysen, 2003; Gomez-Skarmeta et al., 2003; Ball et al., 2004; Matus et al., 2006; Denes et al., 2007; Jacobs et al., 2007; Arendt et al., 2008; Watanabe et al., 2009; Hirth, 2010], but some nervous systems are more closely related than others. Any argument for when animals evolved nervous systems must offer an explanation for the varying degrees of genetic conservation that we observe in nervous systems from different lineages.

This paper reviews fossil, ecological and molecular evidence, and discusses what each tells us about when and why animals first evolved spiking neurones.

Fossils and the Morphology and Behaviour of Ancient Animals

The fossil record shows that animals experienced profound changes in their morphology and behaviour between 550 and 525 million years ago (MYa).

Figure 1 shows body fossils of putative animals before, during and after this 25-million-year period. Most animals before 550 MYa probably have no descendants that exist today. The taxonomic classification of those fossils is notoriously difficult, even at the kingdom level [Narbonne, 2005; Conway-Morris, 2006; Xiao and Laflamme, 2008]. Sponges are one of the few extant animals we can recognise in the body fossil record before 550 MYa. The oldest fossil evidence for animal existence are body fossils from Namibia that are interpreted as sponges, dated to 760 MYa [Brain et al., 2012]. The chemical fossil record also supports an ancient presence of sponges, with demosponge biomarkers dated to 635 MYa [Love et al., 2009]. Other putative animals called rangeomorphs appeared between 575 and 560 MYa. Rangeomorphs were frond-like and superficially resembled modern sea pens, though their taxonomic affinity remains unknown [Laflamme and Narbonne, 2008].

Between 560 and 550 MYa, we see a notable increase in animal taxonomic diversity. Bilaterally symmetric animals such as *Dickinsonia*, *Yorgia* and *Kimberella* appear, as do animals with tri-, tetra-, penta- and octaradial symmetry such as *Tribrachidium*, *Conomedusites*, *Arkarua* and *Eoandromeda* [Droser et al., 2006; Xiao and Laflamme, 2008; Tang et al., 2011]. Other animals such as *Parvancorina* show clear anterior-posterior differentiation. While these animals exhibited various symmetries and rudimentary body patterning, they were morphologically very unlike extant animals [Valentine, 2002], as shown in figure 1.

Around 550 MYa, almost all of these simple animals disappear from the fossil record. By 525 MYa, they had been replaced by more complex animals that are recognisable as representatives of extant animal phyla [Valentine, 2002; Narbonne, 2005]. During this time, which includes the Cambrian explosion, we see the appearance of many evolutionary innovations such as calcified skeletons and drills (550 MYa) [Bengtson and Zhao, 1992; Hua et al., 2003], plates and shells (541–530 MYa) [Maloof et

Fig. 1. Animals experienced profound morphological innovations starting at around 550 MYa. **a–g** Soft, defenceless animals. **h–j** Skeletons, nervous systems and spined tentacles. **a–c** The earliest animals were almost exclusively sessile filter feeders. **a** The frond *Charnia masoni*, dated ~570 MYa. Scale bar = 1 cm. **b** Putative sponge body fossil, the oldest known evidence of animals, dated 760 MYa. Scale bar = 0.1 mm. **c** *Charnia wardi* specimen with rangeomorph elements (grey arrow) and primary branches (black arrows) still intact, dated ~575 MYa. Scale bar = 1 cm. **d–f** Various symmetries of animals appeared after 560 MYa. Scale bar = 1 cm. **d** Triradial body plan of *Tribrachidium*. **e** Bisymmetric *Dickinsonia*. **f** Pentaradial *Arkarua*. **g** Exquisitely preserved specimen of the possible bilaterian *Kimberella*. Scale bar = 1-cm increments.

h–j Between 550 and 525 MYa, animal morphology changed significantly. **h** Bore holes in the calcified skeleton of a putative cnidarian *Cloudina*. This image is the oldest known evidence for macrophagy, and amongst the oldest evidence for skeletons and drills (white arrows). Scale bar = 150 μ m. **Inset** A close-up of one of the holes. **i** SEM image of a trilobite eye from the lower Cambrian. Scale bar = 0.1 mm. **j** The spined tentacle of *Anomalocaris*, a lower-Cambrian predator. Scale bar = 2 mm. Images taken from Laflamme and Narbonne [2008] (**a**), Brain et al. [2012] (**b**), Laflamme et al. [2007] (**c**), Xiao and Laflamme [2008] (**d–f**), Fedonkin et al. [2007] (**g**), Hua et al. [2003] (**h**), Clarkson et al. [2006] (**i**) and Wikipedia Commons (**j**). All images reproduced with permissions.

al., 2010; Erwin et al., 2011], and spikes, teeth and jaws (530 MYa; fig. 1).

