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Guest editorial

Evolving understanding of nervous system evolution

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Nervous systems encompass a staggering diversity from nerve nets of just a few hundred neurons — as in the nematode worm *Caenorhabditis elegans* [1] — to the highly centralised and cephalised nervous systems of arthropods that may contain a million neurons [2], as in the honeybee [3], and those of cephalopod molluscs, such as the octopus [4], and amniotes that can contain hundreds of millions to billions in the case of the human brain [5]. Nervous systems have been evolving in concert with the animals that possess them since the Precambrian more than 580 million years ago [6,7]. Arguably, all extant nervous systems are success stories; no single one is inherently better than any other: they are the products of different sets of evolutionary pressures produced by different life histories. Our knowledge of nervous systems is derived from multiple levels and types of analysis: genetics, development, cell signalling, morphology, biophysics, physiology and behaviour. Understanding how so many organisational levels are integrated to produce even a single behaviour is difficult; understanding their evolution even more so. This, then, is the central challenge of studying the evolution of the nervous system — combining all the disciplines that neuroscience typically employs to understand and interpret structure and function with the approaches needed to understand and interpret evolutionary history, ecology, selection and adaptation (or the lack of it). Integrating all this may seem a daunting prospect and few single studies manage to combine more than two or three of these approaches, though those that do often produce insights into the principles that govern neural function and the mechanisms that govern how neural circuits evolve (for example [8,9]).

Yet as the articles in this special issue show, it is possible to obtain substantial insights into principles and mechanisms of neural circuit evolution by combining the conclusions of many disparate studies each of which tackles only one approach or level [10–13]. These articles demonstrate that some of the key components of nervous systems were in place very early in evolution [3], and indeed some features of gross neuroanatomy have been retained since the Cambrian [6,7]. At the same time, there is evidence for rapid evolution, with seemingly radical changes in behaviour evolving through relatively minor tweaking of existing neural circuitry [14,15]. Understanding how novel functions are added to neural circuits while retaining previous ones is a major challenge. Perhaps unsurprisingly for tissues of such antiquity, nervous systems can also maintain function despite substantial changes in the environment, through plasticity and modulation. This raises another major issue: with plasticity capable of compensating for environmental perturbations, how do neurons, neural circuits and nervous systems evolve?

There is a tendency to try to understand the function of neural circuits through analogy between nervous systems and computers. Whilst there is no doubt that analytical tools from engineering have been enormously beneficial in understanding signal processing within neural circuits, when considering the evolution of these circuits such approaches can be misleading. Brains are not designed but evolve 'blindly' through selection. Brains cannot be optimised as easily as machines: as nervous systems evolve they cannot disconnect the wires and 'start over'. This means that solutions are constrained by history, and in some cases may be suboptimal.

An interest in the evolution of the nervous system and neural circuits is not new; many of the reviews gathered together for this special issue have antecedents from the 1980s and 90s (for example [16–18]), and those in turn were rooted in earlier work (for example [19]). These early studies, and the reviews that integrated and interpreted their findings, revealed much about the evolution of neural circuits and principles that govern information coding and coding within them. Even with a more limited palette of techniques at their disposal, particularly fewer molecular and computational techniques, early researchers interested in the evolution of the nervous system revealed key aspects of nervous system function and evolution through anatomy, electrophysiology and comparative analysis. At the same time, they encountered problems that remain central to studying the evolution of the nervous system, for example the question of how to determine whether features are homologous and how to assign function to specific components, how to reconcile plasticity and modulation within the nervous system with evolvability, and how to determine whether neural circuits or their components are optimal.

Comparison, homology, convergence and divergence

Comparisons are fundamental to determining how neurons, neural circuits and nervous systems have evolved. They can be made at many levels, but their interpretation depends upon the evolutionary history of the traits being compared. Comparisons between neural circuits from disparate lineages, such as insects and vertebrates (for example [11,13,20,21]), have revealed fundamental shared computational and organisational principles, and have been particularly effective in determining principles of sensory coding because these systems have to extract information from the same physical and chemical stimuli and solve the same problems. For example, numerous similarities exist in the visual systems of insects and vertebrates, including multiple layers of graded information processing, centre–surround receptive fields and the occurrence of ON and OFF pathways (processing responses to light increments and decrements, respectively) [22].

