1.01 A History of Ideas in Evolutionary Neuroscience

G F Striedter, University of California, Irvine, CA, USA
© 2007 Elsevier Inc. All rights reserved.

1.01.1 Common Plan versus Diversity
1.01.2 Scala Naturae versus Phylogenetic Bush
1.01.3 Relative Size versus Absolute Size
1.01.4 Natural Selection versus Developmental Constraints
1.01.5 One Law, Many Laws, or None
1.01.6 Conclusions and Prospects

Glossary

allometry The notion that changes in the size of an object (e.g., the body or the brain) entail predictable changes in the proportional sizes of its components. In contrast, isometric scaling involves no changes in an object’s proportions.

convergence The independent evolution of similar structures or functions from non-homologous ancestral precursors.

developmental constraint The notion that the mechanisms of development bias the production of phenotypic variants that natural selection can act on.

encephalization Brain size relative to what one would expect in an organism of the same type (i.e., species or other taxonomic group) and body size. Synonym: relative brain size.

heterochrony Phylogenetic changes in the relative timing of developmental events or in the relative rates of developmental processes.

homology The relationship between two or more characters that were continuously present since their origin in a shared ancestor. For a more detailed definition, especially for neural characters, see Striedter (1999).

mosaic evolution The notion that, as brains evolve, individual brain regions may change in size independently of one another. In contrast, concerted evolution indicates that brain regions must change their size in concert with one another.

The field of evolutionary neuroscience is more than 100 years old, and it has deep pre-evolutionary roots. Because that illustrious history has been reviewed repeatedly (Northcutt, 2001; Striedter, 2005) and is treated piecemeal in several articles of this book, I shall not review it fully. Instead, I will discuss a selection of the field’s historically most important ideas and how they fit into the larger context of evolutionary theory. I also emphasize ideas that are, or were, controversial. Specifically, I present the field’s central ideas in contrast pairs, such as ‘common plan versus diversity’ and ‘natural selection versus constraints’. This approach scrambles the chronology of theoretical developments but helps to disentangle the diverse strands of thought that currently characterize evolutionary neuroscience. It also helps to clarify which future directions are likely to be most fruitful for the field.

1.01.1 Common Plan versus Diversity

One of the most famous battles of ideas in comparative biology was that between Etienne Geoffroy St. Hilaire and George Cuvier over the existence, or not, of a common plan of construction (or Bauplan) for animals (Appel, 1987). Geoffroy was of the opinion, previously developed by Buffon (1753), that all animals are built according to a single plan or archetype, but Cuvier, France’s most illustrious morphologist, recognized at least four different types. Their disagreement erupted into the public sphere when Geoffroy in 1830 endorsed the view that the ventral nerve cord of invertebrates is directly comparable (today we say ‘homologous’) to the spinal cord of vertebrates. Cuvier responded that Geoffroy was speculating far beyond the available data, and he reasserted publicly that the major types of animals could not be linked by intermediate forms or topological transformations. This Cuvier–Geoffroy debate was followed closely by comparative biologists all across Europe, who
were already flirting with the idea of biological evolution or, as they called it, the transmutation of species. If Cuvier was right, then evolution was impossible. On the other hand, some of Geoffroy’s hypotheses (e.g., his proposal that insect legs correspond to vertebrate ribs) did seem a trifle fanciful. Thus, the Cuvier–Geoffroy debate embodied much of the ambivalence surrounding evolution in the first half of the nineteenth century.

After Darwin offered a plausible mechanism for the transmutation of species, namely, natural selection (Darwin, 1859), the idea of biological evolution took hold and, by extension, Geoffroy’s ideas gained currency. Innumerable homologies were sought and, frequently, revealed (Russel, 1916). Most impressive was the discovery of extensive molecular homologies between species that span the metazoan family tree (Schmidt-Rhaesa, 2003). It was striking, for example, to discover that many of the genes critical for early brain development are homologous between insects and vertebrates (Sprecher and Reichert, 2003). Indeed, the invertebrate and vertebrate genes are sometimes functionally interchangeable (Halder et al., 1995; deRobertis and Sasai, 1996). Those discoveries supported Geoffroy’s view that all animals were built according to a common plan, which could now be understood to be a common genetic blueprint or ‘program’ (Gehring, 1996). Indeed, many biologists proceeded to search for molecular genetic homologies that could reveal previously unimagined morphological homologies (Janies and DeSalle, 1999). Geoffroy would have been thrilled. There are, however, problems with the view that animals are all alike.