Nervous systems might have been another innovation from this era; the oldest known direct evidence for nervous systems appears at 525 MYa as the eyes of various arthropods [Clarkson et al., 2006; Zhang and Shu, 2007; Paterson et al., 2011]. These eyes were well developed, suggesting that they had already existed for an evolutionarily significant amount of time. Some of these innovations are shown in figure 1.

As animal bodies increased in complexity, so too did their behaviour. Trace fossils are fossils of biological activity on a substrate. They are good indicators of animal behaviour and ecological change [Mangano and Buatois, 2007; Bengtson and Rasmussen, 2009; Plotnick, 2012]. Figure 2 shows examples of animal traces before and after 550 MYa. The first indisputable animal trace fossils appear around 560 MYa [Budd and Jensen, 2000; Jensen,

2003; Seilacher et al., 2005; Liu et al., 2010]. For 10 million years, the vast majority of these first trace fossils were unbranched, simple, horizontal traces [Jensen, 2003; Jensen et al., 2005; Liu et al., 2010]. The shallowness of these traces indicates that they were probably caused by a bilaterian pushing through the sediment, forming ridges on either side [Jensen et al., 2006]. Other traces from this era include repeated imprints of *Yorgia* [Ivantsov and Malakhovskaya, 2002] and *Dickinsonia* [Xiao and Laflamme, 2008], which may (or may not [McIlroy et al., 2009]) have been capable of passive intermittent movement. *Kimberella* seemed to move itself actively on microbial mats, scratching the mats where it pleased [Seilacher et al., 2005; Mangano and Buatois, 2007; Peterson et al., 2008].

At 550 MYa, animal traces became noticeably more complex and diverse, just as body fossils did. Figure 2 shows pictures of bilaterian trace fossil evidence dated 551–541 MYa. Instead of pushing themselves through

560–550 MYa

550–543 MYa

Fig. 2. Animal traces increased in complexity and diversity in parallel with animal morphology. There are no known, indisputable trace fossils dated before 560 MYa. **a** *Archeonassa*: ridges on either side of the trace indicate displacement by pushing sediment up either side, presumably by a bilaterian. Scale bar = 1 cm. **b** *Helminthoidichnites* are simple, unbranched, horizontal traces that form the majority of animal traces from this era. **c** Series of three *Dickinsonia* resting traces, 1 marks the oldest and 3 the youngest, presumed to have been made by the same organism. Scale bar = 1 cm. **d–f** More complex animal behaviour at the end of the pre-Cambrian.

d Surface tracks and scratch marks (white arrowheads) connecting full reliefs of tunnels (white arrows). Scale bar = 1 cm. **e** Horizontal, cross-cutting, under-mat tunnels. The black arrows denote cross-cutting tunnels. Scale bar = 2 cm. **f** Vertical structures (arrows) connected by horizontal tunnels. Scale bar = 1 cm. For more beautiful pictures of late pre-Cambrian animal trace fossils, see Jensen et al. [2006]. Images taken from Jensen [2003] (**a**), Wikipedia Commons (**b**), Xiao and Laflamme [2008] (**c**) and Chen et al. [2013] (**d–f**). All images reproduced with permissions.

sediment [Jensen et al., 2006], these bilaterians dug cross-cutting and branching tunnels in the microbial mats [Jensen et al., 2000; Chen et al., 2013]. We see examples of surface traces that connect the openings of two tunnels, indicating epibenthic locomotion and perhaps appendages, and vertical structures, interpreted as resting traces or access holes to the under-mat tunnels [Chen et al., 2013]. We also see the first trace fossils resembling modern annelid and molluscan burrows [Narbonne, 2005]. The existence of more complex traces suggests that at least some bilaterian animals were capable of a degree of behavioural complexity just a few million years before the Cambrian explosion, 543 MYa.

Ancient Animal Ecology and an Affordance for Nervous Systems

Neurones are highly specialised and energetically expensive cells [Laughlin et al., 1998; Laughlin, 2001; Niven et al., 2007; Niven and Laughlin, 2008]. Many examples of nervous system reduction have been interpreted as a consequence of the energetic expense of neural tissue. Some ascidian [Cloney, 1982] and anthozoan [Ball et al., 2004] larvae disassemble their nervous system after their metamorphosis into sessile adults. There are many examples of cave-dwelling species that have lost their eyes and much of their visual processing centres [Niven and

Laughlin, 2008]. These observations suggest that nervous systems could not have evolved unless they provided some substantial ecological benefit to compensate for their expense.