In an evolutionary context, however, determining whether neurons or neural circuits share a common ancestry — that is, are homologous — is essential for interpreting comparisons [23,24]. Similarities in early sensory systems could be the result of a common heritage or separate evolutions of a strategy that solves a problem posed by common environmental factors [13,25–27]. Homology can be

considered at many different levels: it can be applied to sub-cellular structures such as synapses, to individual neurons, motifs within neural circuits, tracts and/or regions within nervous systems, and even to behaviours and cognitive capacities.

Once homology (or the lack of it) is established, then traits can be compared and contrasted in appropriate ways. For example, comparison of homologous neurons in different segments of the locust revealed segment-specific divergence in structure, function and connectivity linked to the specialisation of limb control and behaviour [28]. In contrast, the eyes of vertebrates and cephalopods are analogous, separate evolutionary innovations of a simple image-forming eye [29]. Comparisons can be made among species by mapping homologous traits onto established phylogenetic trees to determine whether patterns exist that are linked to the ecology of extant species. Once neural traits have been mapped onto a phylogenetic tree, molecular estimates calibrated with fossils can be used to determine their antiquity. Whilst it may not be possible to detect neurons or neural circuits within fossils, brain regions have been discerned in some exceptionally well-preserved fossils and the antiquity of brain structure demonstrated (for example [30]). In the case of arthropods, remarkably well preserved eyes and central nervous systems have been found in fossils from the Cambrian more than 480 million years ago [7].

Several factors make determining homology fraught with difficulties. As mentioned above, the prevalence of widespread convergence in biological systems means that traits appearing similar in form and/or function may be analogous, having vastly disparate evolutionary histories. Equally, homologous structures may undergo such divergence during their evolutionary history that their identity and origins are obscured. The developmental origins and trajectories of structures are often highly informative for teasing apart homologous from analogous features, a fact appreciated early in the study of neural evolution. Yet some traits within extant species may be so divergent that their origins and homologies remain obscure even during development.

Molecular analyses have also been employed to augment or even replace other means of demonstrating homology [14]. For many researchers, however, their use remains controversial because a relatively small number of signalling pathways have been redeployed during development, so that finding cells or tissues expressing the same sets of genes may not be an unequivocal proof of homology [31]. Recent claims of deep homologies between vertebrate and invertebrate brain structures, and the debates that surround these claims [32], emphasise not only the importance of determining homology but also that new techniques do not necessarily solve the problems faced by earlier researchers.

One neuron, one function?

Closely associated with the concept of homology among neurons and neural circuits is that of the identified neuron. Much of what we know about neural circuit evolution has been discerned from the comparison of the structure and function of identified neurons in invertebrates (for example [33]). In particular, comparisons of identified neurons within or among species have not only revealed the structural and functional changes that can occur during evolution (for example [28]) but also the variation that may be the basis of evolutionary change and innovation.

Nevertheless, there are drawbacks to viewing neural circuit evolution through the prism of identified neurons. Typically, such neurons are 'identified' based upon their structure, relatively few studies relying on developmental lineages and molecular signatures. This may not be such a problem when comparisons are made among closely-related species in which structure is highly conserved. But as the phylogenetic distances across which comparisons are made increase, the guarantee of finding conserved structure diminishes, potentially obscuring homologies. Moreover, homologous neurons can undergo substantial structural divergence even among different segments of the same species in relation to functional/behavioural specialisation (for example [28]).

Neurons identified through common structural motifs may still not function in similar ways to homologous neurons in other, even closely-related species [8]. In part this is due to a reliance on major dendritic and/or axonal branches to find structural motifs; small changes in branching may have major consequences in terms of connectivity changing both inputs and outputs with accompanying functional implications. In part, this is because structure does not completely determine neuronal function: physiology is essential. Although neuronal biophysics is clearly affected by branching structure, synapses, channels, exchangers, pumps and intracellular signalling pathways all have major influences on the functional output of neurons.