The most serious problem, in my view, is that homologous genes may sometimes be involved in the development of adult structures that are clearly not homologous (Stiedrer and Northcutt, 1991). For example, insect wings and vertebrate nervous systems both depend on hedgehog function for normal development, but this does not make neural tubes and insect wings homologous (Baguña and Garcia-Fernandez, 2003). Instead, findings such as this suggest that evolution tends to work with highly conserved ‘master genes’ (Gehring, 1996) or, more accurately, tightly knit assemblies of crucial genes (Nilsson, 2004), which it occasionally reshuffles by altering their upstream regulatory elements and/or downstream targets. Evolution is a terrific tinkerer that manages to create novelty from conserved elements. This conclusion echoes Geoffroy’s arguments insofar as it acknowledges that “Nature works constantly with the same materials” (Geoffroy, 1807), but it does not mesh with the view that evolution built all animals according to a single plan. What we have, then, is at least a partial rapprochement of the positions held by Cuvier and Geoffroy: adult organisms do conform to several different body plans, but they are built by shuffling repeatedly a highly conserved set of genes (Raff, 1996). Therefore, a crucial question for research is how evolutionary changes in networks of developmentally important genes influence adult structure and function.

Implicit in the preceding discussion has been the idea that adult species differences arise because of evolutionary changes in development (Garstang, 1922). This idea is commonly accepted now, but, back in the nineteenth century, Haeckel (1889) used to promote its polar opposite, namely, the notion that phylogeny creates ontogeny (see Gould, 1977). Haeckel also promoted the idea that all vertebrates pass through a highly conserved phylotypic stage of embryonic development (Slack et al., 1993). Studies have, however, challenged the phylotypic stage idea by showing that the major groups of vertebrates can be distinguished at all stages of embryogenesis (Richardson et al., 1997). An intriguing aspect of that early embryonic variability is that it consists mainly of differences in the timing of developmental processes (Richardson, 1999). Little is known about the genes that generate those changes in developmental timing (also known as heterochrony), but some of them, at least, are likely to be fairly well conserved across species (Pasquinelli and Ruvkun, 2002). More importantly, the notion that adult diversity is based on evolution changing the temporal relationships of conserved processes represents another reconciliation of Cuvier’s insistence on adult diversity with Geoffroy’s belief in a common plan. Thus, the field of evolutionary developmental biology (evo-devo for short) has overcome the once so prominent dichotomy between conservation and diversity. Its major challenge now is to discover the mechanistic details of how conserved genes and processes are able to produce such diverse adult animals.

Evo-devo thinking has also invaded neuroscience, but evo-devo neurobiology still emphasizes conservation over diversity. For example, we now have extensive evidence that all vertebrate brains are amazingly similar at very early stages of development (Puelles et al., 2000; Puelles and Rubenstein, 2003). However, we still know very little about how and why brain development diverges in the various vertebrate groups after that early, highly conserved stage or period. Looking beyond vertebrates, we find that insect brain development involves at least some genes that are homologous to genes with similar functions in vertebrates (Sprecher and Reichert, 2003). This is
remarkable but does not prove that insects and vertebrates are built according to a common plan – if by that we mean that the various parts of adult insect brains all have vertebrate homologues. For example, the finding that several conserved genes, notably \textit{Pax6}, are critical to eye development in both invertebrates and vertebrates, does not indicate that all those eyes are built according to a common plan. The crucial question, which we are just beginning to explore, is how the conserved genes are tinkered with (reshuffled, co-opted, or redeployed) to produce very different adult eyes (Zuber et al., 2003; Nilsson, 2004). This, then, seems to be the future of evo-devo neurobiology: to discover how highly conserved developmental genes and processes are used to different ends in different species. As I have discussed, this research program has ancient roots, but it is just now becoming clear.

### 1.01.2 Scala Naturae versus Phylogenetic Bush

The idea of evolution proceeding along some kind of scale from simple to complex also has pre-evolutionary roots. Aristotle, for example, ordered animals according to the degree of perfection of their eggs (see Gould, 1977). Later religious thinkers then described an elaborate scale of nature, or \textit{scala naturae}, with inanimate materials on its bottom rung and archangels and God at the other extreme. The early evolutionists, such as Lamarck, transformed this static concept of a \textit{scala naturae} into a dynamic phylogenetic scale that organisms ascended as they evolved. Darwin himself had doubts about arranging species on a scale, but most of his followers had no such qualms (Bowler, 1988). Even today, the phylogenetic scale is taught in many schools and it persists in medicine and academia. For example, the National Institutes of Health’s (NIH) guide for institutional animal care and use still recommends that researchers, whenever possible, should work with “species lower on the phylogenetic scale” (Pitts, 2002, p. 97). On the other hand, most contemporary evolutionists have pronounced as dead both the \textit{scala naturae} and its postevolutionary cousin, the phylogenetic scale (Hodos and Campbell, 1969). What do those modern evolutionists cite as the scales’ cause of death?