The simple morphology and behaviour of pre-Cambrian animals were likely a reflection of their simple ecological lifestyle. Before 560 MYa, it seems that animals were exclusively sessile filter feeders (e.g. sponges and frond-like rangeomorphs) [Narbonne, 2005; Bottjer and Clapham, 2006; Laflamme and Narbonne, 2008]. These animals might have experienced many ecological selection pressures that extant sessile animals face, such as dispersal strategies, intraspecific competition and epifaunal tiering [Clapham and Narbonne, 2002; Clapham et al., 2003; Droser et al., 2006]. The bi-, tri-, tetra-, penta- and octaradial taxa existing between 550 and 560 MYa probably exploited the abundant microbial mats or suspension fed in the water column for nutrients [Seilacher, 1999; Bottjer and Clapham, 2006; Tang et al., 2011], each occupying a specific ecological niche [Seilacher, 1999].

Animals apparently did not eat each other (macrophagy) throughout almost all of the pre-Cambrian [McMenamin, 1986; Waggoner, 1998; Clapham et al., 2003; Hua et al., 2003; Narbonne, 2005; Xiao and Laflamme, 2008; Northcutt, 2012; Sperling et al., 2013]. The fossil record is notoriously incomplete, but excellent pre-Cambrian taphonomic conditions [Bottjer and Clapham, 2006] preserved a surprising number of body and trace fossils from hundreds of species, some of which are globally distributed [McCall, 2006; Shen et al., 2008; Xiao and Laflamme, 2008]. None of those pre-Cambrian fossils reveal evidence of injuries, healed wounds, body fragments, trace fossils or functional interpretations of body parts that are consistent with the existence of macrophagy (e.g. shells and drills) [McMenamin, 1986; Waggoner, 1998; Clapham et al., 2003; Hua et al., 2003; Narbonne, 2005; Xiao and Laflamme, 2008; Northcutt, 2012; Sperling et al., 2013]. Furthermore, survivorship curves of pre-Cambrian animals imply age-independent mortality and are consistent with a lack of predation [Waggoner, 1998]. It is possible that macrophagy has a substantial pre-Cambrian history, but evidence for its practise escaped the fossil record, e.g. if the earliest predators and prey were exclusively pelagic. However, such scenarios would require an explanation for why the soft, defenceless, slow animals on the benthos remained unexploited.

In the absence of macrophagy, pre-Cambrian animals would have only needed to move according to nutritional, chemical, light or temperature gradients [Bengtson, 2002] and filter water or forage for sustenance. Extant

sponges and *Trichoplax* indicate that animals do not require neurones to accomplish these tasks. Extant sponges and their larvae show that animals do not require neurones to filter feed [Leys et al., 1999; Leys and Meech, 2006; Nickel, 2010; Ludeman et al., 2014]. *Trichoplax* demonstrates that animals do not require neurones to crawl on a substrate and forage for food [Schierwater, 2005; Pearse and Voigt, 2007; Liebeskind et al., 2011]. Sponge larvae show that animals do not require neurones to follow gradients or respond to environmental stimuli [Woollacott, 1993; Leys et al., 2002; Maldonado, 2006; Ettinger-Epstein et al., 2008; Wahab et al., 2011; Rivera et al., 2012]. There are cheaper alternatives than neurones to fulfil these tasks.

Figure 3 contains examples of such cheaper alternatives. Many sponge larvae possess a ring of cells with long cilia. The distal protrusions of these cells are filled with pigment and mitochondria [Maldonado et al., 2003] and express a sponge gene that was shown to be photoresponsive [Rivera et al., 2012]. These cells collectively form a rudimentary eye and steer larvae according to light intensity [Maldonado, 2004]. Cilia lining the osculum of freshwater sponges are probably sensory cells that trigger body contractions in response to changes in expelled water flow [Ludeman et al., 2014]. Globular cells protrude from the epithelia of almost all sponge larvae and probably serve neurone-like functions by secreting chemicals in response to stimuli (i.e. paracrine signalling) [Woollacott, 1993; Richards et al., 2008]. Neurones are not the only cell type that animals could utilise for sensory capabilities.

The fossil record indicates that a major event in the evolutionary history of animals occurred at around 550 MYa: the introduction of macrophagy. Unmistakable bore holes in the calcified sessile animal *Cloudina* are currently the oldest evidence of animals eating each other, with fossils dated at 550 MYa (fig. 1h) [Bengtson and Zhao, 1992; Hua et al., 2003]. Subsequently, and perhaps not coincidentally, the vast majority of defenceless filter feeders and mat grazers (fig. 1a–g) disappeared from the fossil record [Waggoner, 2003; Narbonne, 2005; Xiao and Laflamme, 2008], replaced instead by animals with weapons and armour.