Typically, identified neurons are large in comparison to the majority of neurons, even within invertebrate nervous systems. This bias is partly a result of the methods through which they have traditionally been identified, and the ease with which they may be found in multiple species. Nevertheless, it means that they may not be entirely representative of most neurons that exist in populations within nervous systems [34]. Often these neurons may be highly specialised in both structure and biophysical properties for a specific task or function, such as the squid giant axon [34,35]. Yet much of our understanding of the evolution of the nervous system and neural circuits is based upon studies of this relatively small subset of neurons.

One impact of this has been the perception that separate neural circuits exist for all behaviours. Such specialisation and segregation might represent an idealised, 'neat' scenario, where there is no interference between responses underpinning different behaviour routines, and where separate circuits can be tuned independently over evolutionary time, without disrupting the function of others [22]. Yet the common sets of sensory and motor neurons shared by numerous behaviours are an obvious demonstration that this perception is misleading [36]. Even components of central pattern generators may be recruited into multiple rhythm generating circuits, as occurs in the stomatogastric ganglion of *Cancer borealis* (for example [37]). In some neural circuits, the very definitions of neurons into sensory neurons, interneurons and motor neurons are blurred (for example [38]). Nevertheless, there has been

a tendency to associate specific neurons with specific tasks, even going so far as to give identified neurons names that describe their supposed function. Naming neurons based upon a supposed functional role can entrench thinking and prevent a broader appreciation of the contributions of neurons to many behaviours and circuits. The names ascribed to neurons can themselves be misleading; in visual interneurons, for example, they often caricature receptive field structures, capturing only the most striking features (typically those stimuli that evoke the highest spike rates) and ignoring the restructuring of receptive fields that can occur during behaviour and/or as a consequence of modulation.

This tendency to ascribe specific behavioural roles to neurons is unlikely to reflect the way in which selection pressures act on the nervous system through the behaviour and ultimate outcomes it generates in terms of survival and reproduction rather than specific neurons. Selection pressures will act on any component of a neural circuit that affects a behavioural output with ultimate consequences, whether by reducing costs or increasing benefits. At bottlenecks that limit behavioural output, such as the speed of transmission of a signal indicating danger, selection pressures are likely to be particularly strong but still act throughout a circuit. Where neurons contribute to multiple behaviours, they will be subject to numerous selection pressures that do not necessarily act in the same direction.

Modulation, plasticity and evolvability

The presence of modulation and plasticity within nervous systems compounds the difficulties of assigning function to specific components. Nervous systems are rife with the means to adjust their components over a range of timescales from seconds to years, altering behaviour. Modulation and plasticity can themselves evolve so that they differ even among closely-related species, increasing the difficulty of identifying homologous components and making comparisons (for example [39]).

Neuromodulators and neurohormones can alter the outputs of circuits so that the same circuits can produce different behaviours [40]. Moreover, the components of neural circuits can be reconfigured so that neurons are recruited into different circuits producing new behavioural outputs [37,40]. The evolution of neuromodulatory and/or neurohormonal systems can, therefore, produce entirely new behavioural output without requiring substantial changes in the structure of particular components. Changes in the relative timing of release of modulators and/or hormones can enable behaviours to be expressed at different times within an animal's life history, placing animals in novel behavioural environments and exposing them to new selection pressures.

Plasticity can also occur over a broad range of timescales, occurs in both structure and function, and fulfils multiple roles. In some cases, plasticity can enable neural circuits to produce relatively constant outputs despite changes in the environment (for example [41]). This homeostatic role of plasticity enables an animal to absorb change, adjusting to perturbations such as mutations, injury or sensory deprivation. Thus, mutations that alter neural structure and function may have substantially less of an effect than might be supposed. In this sense, homeostatic plasticity could act as a phenotypic capacitor allowing animals to absorb change under one set of environmental circumstances only to reveal these changes when the environment is perturbed. Potentially, this canalisation of neural circuit function could be a powerful means of producing innovation.

Another form of plasticity is linked to the formation of learning and memory. Again, this permits animals to adjust to their environment, allowing them to predict and exploit its features. Indeed, plasticity linked to learning and memory can allow animals to produce entirely different/novel sets of behaviours and to become more efficient within a particular environment. Yet this plasticity can also expose animals to entirely new environments that they can exploit and to new selective pressures.