One fatal flaw in the idea that species evolve along a single scale is that, as we now know, evolution made at least some species simpler than their ancestors. Salamanders, for example, are much simpler, especially in brain anatomy (Roth et al., 1993), than one would expect from their phylogenetic position. Even more dramatically, the simplest of all animals, the placozoans, are now thought to have evolved from far more complicated ancestors (Collins, 1998). As more and more molecular data are used to reconstruct phylogenies, it is becoming apparent that such secondary simplification of entire animals has occurred far more frequently than scientists had previously believed (Jenner, 2004) – perhaps because they were so enamored of the phylogenetic scale. A second major problem with \textit{scala naturae} thinking is that the order of species within the scale depends on which organismal features we consider. For example, many fishes would rank higher than mammals if we based our scale on skull complexity, which was reduced dramatically as early mammals evolved (Sidor, 2001). Similarly, dolphins rank high if we look only at brain size, but relatively low if we consider neocortical complexity, which was reduced as the toothed whales evolved (Morgane and Jacobs, 1972). Most people tacitly agree that ‘higher animals’ are warm-blooded, social, curious, and generally like us, but once we try to be more objective, the single ‘chain of being’ (Lovejoy, 1936) fractionates into a multitude of different chains, none of which has any special claim to being true.

This multiple-chains idea becomes self-evident once we have grasped that species phylogenies are just like human family trees; they are neither ladders, nor trees with just a single trunk, but bushes or tangleweds (Striedter, 2004) with branches growing in divergent directions. Within a given branch, or lineage, complexity may have increased at some points in time and decreased at others, but even if complexity increased more frequently than it decreased, the overall phylogeny would fail to yield a single scale, because complexity tends to increase divergently in different lineages. For example, bats, honeybees, and hummingbirds are all incredibly complex, compared to their last common ancestor, but they are each complex in different ways. Of course, we can pick one parameter and build a scale for that – we can, for instance, compare the ability of bats, honeybees, and hummingbirds to see ultraviolet (UV) radiation – but different parameters might well yield different scales. Simply put, changes that occurred divergently in different lineages will not, in general, produce a single overarching scale. This insight is old hat to evolutionary biologists, but news to many neuroscientists (Hodos and Campbell, 1969). In part, therefore, the persistence of \textit{scala naturae} thinking in the neurosciences reflects a lack of proper training in contemporary evolutionary theory. In addition, I suspect that human minds possess a natural tendency for ordering disparate items linearly. Such a bias would be useful in many contexts, but it would make it
difficult to comprehend (without training) the divergent nature of phylogeny.

Although *scala naturae* thinking persists in neuroscience generally, evolutionary neuroscientists have labored to expunge its ghost. For example, a consortium of 28 comparative neurobiologists revised the nomenclature of avian brains to replace the terms neostriatum, archistriatum, and paleostriatum – which suggested that brains evolved by the sequential addition of new brain regions – with terms devoid of *scala naturae* overtones (Reiner et al., 2004a, 2004b; Jarvis et al., 2005). Some of the replacement names are terms that were already used for brain regions in other vertebrates; they reflect our current understanding of homologies. However, some of the new terms – e.g., nidipallium and arcopallium – are novel and intended to apply exclusively to birds. These novel names were coined because bird brains, particularly bird forebrains, have diverged so much from those of other vertebrates (including reptiles) that strict one-to-one homologies are difficult, if not impossible, to draw for several regions (Striedter, 1998, 1999). Thus, the revised terminology reflects a new consensus view that avian brains did not evolve by the sequential addition of new brain areas, yet also reminds us that bird brains are full of features that evolved quite independently of those that feature in mammalian phylogeny. In other words, the new terminology avoids *scala naturae* overtones and, instead, combines the notion of a common plan with that of divergent complexity.