Still, the first predator-prey interactions did not necessarily require neurones. All animals emit mechanical, chemical, electrical and other signals in their vicinity, and other animals could have detected that signal and followed its gradient toward its source (or away from it). As sponge larvae show, animals do not require neurones to follow gradients or respond to stimuli [Leys et al., 2002; Maldonado, 2006; Ettinger-Epstein et al., 2008; Wahab et

Fig. 3. Sponges do not have neurones, but they do have specialised cells that can detect stimuli. **a** General view of *Amphimedon queenslandica* (demosponge) larvae. The ring of long-ciliated cells at the posterior end of the larvae are pigmented, facilitating phototaxis. **b** Sensory cilia line the osculum of the freshwater sponge *Ephydatia muelleri* and trigger body contractions in response to changes in the flow of expelled water. Scale bar = 1 μm . **c–f** Globular cells (black arrowheads) migrating through the epithelium of

an *Amphimedon* larvae (**c–e**) until they eventually protrude from the epithelium. These globular cells express genes that suggest that these cells are ancient animal sensory devices. **f** TEM image of a globular cell of an *Amphimedon* larva. The apex of the cell protrudes into the environment (open arrowhead). Images taken from Sally Leys (photo credit; **a**), Ludeman et al. [2014] (**b**) and Richards et al. [2008] (**c–f**). All images reproduced with permissions.

al., 2011; Rivera et al., 2012]. In fact, unicellular organisms [Berg, 1975] and plants [Trewavas, 2005] can also perform these feats without the aid of neurones. The earliest predators and prey could have utilised similar non-neuronal sensory capabilities to follow gradients in pursuit or retreat of one another.

While the first predator-prey interactions probably transpired slowly by modern standards, macrophagy must have pressured animals to detect and react to other animals increasingly quickly. Over evolutionary time, animals must have decreased their reaction times and moved ever faster when other animals approached them. Eventually, their success in predator-prey interactions depended on events that happen on a millisecond time scale.

Extant nervous systems can make decisions on a millisecond time scale [Johansson and Birznieks, 2004; Bodelon et al., 2007; Olberg et al., 2007; Stanford et al., 2010; Stewart et al., 2013]. This reaction time may reflect a biophysical limit on the speed at which biological cells can

create and process signals. Predation still pressures extant animals to detect and react to the proximity of other animals as quickly as possible; if they could react on a microsecond or nanosecond time scale, then we expect that they would. However, faster reaction times may not be biologically possible, in which case reaction times have achieved their biophysical limit.

Macrophagy pressures animals to react to threats and opportunities in a precisely timed and well-coordinated way [Broom and Ruxton, 2005; Chittka et al., 2009; Zylberberg and DeWeese, 2011; Stewart et al., 2013]. Neurones can create more precisely timed signals than paracrine-signalling sponge-like ‘proto-neurones’. Networks of neurones can propagate those signals throughout a body quickly, facilitating well-coordinated behaviours. In predator-prey interactions, these abilities are ecological benefits that could compensate the energetic expense of nervous systems.

Ctenophora [Dunn et al., 2008; Ryan et al., 2013; Moroz et al., 2014]. Almost all agree that cnidarians and ctenophores are basal to or sisters of bilaterians [Peterson and Eernisse, 2001; Manuel et al., 2003; Glenner et al., 2004; Wallberg et al., 2004], and that sponges, cnidarians, ctenophores and several bilaterian phyla crossed the Ediacaran-Cambrian boundary 543 MYa [Halanych, 2004; Peterson et al., 2004, 2005; Peterson and Butterfield, 2005].

A current and important conflict concerns the monophyly [Peterson and Eernisse, 2001; Wallberg et al., 2004; Phillippe et al., 2009] versus paraphyly [Borchiellini et al., 2001; Peterson and Eernisse, 2001; Manuel et al., 2003; Halanych, 2004; Peterson et al., 2005; Sperling et al., 2012] of sponges. If sponges are paraphyletic, then all animals with nervous systems must have descended from a sponge, as shown in figure 4. We will later discuss why this issue is of particular importance to nervous system evolution.

