Introduction

This year (2009) commemorates both Charles Darwin's 200th birthday and the 150th anniversary of the publication of the first edition of *On the origin of species* (Darwin 1859). To celebrate these events, *Biology Letters* is publishing a number of special features on topics related to evolution. This first special feature focuses on brain evolution. At first glance, this is a strange choice: in the first edition of the *Origin*, Darwin had very little to say about the brain. A search through the digitized version of this work (http://darwin-online.org.uk) brings up only one mention of the word 'brain', and that is in the context of describing the skull and the axial skeleton (Darwin 1859; p. 437). This is deceptive, because in his notes, Darwin frequently refers to the brain as the organ of thought and behaviour, and to heredity of behaviour as being dependent on the heredity of brain structure (e.g. de Beer 1960). In later editions of the *Origin*, additional mentions of the brain do crop up. The sixth edition, for example, contains a passage, which explicitly states that natural selection applies to the brain as it does to all the other organs (Darwin 1872; p. 98).

The increased focus on the brain in later editions is probably due to the ongoing debates at the time about the position of humans as part of the animal kingdom. By the time Darwin published the sixth edition of the *Origin*, he had already published the first edition of *The descent of man* (Darwin 1871). This entire book is an argument for the similarities and continuity between apes and humans, and it emphasizes the importance of the brain: 'It is notorious that man is constructed on the same general type or model with other mammals. All the bones in his skeleton can be compared with corresponding bones in a monkey, bat, or seal. So it is with his muscles, nerves, blood-vessels and internal viscera. The brain, the most important of all the organs, follows the same law, as shewn by Huxley and other anatomists'. (Darwin 1871; p. 10). It is clear, therefore, that in his lifetime, Darwin advocated the idea that the human brain, as any other organ, shared a history with the brains of other animals (i.e. descent with modification), and were subject to the pressures of natural selection.

Since Darwin's time, the topic of brain evolution has remained of interest. As in Darwin's works mentioned above, the main reason for this interest is a general interest in what makes humans different from other animals. But of course, the study of brain evolution cannot be about the human brain alone. As Darwin showed us for many other characteristics, the evolutionary framework helps us to understand the wide variety of brains, and the behavioural variability that can go alongside it. The research on brain evolution, therefore, has involved the brains of many animals, not just humans and our closest relatives, and this is reflected in this special feature. A large proportion of the research in this field is focused on describing and understanding the patterns of descent with modification. This makes sense, because it is impossible to explain the variability that exists in terms of morphology, mechanism or function, without first knowing its extent and pattern of descent. A smaller proportion of the research focuses on (or speculates about) the selective pressures that have shaped and still shape brains. These studies typically only look at the easy-to-measure aspects of brain morphology, such as the overall size or the sizes of major subdivisions (for a review, see Healy & Rowe 2007). In this special feature on brain evolution, we present a selection of articles that spans this entire range of topics.

The first two papers focus on aspects of common descent across very distantly related groups of animals: they emphasize the continuity and similarity of molecular aspects of neural function and development. Kosik (2009) reviews how the molecular complexes involved in synaptic transmission are thought to have evolved, while making an argument for the comparative approach in order to understand all types of complex cellular machinery. Reichert (2009) shows us how very different adult nervous systems (those of insects and vertebrates) can be based on very similar (and presumably conserved) molecular machinery. Both papers address a very important question, which has come up in the debate about evolution many times in different guises: how can complex systems have evolved, if taking away even one component today damages the system beyond repair? The answer seems to be that the same molecules can serve different functions in different contexts (and do so in different organisms), as both papers illustrate beautifully.

The next two papers address a question with important implications for understanding the structure-function relationships in the brain. We all know that humans can do very complex cognitive tasks, and that, as mammals, humans have a six-layered cortex. Many theories have
been put forward about why this cortical organization is crucial for the efficient functioning of the brain, and have argued that it is this cortical organization that has allowed humans to become what we are today. But why do only mammals have such a laminated cortex, and more importantly, does it really make a qualitative difference in behaviour? Both Ito & Yamamoto (2009) and Reiner (2009) address this question, focusing on birds and fishes, respectively. In their papers, bird and fish forebrains are shown to have a lot more in common with the mammalian forebrain than previously thought, without the laminar organization. Their ideas suggest that similar behavioural problems can be solved with different neural architectures, a conclusion that may give us important insights into exactly what is necessary for brains to produce complex behaviours.

The question of the total brain size has always been at the forefront of arguments about brain evolution. After all, humans have relatively large brains compared with other animals, so the question is intrinsically interesting to us. Isler & Van Schaik (2009) and Sol (2009) address two opposing selective pressures on the evolution of brain size. On the one hand, Sol points out that large brains may be advantageous for dealing with unexpected circumstances (the cognitive buffer hypothesis), while on the other hand, Isler and Van Schaik present the data from a new comparative analysis which shows that population dynamics of species are limited by the demands of developing a larger brain. While these two papers address the selective pressures that apply to brain size, Striedter & Charvet (2009) investigate developmental mechanisms that allow brains to get larger, both in birds and mammals. They conclude that similar developmental mechanisms leading to larger brains may have evolved in these two lineages.

Finally, there remains the question about whether it is important to learn about brain evolution at all. Of course, we are all interested in knowing why we as humans are intellectually so different from other animals (or at least that is how we see it), and why we have such large brains. But is this just a bit of narcissism? Are we just interested because it is about us or is this knowledge important from a more practical point of view? For most of the neuroscience community, many of whom study the brain from a more applied, medical point of view, studying brain evolution may seem as an interesting, but irrelevant, pastime. In a separate contribution, I (Smulders 2009) argue that as long as biomedical researchers use other animals to help us understand the human brain, understanding the processes and patterns of brain evolution will be important. The comparative analyses among many species are also important to give us insights into the structure–function relationships in the brain, which we might not discern when studying just one or a few species. Examples of this latter argument are present in many of the papers in this special feature, but especially in the final contribution by Amrein & Lipp (2009). They use comparisons between the different groups of mammals to gain insights into the function of a relatively novel discovery in neuroscience: the fact that adult mammals continue to create new neurons in the hippocampus, a brain structure involved in learning and memory. Their findings call into doubt some of the proposed functions that were based on work done purely with laboratory mice and rats.

In conclusion, 150 years after Darwin published On the origin of species, we have learned much about how brains have evolved and about what this means for us as humans. However, as is clear from the eclectic selection of papers in this special feature, many questions remain unanswered and evolutionary neuroscientists still have a significant challenge ahead of them.