As comparative neurobiologists reject the notion of a *scala naturae*, they stand to lose a central part of their traditional justification for working on nonhuman brains. No longer can they argue that research on other brains must be useful because nonhuman brains are always simpler, and therefore easier to comprehend, than human brains. Instead, they must admit that some nonhuman brains are stunningly complex and, more importantly, that their phylogenetic paths toward complexity diverged from the primate trajectory. That is, complex bird, fish, or insect brains are not mere steps along the path to human brains, but the outcome of divergent phylogenies (see Evolution of the Nervous System in Fishes, Do Birds and Reptiles Possess Homologues of Mammalian Visual, Somatosensory, and Motor Cortices?, Evolution of Color Vision and Visual Pigments in Invertebrates). Does this suggest that research on nonhuman brains should cease to be funded? I do not think so, but the justification for working on nonhuman brains ought to be tweaked.

One obvious alternative justification is that all brains are likely to share some features, especially if they come from close relatives. Another good justification for research on nonhuman brains is that, compared to human brains, the former are much more amenable to physiological and anatomical research. This line of justification assumes that the model differs from the target system only in those respects that make the model easier to study, and not in the respects that are modeled – an assumption that sometimes fails. It now appears, for example, that the auditory system of owls, which was generally regarded as an ideal model for sound localization in vertebrates, exhibits some highly specialized features (McAlpine and Grothe, 2003). This finding, at first glance, suggests that research on bird brains is wasteful, but this is a simplistic view. Research on the owl’s auditory system has taught us much about how neurons compute behaviorally relevant information and it serves as an invaluable reference against which we can compare sound processing in other species, including humans. Furthermore, some differences between a model and its target can lead to surprising discoveries. Much might be gained, for example, from studying why some nonhuman brains are far more capable than primate brains of repairing themselves (Kirsch and Kirsch, 1964). Thus, model systems research can be useful even if the model is imprecise.

A third, less frequently discussed, justification for examining the brains of diverse species is that comparative research can bring to light convergent similarities, which in turn might reveal some principles of brain design. For example, the discovery that olfactory systems in both vertebrates and many different invertebrates exhibit distinctive glomeruli strongly suggests that those glomeruli are needed for some critical aspects of odorant detection and analysis (Strausfeld and Hildebrand, 1999).

Therefore, research on nonhuman brains need not be justified in terms of a presumed phylogenetic scale. Instead, comparative neurobiology is valuable because (1) all brains are likely to share some features, (2) nonhuman brains are more amenable to some types of research, and (3) the study of diverse nonhuman brains can lead to the discovery of design rules for brains. Historically, only the first of these alternatives has been widely discussed, but all are logically sound, and none depend on the existence of a *scala naturae*.

### 1.01.3 Relative Size versus Absolute Size

The most obvious difference between species is that they differ enormously in size. Because life began with tiny organisms, evolutionary increases in body size must have outnumbered or outpaced the decreases. This is true of organisms generally, but it
also holds for several individual lineages, including mammals and, within mammals, primates (Stanley, 1973; Alroy, 1998). The most fascinating aspect of those changes in body size is that they involved much more than the isometric scaling up or down of the ancestral condition; they involved allometric changes in the proportions of body parts and physiologic processes. For example, skeletal mass increases disproportionately with increasing body size, whereas heart rate decreases. Countless studies – on both vertebrates and invertebrates – have documented these allometries and explored their functional implications (Calder, 1984; Schmidt-Nielsen, 1984).

Much less is known about the causes of allometry. Studies on allometry in insects showed that some scaling relationships are readily modifiable by natural or artificial selection (see Emlen and Nijhout, 2000; Frankino et al., 2005). This finding suggests that even tight scaling laws are not immutable, which would explain why many traits scale differently (e.g., with different exponents) in different taxonomic groups (Pagel and Harvey, 1989). A very different, more theoretical line of research has shown that numerous allometries, specifically those with power law exponents that are multiples of 1/4, have evolved because the optimal means of delivering metabolic energy to cells is through an hierarchically branching, fractal network of vessels whose termini (e.g., capillaries) are body size-invariant (West et al., 1997; Savage et al., 2004; West and Brown, 2005). This theory is mathematically complex and still controversial (Kozlowski and Konarzewski, 2004; Brown et al., 2005; Hoppeler and Weibel, 2005), but it is elegant. Furthermore, because the theory of West et al. is based in part on the assumption that natural selection optimizes phenotypes, it is consistent with the aforementioned finding that allometries are modifiable by selection. However, West et al.’s (1997) theory cannot explain (or does not yet explain) why some organs, such as the brain, scale with exponents that are not multiples of 1/4. Nor can it easily explain taxonomic differences in scaling exponents. Thus, the causal – physiological and/or developmental – bases of allometry are coming into focus but remain, for now, mysterious.