Fossils and molecular clock studies give different answers as to when these basal animal lineages diverged. While taxonomic classification of pre-Cambrian animal fossils is highly controversial, fossil evidence tentatively suggests that cnidarians, ctenophores and bilaterians split from each other by 550 MYa. *Eoandromeda* is interpreted as an early ctenophore, as it possesses characteristics observed exclusively in the Ctenophora phylum [Tang et al., 2011]. It appeared no later than 560–550 MYa [Xiao and Laflamme, 2008; Zhu et al., 2008]. There are many fossil candidates for the existence of cnidarians at this time, including *Palaeophragmodictya spinosa* [Serezhnikova, 2007], axially patterned fronds [Erwin, 2008] and calcified *Cloudina* and *Namacalathus* (fig. 1) [Cortijo et al., 2010; Gaucher and Germs, 2010; Wood, 2011]. *Kimberella* is perhaps the strongest body fossil evidence that bilaterians existed before 550 MYa, though the existence of bilaterally symmetric organisms does not necessarily imply that those organisms were bilaterians [Ball et al., 2004; Matus et al., 2006]. Trace fossils dated at 551–543 MYa reflect peristaltic locomotion, indicating the presence of bilaterians [Mangano and Buatois, 2007; Chen et al., 2013]. A conservative reading of the body fossil and trace fossil records suggests that basal animal clades, including ctenophores, cnidarians and bilaterians, had diverged by 550 MYa [Jensen et al., 2005].

Molecular clock studies are another source of evidence regarding when these lineages diverged. Though molecular clock methodology has improved in recent years, they can still be sensitive to methodology, model assumptions and the taxa included in the data set [Welch et al., 2005; Northcutt, 2012]. Recent molecular clock studies still

vary widely in their reported branching times, and molecular clocks become increasingly unreliable as they attempt to estimate older branching times [Marshall and Valentine, 2010]. However, molecular clock studies assert an earlier divergence of these lineages than the fossil record indicates. Current molecular clock estimates for the branching time of cnidarians from bilaterians range from 700 to 600 MYa [Peterson et al., 2004, 2005; Erwin et al., 2011]. Estimates for the branching time of bilaterians into protostomes and deuterostomes range from 670 to 570 MYa [Aris-Brosou and Yang, 2003; Peterson et al., 2004, 2005; Erwin et al., 2011].

Genetic Relatedness of Nervous Systems

Modern molecular genetics has revolutionised our understanding of relatedness, but we must be careful in our interpretation of such evidence. As we will soon discuss, all nervous systems share some degree of genetic conservation. Therefore, the last common ancestor of animals developing nervous systems possessed those conserved genes, and it is tempting to infer that this ancestor must have used them to develop a nervous system as well. This inference is not necessarily true; there are many counterexamples of genes that have some conserved function in a number of 'higher' lineages, but have a different function in more basal lineages [Marshall and Valentine, 2010].

Sponges and *Trichoplax* provide examples of this principle that are specific to nervous systems. Sponges have many genes that are related to important neural genes in 'higher' animals. Comprehensive lists of these genes exist [Renard et al., 2009]. A few can be transferred into bilaterians and successfully function in neurogenic roles [Richards et al., 2008]. Sponges possess a 'nearly complete' set of post-synaptic proteins [Sakarya et al., 2007], potassium ion channels [Tompkins-MacDonald et al., 2009], and many known neurotransmitters and neuromodulators [Renard et al., 2009]. *Trichoplax* contains genes involved in neurone specification (and muscle and circulatory system development) [Schierwater et al., 2008; Srivastava et al., 2008; Marshall and Valentine, 2010]. Neither sponges nor *Trichoplax* have neurones (or muscles or circulatory systems); those genes must serve some other purpose for them. The molecular genetics of sponges and *Trichoplax* show that the presence of conserved neurogenic genes in conserved neurogenic roles in 'higher' animals does not necessarily imply the presence of neurones in their ancestors.

Fig. 5. Evidence for the genetic conservation of nervous system development between cnidarians and bilaterians. **a** Oral region of *Hydra oligactis* (cnidarian), showing the nerve ring that connects to tentacles and a dense population of epidermal sensory cells surrounding the mouth (centre). Concentrations of neurones in specific regions of the body plan are reminiscent of neural regionalisation in bilaterians. Scale bar = 100 μ m. **b** The genetic pathway leading to neural differentiation in *Hydra* (cnidarian) and vertebrates

(chordate) share some genetic homologues (top two boxes), but not others (lowest box). **c-f** Injecting a cnidarian proneural gene into *Drosophila* (a bilaterian) induces the development of sensory structures. **c** Control *Drosophila* thorax. **d** Mechanoreceptor bristles on *Drosophila* thorax induced. **e** Control *Drosophila* wing. **f** Bristles and chemoreceptors (black arrows) induced. Images taken from Koizumi et al. [1992] (**a**), Lindgens et al. [2004] (**b**) and Grens et al. [1995] (**c-f**). All images reproduced with permissions.