Understanding the impact of plasticity on the evolvability of the nervous system and neural circuits is, then, a considerable challenge. Whilst the benefits of plasticity are often obvious, in that it preserves function or enables animals to exploit correlations within their environments, the costs are more difficult to discern. Moreover, the mechanisms underlying plasticity are able to evolve just as those of modulation. For instance, changes in the duration and timing of critical periods can have major effects upon which changes can be compensated for or which correlations learnt.

Optimality and the adaptionist programme

There is a pervasive view that evolution is a 'natural engineer' honing each trait of an organism to reach its theoretical optimum. The fallacy of this view was highlighted by Gould and Lewontin [42], in which they likened this idealised view of evolution to Voltaire's blue-eyed philosopher Pangloss, who finds divine design and meaning even in the face of utter disaster surrounding him. Engineered systems and circuits can be reconfigured extensively to accommodate new components and technologies. Moreover, components from early designs may bear little resemblance to those in later iterations producing substantial improvements in terms of performance and materials (consider, for example, vacuum tubes and transistors). Unlike engineered systems, organisms cannot simply invent new components but rather must adapt existing ones; they are the product of an evolutionary history that influences all aspects of their structure and function.

As a consequence of this evolutionary history, the molecular components of nervous systems are similar throughout animals, with the same sets of proteins and signalling molecules being used again and again in different contexts [43]. Key steps in signal processing can be achieved through entirely different molecular processes involving different components, acting at different points within neurons and neural circuits. For example, gain control can occur in a huge variety of ways within neural circuits, at the synaptic inputs, through shunting inhibition, through changes in the spatial location of the spike initiation zone, and through pre-synaptic inhibition (for example [44] and references therein).

Selection acts on these components through ultimate costs and benefits to produce adaptations within the bounds set by physical constraints, which include both the size of

molecules themselves and factors such as thermal noise [45]. Numerous studies have demonstrated that features of the nervous system that are adapted to specific functions perform certain information coding tasks particularly efficiently [22]. Investment in computational resources may be matched to the salience of particular sensory cues or the demands of fine motor control; many animals devote proportionally more of their sensory coding regions to the cues upon which they rely most heavily and which will yield substantial ultimate reward [3]. A particularly obvious example is the primary sensory neuropile region (glomerulus) of the male moth that processes signals from pheromone receptors, which is larger than other olfactory glomeruli [46].

Yet investment in and adaptation of some features does not necessarily imply that all features of nervous systems are adapted to specific functions or that selection has optimised them for these functions. There are clear examples of not-quite optimal adaptations within nervous systems. For example, the specific placement of components within nervous systems are arranged to closely match the positions that would minimise wiring length, though they do not match exactly [47]. Wiring length is thought to be a proxy for resource allocation and, consequently, this is assumed to be an adaptation that reduces the consumption of resources including energy [21,22]. Nevertheless, even when considering component placement within nervous systems, it is clear that developmental constraints can and do prevent nervous systems from achieving optimal solutions. The recurrent laryngeal nerve (specifically the left one) is a particularly clear example of developmental constraints causing deviations from optimality. This branch of the vagus nerve passes under the aortic arch, a consequence of the development origin of the larynx from pharyngeal arches. This increases the length of the nerve far beyond the minimum length that could occur without recurrence in vertebrates with long necks such as giraffes or sauropod dinosaurs. In modern giraffes (*Giraffa camelopardalis*) this nerve can exceed 4.5 metres in length, despite linking two locations just centimetres apart: the hindbrain and the larynx at the top of the neck, controlling vocalisations, breathing, and trachea protection while swallowing [48].

The participation of neurons in the generation of multiple behaviours may also prevent them from being optimally adapted to any specific behaviour. Whilst neuromodulators and neurohormones can alter neural components to make them more suited to particular tasks [40], it seems unlikely that they can shift a neuron or neural circuit from being optimised for one task to being optimised for another. Indeed, in many cases it is difficult even to define the specific functions that would be optimised because of the many ways in which the performance of neurons and neural circuits can be assessed. But where performance can be quantified, computational approaches offer the possibility of simulating different combinations of components at scales from ion channel biophysics to entire neural networks. In such cases, it is possible to assess the performance of the actual components that have evolved and compare them to the possible combinations that could have evolved to directly assess optimality and adaptation.