Brain scaling, in particular, remains quite poorly understood (see Principles of Brain Scaling, Scaling the Brain and Its Connections, How to Build a Bigger Brain; Cellular Scaling Rules for Rodent Brains). The discovery that brains become proportionately smaller with increasing body size dates back to the late eighteenth century (Haller, 1762; Cuvier, 1805–1845). Since then, numerous studies have documented brain allometry in all the major groups of vertebrates (Deacon, 1990a; van Dongen, 1998) and even some invertebrates (Julian and Gronenberg, 2002; Mares et al., 2005). Generally speaking, those studies confirmed that in double logarithmic plots of brain size versus body size, the data points for different species within a given lineage tend to form a reasonably straight line, indicating the existence of a simple power law. The slope of those best-fit lines are almost always less than 1, which reflects the aforementioned fact that brains generally become proportionately smaller with increasing body size. The large body of work on brain–body scaling further revealed that data points for different taxonomic groups often form lines with similar slopes but different y intercepts. These differences in y intercepts are known as differences in relative brain size or encephalization. They seriously complicate efforts to draw a single allometric line for any large taxonomic group (Pagel and Harvey, 1989), but they allow us to identify evolutionary changes in relative brain size among some smaller taxonomic groups. For example, they allow us to determine that relative brain size increased with the origin of mammals, with the origin of primates, several times within primates, with the origin of the genus Homo, and, last but not least, with the emergence of Homo sapiens (see Primate Brain Evolution in Phylogenetic Context, The Hominin Fossil Record and the Emergence of the Modern Human Central Nervous System, The Evolution of Human Brain and Body Growth Patterns). Overall, such phylogenetic analyses suggest that, among vertebrates, relative brain size increased more frequently than it decreased (Striedter, 2005).

Enormous effort has gone into determining the functional significance of evolutionary changes in brain–body scaling. Darwin, for example, had argued that relative brain size is related to “higher cognitive powers” (Darwin, 1871), but defining those powers and comparing them across species has proven difficult (Macphail, 1982). Consequently, most subsequent investigators shied away from the notion of general intelligence, or ‘biological intelligence’ (Jerison, 1973), and focused instead on more specific forms of higher cognition. Parker and Gibson (1977), for example, proposed that a species’ degree of encephalization is related to its capacity for extracting nutritious fruits and nuts from their protective shells. Several authors have stressed correlations between brain size and ‘social intelligence’ (Byrne and Whiten, 1988; Dunbar, 1998; Reader and Laland, 2002). Collectively, these studies reinforced the sense that relative brain size is, somehow, related to some forms of intelligence. However, relative brain size also correlates with several other attributes, such as longevity, home-range size, diet, and metabolic rate (for a review, see van Dongen, 1998). The latter correlations, with diet and metabolism, have received...
particularly lavish attention (Martin, 1981; McNab, 1989; Aiello and Wheeler, 1995). Paradoxically, the discovery of so many correlations has led some evolutionary neuroscientists to despair: there are too many correlates of relative brain size, and many of them come and go, depending on which taxonomic group is being examined and which statistical methods are used for the analyses (e.g., Bennet and Harvey, 1985; Iwaniuk et al., 1999; Deaner et al., 2000; Beauchamp and Fernández-Juricic, 2004; Jones and MacLarnon, 2004; Martin et al., 2005). Too many contested hypotheses, too little certitude.

There is not much clarity on why brains scale so predictably with body size. Early workers argued that brains generally scale against body size with a power law exponent close to 2/3 because the brain’s sensory and motor functions were related to the body’s surface area, which presumably scales with that same exponent (Snell, 1891; Jerison, 1973). According to this view, brain sizes in excess of that predicted by the 2/3 power law are due to increases in the brain’s nonsomatic, cognitive regions. This would explain the correlations between relative brain size and some forms of intelligence. Unfortunately, there are two major problems with this view. First, brain–body scaling exponents often differ substantially from 2/3 (van Dongen, 1998; Nealen and Ricklefs, 2001). The second problem is that the brain’s more cognitive regions also scale predictably with body size (Fox and Wilczynski, 1986), undermining the assumption that brains are divisible into regions that scale with body size and regions that do not. Therefore, the excess neuron hypothesis (Striedter, 2005) is dead.