Sponges possess much of the core molecular toolkit required to develop a nervous system. If sponges are paraphyletic (fig. 4), then all other animals must have inherited that toolkit from their sponge ancestor. If sponges are monophyletic, then it remains likely that all other animals inherited a similar toolkit from some sponge-like predecessor. Either way, one might expect to observe a degree of genetic conservation in the nervous systems of 'higher' animals. Indeed, figure 5 contains examples of genetic similarities we observe in the nervous systems of cnidarians and bilaterians, including genetic homologues be-

tween the two lineages [Hayakawa et al., 2004; Lindgens et al., 2004; Matus et al., 2006; Jacobs et al., 2007; Galliot et al., 2009; Marlow et al., 2009; Watanabe et al., 2009]. These observations have led to a widespread belief that cnidarian and bilaterian neurones are genetically homologous.

While all nervous systems share a degree of genetic conservation, those of cnidarians and bilaterians display many disparities that collectively lead to 'strikingly different' overall nervous system organisations [Nakanishi et al., 2012]. The nervous systems of bilaterians contain gli-

Fig. 6. Medirolateral neurogenic domains between annelid (proto-stome, P) and vertebrate (deuterostome, D) trunk nervous systems. Vertical bars represent medirolateral domains of neural specification gene expression during development. Homologous genes are vertically aligned; for example, *pax3/7* in *Platynereis* is located directly above *pax3* and *pax7* in the vertebrate. Horizontal dashed lines represent spatial domains with distinct combinations of neural specification gene expression. The resultant neurone types and their spatial distributions are highly conserved, as indicated in the margins. The expression of homologous neurogenic genes in similar spatial distributions in protostomes and deuterostomes is strong evidence that nervous systems evolved exactly once in bilaterians. Figure taken from Denes et al. [2007] and reproduced with permission.

al cells, but no analogous cell types have been reported in cnidarians or ctenophores [Galliot et al., 2009; Marlow et al., 2009]. During development, only the ectoderm of bilaterians shows neurogenic potential, whereas neurones may arise from both the ectoderm and the endoderm in

cnidarians [Galliot et al., 2009; Marlow et al., 2009; Nakanishi et al., 2012]. Furthermore, the development of the endodermal and ectodermal nervous systems in cnidarians occur through independent guidance mechanisms [Nakanishi et al., 2012]. No shared 'pan-neural' genes have been reported in cnidarians and bilaterians [Moroz, 2009]. Even within the cnidarian phylum, no pan-neural markers have been shown to cross-hybridise between cnidarian species [Galliot and Quiquand, 2011]. On this basis, it has been suggested that not only did nervous systems evolve independently in bilaterians and cnidarians, but perhaps even several times in the cnidarian phylum alone [Moroz, 2009].

In bilaterians, nervous systems are highly genetically conserved, as shown in figure 6. All known bilaterians utilise conserved genes that are expressed in conserved spatial patterns to develop specific neural types in specific regions of their bodies [Gomez-Skarmeta et al., 2003; Lowe et al., 2003; Denes et al., 2007; Arendt et al., 2008]. Many of these genes can be transferred between disparate bilaterian lineages and function successfully. This molecular evidence strongly suggests that the last common ancestor of all bilaterians also had a nervous system, i.e. bilaterians evolved nervous systems exactly once [Hirth, 2010].

Discussion

Summary

We have reviewed fossil, ecological and molecular-comparative evidence to see what each tells us about when and why animals evolved nervous systems. Collectively, these lines of evidence indicate that animals evolved nervous systems soon after the advent of macrophagy.

The fossil record testifies that animals underwent profound morphological innovations soon after they started eating each other, 550 MYa. Over the next 20 million years, we see the first appearances of teeth, claws, spines, shells, skeletons and drills. Given the first fossil appearance of highly developed eyes 525 MYa, it is plausible that nervous systems should be added to this list of innovations. The sudden increase in animal trace complexity and diversity, starting at 550 MYa, might be explained by the appearance of neurones at that time.

Before 550 MYa, it seems that animals were either filter feeders or mat grazers. Animals could have employed cheaper alternatives than neurones to meet their ecological demands. Thus, although these animals probably had much of the requisite molecular toolkit to develop ner-

vous systems, it may not have been advantageous for them to do so.

Cnidarian, ctenophore and bilaterian nervous systems exhibit varying degrees of genetic conservation. Their ancestor must have possessed much of the core molecular toolkit required to develop a nervous system. Ancient cnidarians, ctenophores and bilaterians must have inherited that toolkit and might have used it to develop and distribute 'proto-neural' sensory cells such as those of extant sponges. If those lineages split before neurones evolved, then they must have independently co-opted their distributed 'proto-neural' sensory cells into networks of neurones. While this scenario somewhat contradicts the widespread belief that cnidarian and bilaterian neurones are genetically homologous, it potentially explains the profound developmental and design discrepancies of their nervous systems today.