Conclusions

In opening up a new chapter in the study of the evolution of the nervous system, it is essential that we build upon earlier work. Many of the problems that early researchers faced remain critically important when studying the evolution of neurons, neural circuits and the nervous system even if the arsenal of anatomical, computational and molecular techniques used to address them has expanded. Moreover, new techniques, for example those based on CRISPR/Cas9, show enormous promise addressing questions about the evolution of the nervous system and neural circuits in relation to a broad range of animals that have traditionally not been accessible [49]. Such molecular techniques have the potential to democratise the study of the molecular mechanisms of neural circuit formation and function. Coupled with comparative analysis and phylogenetics this has the potential to reveal the mechanisms underpinning evolutionary changes in neurons, neural circuits and nervous systems and their relation to behaviour.

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Feature

The cryptic cortex

New data are overturning the classical view of the cerebral cortex as a mammalian invention. The closer we look, the more cortex-like features we see in a number of other vertebrates, including birds, which have evolved impressive cognitive abilities. **Cyrus Martin** reports.

Nothing sets us humans apart from the rest of the animal kingdom quite like our brains. Our prodigious craniums allow us to communicate with each other in spoken language and give us insight into one another's thoughts and feelings. The human mind is also capable of extraordinary creativity and abstraction, epitomized by our works of art and literature. And our powers of logic and reasoning have unraveled the fundamental forces governing the cosmos, and the inner workings of life itself. The downside of such a potent brain, and a great irony, is that it has allowed us to multiply to such an extent that we are quickly fouling our own nest. This, together with the technology in hand to incinerate each other in a nuclear apocalypse, suggests the possibility that our brilliant minds will be our downfall. Oh, and lest we get too full of our cognitive powers, it should be pointed out that the human brain was also responsible for the pet rock.

From where in the human brain does all of this intellectual horsepower originate? Well, starting from the back and moving forward, the human brain, and in fact all mammalian brains, at first appears to follow a blueprint common to all vertebrates. There is the requisite brainstem, for example, which controls the pace of our heartbeat and our breathing, or, as another example, the hypothalamus, which tells us whether we are hungry or sated, and keeps our bodies on a 24-hour rhythm. While essential, these functions are more concerned with the day-to-day business of existing rather than the intelligent behaviors we typically associate with a fully animated human being. It isn't until we move to the front that we see a remarkable shift in mammals. Where in other vertebrates the forebrain is a smooth, mostly featureless surface, in mammals we see a kind of wrinkling occurring where the surface has started to undulate. In primates and a few species like dolphins and elephants the folding is even more accentuated, to the point where it gives the appearance of Play-Doh snakes intertwined with one another, or an intestine coiled in on itself. This is the cerebral cortex.

We now understand that it is the cerebral cortex and several structures underneath it that mediate most of the brain's 'higher level' functions — its ability to learn and remember, to track the body's position in space, and to control intricate movements with the hands, among many other things. At the most basic level, the function of the cortex is to use information sampled from the outside world by the eyes, ears, nose, and skin, and generate appropriate behaviors. In fact many neuroscientists argue that movement is the cortex's raison d'être, as movement, in the end, is what natural selection acts on.

If we take a cross-section through the cortex, we see a striking degree of organization. Early neuroanatomists like Cajal noted that the cortex is arranged like a layer cake, each layer being easily distinguished by the characteristic features of the neurons and fiber types present. The work of pioneering electrophysiologists like Vernon Mountcastle then showed that, as we move up and down in the different layers of the cortex, the cells in a column function together in little microcircuits. And, fascinatingly, as we move laterally across the surface of the cortex, we find that there is a tight correspondence between the function of the columns and the spatial arrangement of the receptors they receive input from, or the muscle fibers they control. So, for example, in the visual cortex, which receives sensory information from the eye, a two-dimensional map of the activity patterns of the microcircuits would match a corresponding map of retinal activity.