In searching for an alternative, some have suggested that brain–body allometry is linked to the scaling of metabolic rates. This hypothesis is based on the observation that, in at least some taxonomic groups, brain size and basal metabolic rate scale against body size with similar exponents (Martin, 1981; Mink et al., 1981). However, other studies have shown that the correlation between brain size and metabolism is not tight, once the mutual correlation with body size is factored out (McNab, 1989). This correlational slack presumably arises because species differ in how much of the body’s total energy supply they deliver to the brain (Aiello and Wheeler, 1995; Kaufman, 2003), but this just underscores that relative brain size is not so tightly linked to metabolic rate.

Overall, the lack of clarity on what causes brains to scale predictably with body size, and how to interpret deviations from the scaling trends, has caused interest in relative brain size to fade. Increasingly, evolutionary neuroscientists have turned away from relative brain size and asked, instead, how the size of individual brain regions correlates with various behavioral parameters (Harvey and Krebs, 1990; see Brain Size in Primates as a Function of Behavioral Innovation, Mosaic Evolution of Brain Structure in Mammals). This shift in research strategy makes sense, because, after all, the brain is functionally heterogeneous. However, even studies that focus on correlations between single brain areas and specific behaviors – some refer to them as neuroecological studies – are controversial because: (1) the behavioral parameters are difficult to quantify and/or define (Bolhuis and Macphail, 2001), (2) neuronal structure–function relationships are complex and often poorly understood, (3) it is difficult to decide a priori whether one should correlate behavioral parameters against a region’s absolute size, its proportional size, or its size relative to expectations (Striedter, 2005), and (4) the methods for establishing statistically significant correlations in phylogenetic data remain debatable (Felsenstein, 1985; Garland et al., 1992; Smith, 1994; Martin et al., 2005). Brave neuroscientists are continuing to tackle those problems, but the larger problem of how to deal with relative brain size – how to find its causes and its functional significance – is fading from view.

Perhaps we need a new approach to understanding relative brain size – perhaps one that is linked more directly to the physiological and geometric properties of brains (West and Brown, 2005) – but this novel direction is not yet apparent.

As interest in relative brain size waned, interest in absolute brain size waxed, mainly because many of the brain’s internal structural and functional features turn out to scale predictably with absolute brain size. Best studied is the phenomenon of size-related shifts in brain region proportions (Sacher, 1970; Finlay and Darlington, 1995). In mammals, for example, the neocortex becomes disproportionately large as absolute brain size increases, whereas most other regions become disproportionately small. A second interesting scaling law is that a brain’s degree of structural complexity tends to increase with absolute brain size. Within the neocortex, for example, the number of distinct areas increases predictably with neocortex size (Changizi and Shimojo, 2005). A third fascinating aspect of brain scaling is that the amount of white matter within mammalian brains scales allometrically with absolute brain size (Ringo, 1991; Zhang and Sejnowski, 2000). This connectional allometry, taken together with the fact that synapse size and density are relatively size-invariant, indicates that brains become less densely interconnected, on average, as they increase in size (Stevens, 1989; Deacon, 1990a, 1990b; Striedter, 2005; see Scaling the Brain and Its Connections). All of this signifies that brains change structurally in many ways as they vary in absolute size. Many of those changes have clear functional
implications. For example, it has been suggested that, as hominid brains increased in size, the axons interconnecting the two cerebral hemispheres became so sparse and long that the hemispheres became less capable of interacting functionally, which led to an increase in functional asymmetry (Ringo et al., 1994; see Cortical Comissural Connections in Primates, The Evolution of Hemispheric Specializations of the Human Brain). Considerations such as these suggest that absolute brain size is a much better predictor of brain function than relative brain size, at least among close relatives (Striedter, 2005).