A Potential Utility for Fast Threshold Detectors

Before animals ate each other, they followed gradients to find more favourable environments. When macrophagy became a viable feeding strategy, a dynamic state of the world became crucial to an animal's survival: the proximity of other animals. Knowing that state, and particularly the moment when that state indicated the presence of a threat or opportunity, would have provided utility. As soon as another animal came sufficiently close, predators and prey needed to make an immediate decision to attack or defend. That decision needed to be made at precisely the right time; striking or fleeing a bit too early or a bit too late can result in the loss of a potential meal for predators, or death for prey [Stewart et al., 2013]. Animals must have experienced a selection pressure to react as soon as they had evidence that a state of the world (e.g. the proximity of another animal) became critical.

How might that selection pressure be satisfied by spiking neurones, but not other signalling cell types? Consider a hypothetical late pre-Cambrian predator that is approaching a prey. If the prey can initiate some defensive strategy, e.g. fleeing, when the predator is some particular distance D away, it maximises its chances of surviving the encounter [Stewart et al., 2013]. Assume that the predator produces some physical signal (e.g. chemical, electrical or mechanical) that protrudes into the open environment and assume that the prey has a thresholding cell whose membrane potential depends on the strength of that signal. As the predator approaches the prey, its signal strengthens, and the membrane potential of the prey's thresholding cell rises. When the distance between the predator and prey reduces to D , the membrane poten-

tial meets its threshold, and the cell produces a spike. That spike is a precisely timed assertion that a state of the world has reached some critical value, so a decision needs to be made at that moment. *Nota bene*, this proposal for the origin of sensory neurones is hypothetical and abstract; it is only intended to illustrate a potential utility for fast thresholding cells in predator-prey interactions that paracrine-signalling cells cannot provide.

Implications for Neural Computation

Predator-prey interactions require animals to make precisely timed decisions in accordance with potentially fatal world states. Intuitively, animals should value real-time information about the criticality of world states, as they could make better and more precisely timed decisions in response to them. Extant sensory neurones are devices that produce spikes conditional on world states. How can an animal extract the most information about critical world states from those sensory spikes?

Since sensory spikes are conditional on world states, it is possible in principle to make inferences about the world given the presence or absence of each individual sensory spike. If an animal could implement Bayes' rule to perform this inference, then that animal would extract the most possible information about world states from sensory spikes [MacKay, 2004]. If an animal could perform Bayes' rule as quickly as sensory spikes are streamed, then that animal would have the most possible information about world states at any instant in time. In situations demanding fast decision making and reaction in accordance with potentially fatal world states, e.g. predator-prey interactions, continuous and direct inference about critical world states from sensory spikes cannot be outperformed in bits per second.

It seems plausible that nervous systems actually implement this computation, or something like it. Psychophysical evidence suggests that animals act as if they are performing bayesian inference in many tasks [Jacobs, 1999; Ernst and Banks, 2002; Weiss et al., 2002; Knill and Saunders, 2003; Adams et al., 2004; Knill and Pouget, 2004; Kording and Wolpert, 2004, 2006]. Animal reaction times indicate that individual spikes, and not trains or codes of spikes, are the fundamental operands of neural computation [Paulin and Hoffman, 2001; Uchida and Mainen, 2003; Johansson and Birznieks, 2004; Paulin, 2004; Bodelon et al., 2007; Olberg et al., 2007; Deneve, 2008; Stanford et al., 2010; Rolls and Treves, 2011]. We do not know if continuous inference from sensory spikes is biologically possible to implement, nor if the energetic expenditure required to implement it is prohibitively high. Establishing

whether and how nervous systems might implement this computation are major open questions in neuroscience [Rao, 2004; Ma et al., 2006; Huys et al., 2007; Deneve, 2008; Ma et al., 2008; Natarajan et al., 2008; Bobrowski et al., 2009; Gerwinn et al., 2009; Fiser et al., 2010; Koyama et al., 2010; Lochmann and Deneve, 2011; Pouget et al., 2013].

A Contradiction with Molecular Clocks

Molecular clocks dispute the claim that animals evolved neurones after the advent of macrophagy. A strong argument can be made that nervous systems evolved once in bilaterians [Hirth, 2010]. If nervous systems appeared at around 550 MYa, then bilaterians must have split (into protostomes and deuterostomes) after this date. Fossil evidence does not contradict this assertion; trace fossils indicate the presence of bilaterians around 560 MYa, and the first bilaterally symmetric body fossils are dated to 557 MYa (see *Fossils and the Morphology and Behaviour of Ancient Animals*). It seems reasonable that bilaterians split into protostomes and deuterostomes a few million years later. Molecular clocks, on the other hand, assert an earlier bilaterian divergence time. Current molecular clock estimates for the branching time of bilaterians into protostomes and deuterostomes range from 670 to 570 MYa [Aris-Brosou and Yang, 2003; Peterson et al., 2004, 2005; Erwin et al., 2011]. These dates imply that bilaterians remained absent from the fossil record for tens of millions of years. Either the fossil record is incomplete or the clock dates are incorrect.