In retrospect, we can say that evolutionary neuroscientists historically have overemphasized relative brain size. As Dunbar (2006) put it, comparative neurobiologists have too long been “dragooned into worrying about relativizing brain size by a very peculiar view that body size must be the default determinant of brain volume.” Can we explain this undue emphasis? Partly, evolutionary neuroscientists may have worried that focusing on absolute brain size and linking it to higher cognitive powers would force us to conclude that whales and elephants, with their enormous brains, are smarter than humans (see Cetacean Brain Evolution, Evolution of the Elephant Brain: A Paradox between Brain Size and Cognitive Behavior). This is a valid concern, for few would doubt that humans are – or at least can be – the most intelligent creatures on earth. However, whales and elephants are behaviorally complex, and humans may well be special because they are unique in possessing symbolic language (Macphail, 1982). Furthermore, it seems to me that large whales, with large brains, are more intelligent (both socially and in their hunting strategies) than dolphins or small whales. This hypothesis remains to be tested, but it points to a strategy for reconciling absolute and relative brain size: among close relatives, comparisons of absolute brain size are most informative, but in comparisons of distant relatives (e.g., whales and humans), relative brain size is a more potent variable (Striedter, 2005). This view is consistent with the finding that, among primates, social group size correlates more strongly with absolute brain size than with relative brain size (Kudo and Dunbar, 2001; Striedter, 2005). It also serves as a productive counterweight to the field’s traditional, almost exclusive emphasis on relative brain size.

1.01.4 Natural Selection versus Developmental Constraints

Darwin’s theory of natural selection entails two main components, namely, that (1) organisms produce offspring with at least some heritable variation and (2) that organisms generally produce more offspring than their environment is able to sustain. Given those two components, some variants are bound to be fitter than others in the sense that their offspring are more likely to survive and produce offspring. This difference, in turn, will cause the heritable traits of the fitter variants to spread in the population. Given this, Darwin’s most “dangerous idea” (Dennett, 1995), one can explain an organism’s attributes in terms of the selective pressures that promoted their spread and, hence, their current existence. An enormous number of such adaptational explanations have been proposed. Many stress that natural selection optimized features for specific functions; others emphasize that natural selection tends to produce optimal compromises between competing functions and/or costs (Maynard Smith, 1982). Generally speaking, the explanatory power of these adaptational explanations derives solely from natural selection’s second step, the sorting of offspring. Generation of the variants that are sorted is usually assumed to be random and, hence, irrelevant to explanations of the phenotype. This ‘adaptationist paradigm’ (Gould and Lewontin, 1979) has dominated evolutionary theory for most of its history.

In the 1970s and 1980s, however, the adaptationist paradigm was challenged by authors who stressed that the variants available to natural selection may not really be random (Gould and Lewontin, 1979; Alberch, 1982; Maynard Smith et al., 1985). Central to those challenges was the idea that, even if mutations are random at the genetic level, those random genetic mutations are channeled, or filtered, through mechanisms of development that favor the emergence of some phenotypes. Some structures may be impossible for embryos to develop; others are likely to emerge (Alberch, 1982). If this is true, then natural selection chooses not among a random selection of phenotypes but from a structured set that is determined, or at least biased, by the mechanisms of development. This idea is important, because it suggests that development constrains the power of natural selection to set the course of evolutionary change. It threatens natural selection’s widely assumed omnipotence. Some authors carried this threat so far as to exhort biologists to halt their search for adaptive scenarios and to research, instead, the ‘generative’ mechanisms of development (Goodwin, 1984). Fortunately, most evolutionary biologists today seek a more balanced rapprochement of embryology and evolutionary biology (Gilbert et al., 1996; Wagner and Laubichler, 2004).

Specifically, evo-devo biologists today tend to accept the concept that natural selection is the most prominent determinant of who thrives and
who dies, no matter how constrained development might be. They also tend to stress that development itself is subject to descent with modification – i.e., evolution – which means that even fairly tight constraints can change. Therefore, explanations couched in terms of natural selection are not antithetical to those involving developmental constraints, but complementary (Striedter, 2005). Still, the synthesis of natural selection and developmental constraints remains uncertain in one key respect: what if the mechanisms of development were shaped by natural selection to produce variants that are much fitter than one would expect by chance? Then the distinction between the generative and selective components of natural selection (see above) would blur. The developmental production of variants would no longer be random with respect to a species’ ecology. This hypothesis, which was pushed furthest by Riedl (1977), is interesting and potentially profound, but not yet supported by much evidence.