Bilaterian absence from the trace fossil record for tens of millions of years seems unlikely. Before 550 MYa, there were abundant microbial mats that provided excellent taphonomic conditions to preserve traces [Gehling, 1999; Jensen et al., 2005]. It is also possible, though unlikely [Budd and Jensen, 2000], that the first bilaterians were pelagic, tiny or otherwise unable to leave detectable traces. However, the earliest bilaterian traces we observe are extremely simple, unbranched, shallow, horizontal traces depicting bilaterians gently pushing through sediment (see *Fossils and the Morphology and Behaviour of Ancient Animals*). These traces are inconsistent with those we would expect from organisms that had been evolving nervous systems for tens of millions of years. Furthermore, although molecular clock methods have improved, even recent results on the bilaterian split vary by 100 million years. They can be sensitive to methodology, model assumptions and the data set [Welch et al., 2005], and are unreliable when inferring earlier branching times [Marshall and Valentine, 2010]. Thus, we believe that these clock dates are too old.

Phyla Branching Order Does Not Matter

Phylogenetic trees produce notoriously inconsistent results [Nielsen, 2008; Siddall, 2010]. We have assumed that sponges are the most basal extant animal lineage (fig. 4). We made this assumption because most phylogenetic trees place sponges at their base [Nielsen, 2008]. We also used this assumption to provide a potential explanation for how nervous systems can be polyphyletic, yet exhibit a degree of genetic conservation. However, the core arguments of this paper do not depend on the validity of this assumption or the branching order of the animal phyla.

Recently published results indicate that ctenophores, and not sponges, could be the most basal extant animal phylum [Ryan et al., 2013; Moroz et al., 2014]. If this claim is true, it does not follow that animals evolved nervous systems once, even though extant ctenophores possess nervous systems. In fact, both Moroz et al. [2014] and Ryan et al. [2013] acknowledge this potential fallacy; if ctenophores are basal to all other animals, then either animals evolved nervous systems once, and sponges and *Trichoplax* subsequently lost their nervous systems, or nervous systems evolved independently in ctenophores, cnidarians and bilaterians. The latter scenario still accounts for the fossil and ecological evidence that we have reviewed in this paper.

Other Proposals for Nervous System Origin

The 'light switch' hypothesis [Parker, 1998] proposes that the evolution of sensory systems, specifically colour spatial vision, led to the onset of predation at the base of the Cambrian. We contend that causality goes the other way. Animals do not require neurones to detect gradients or move in relation to them, so animals are capable of orienting and moving toward or away from other animals by following the gradient of the signals that they emit. Thus, predation is possible in ecosystems lacking animals with neurones. Conversely, ecological considerations indicate that neurones cannot exist in ecosystems lacking predation.

Keijzer et al. [2013] argue that nervous systems evolved not as an input-output mechanism, but rather as a way to coordinate muscle contraction over large spatial scales. Their argument is based on some of the material we have presented, for example that nervous systems are not necessary for animals to detect stimuli, but does not seem to account for the fact that nervous systems are not necessary for animals to coordinate movement on large spatial scales either [Nickel et al., 2011]. Their point is well taken: a crucial function of the earliest nervous systems was to

facilitate quick muscle contractions over the whole body. However, another crucial function was to detect the presence of states that required such coordinated contractions. Detection of states of the world and reaction to those states are inextricably linked.

Jekely [2011] proposes that the first neural circuits evolved to improve the efficiency of ciliary swimming in the ancestor of cnidarians and bilaterians. The basic idea is that, without nervous systems, sensory and motor functions are performed by the same cell, such as the photoresponsive ring of cilia in sponge larvae (fig. 3a). Each of these cells has a sensory structure whose output affects ciliary beating. The number of sensory structures can be reduced by eliminating the sensory structures of the cili-

ated cells in favour of a smaller number of neurones. Those neurones produce signals in response to light intensity and transmit those signals to the ciliated cells. This transition could have allowed the diversification of sensory modalities and the behavioural repertoire of animals. While Jekely's hypothesis provides an ecological affordance for neurones, it does not explain why the first bilaterian trace fossils are so simple, given that the ancestors of those bilaterians had been evolving nervous systems for at least tens of millions of years. It also assumes that nervous systems evolved once in the cnidarian-bilaterian ancestor. Firmer molecular evidence on the monophyly or polyphyly of nervous systems should be able to support or refute his hypothesis.

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