Brains were historically considered to be shaped by natural selection, unencumbered by developmental constraints. In general, the size and structure of both entire brains and individual brain regions were thought to be optimized. Jerison (1973, p. 8), made this idea explicit when he wrote that “the importance of a function in the life of each species will be reflected by the absolute amount of neural tissue of that function in each species.” How development produced that fine-tuning was never specified. Presumably, the idea was that genetic mutations could vary the size and structure of individual brain regions freely, leading to steady improvements in fitness until an optimum was reached. Little thought was given to the possibility that brains might be constrained in how they could evolve. However, a few authors proposed that trophic dependencies between interconnected brain regions might cause entire circuits or systems to change size in unison rather than piecemeal (Katz and Lasek, 1978). Such ‘epigenetic cascades’ (Wilczynski, 1984) might channel evolution (Katz et al., 1981), but they would not constrain natural selection, because the cascades help to optimize functional brain systems by matching the size of interconnected neuronal populations. That is, epigenetic cascades act not against, but in conjunction with, the optimizing power of natural selection; they are not classical constraints, which may explain why they have rarely been discussed (Finlay et al., 1987).

The idea of brains evolving under a restrictive developmental rule was proclaimed forcefully by Finlay and Darlington (1995). Their argument was founded on the observation that the various major brain regions in mammals scale against absolute brain size with different allometric slopes (Sacher, 1970; Gould, 1975; Jerison, 1989). Although this finding was well established at the time, it had not been explained; it was a scaling rule without a cause. Finlay and Darlington’s major contribution was to propose that the height of a region’s allometric slope was related to the region’s date of birth (i.e., the time at which the region’s precursor cells cease to divide), with late-born regions tending to become disproportionately large with increasing brain size. Why does this relationship exist? Finlay and Darlington (1995) showed that their late-equals-large rule emerges naturally if neurogenetic schedules and cannot, in general, delay or advance the birth of individual regions. In other words, even if evolution ‘wanted’ to increase the size of only one brain region, it would be ‘forced’ to change also the size of many other brain regions. Thus, Finlay and Darlington argued that development constrains brains to evolve concerted, rather than mosaically.

Finlay and Darlington’s developmental constraint hypothesis has been challenged by various authors, who all pointed out that brains do sometimes evolve mosaically (Barton and Harvey, 2000; Clark et al., 2001; de Winter and Oxnard, 2001; Iwaniuk et al., 2004; Safi and Dechmann, 2005). In addition, Barton (2001) has argued that correlations between region size and absolute brain size are due to functional requirements, rather than developmental constraints. Specifically, Barton (2001, p. 281) reported that the sizes of interconnected brain regions in what he called a functional system exhibited “significantly correlated evolution after taking variation in a range of other structures and overall brain size into account.” Finlay et al. (2001) countered that such system-specific evolution may indeed occur, particularly for the so-called limbic system (see also Barton et al., 2003), but that this does not negate the existence of developmental constraints. In a review of this debate, I concluded that most of it may be resolved by arguing that instances of mosaic (and/or system-specific) evolution occur against a background of concerted, developmentally constrained evolution (Striedter, 2005; see Mosaic Evolution of Brain Structure in Mammals). Both Finlay and Barton seem open to this kind of rapprochement (Finlay et al., 2001; Barton, 2006).

The debate on mosaic versus concerted evolution highlights how little we know about the evolution of
neural development or, for that matter, about the role that natural selection played in shaping brains. The developmental data used to support Finlay et al.’s (2001) hypothesis came from just 15 species and were collected by several different laboratories, using diverse methodologies. Moreover, the data are limited to dates of neurogenesis. We know virtually nothing about species differences (or similarities) in how large brain regions are prior to neurogenesis, how quickly the regions grow, or how much cell death they endure. Data on these other, relatively neglected aspects of brain development might reveal additional constraints, and they might clarify how regions can evolve mosaically even if neurogenic schedules are conserved.

Similarly lacking are data on natural selection and the brain. Although several analyses have shown that the size of some brain regions (relative to absolute brain size) correlates with aspects of a species’ behavior or ecology (e.g., Clark et al., 2001; de Winter and Oxnard, 2001; Iwaniuk et al., 2004), such correlations are only indirect evidence for natural selection. More direct data are difficult to gather, because direct demonstrations of natural selection at work require measurements of heritability and fitness functions. As it is, we know so little about how selection acts on brains that debates on its potency are bound to waxes and wanes in popularity (Kincaid, 1996; McIntyre, 1996), but it seems logical in principle. Naturally, one may debate whether human behavior is predictable enough to yield the kind of laws that are needed for nomological–deductive explanations (Beed and Beed, 2000).

Evolutionary biologists have likewise debated the role of general laws in explaining the past, which in their realm is phylogeny. Some have argued that natural selection is a universal law that can be used to explain the emergence of many, if not most, biological features. Others have countered that natural selection is a mathematical truth, rather than an empirically determined law (Sober, 2000). More importantly, many biologists have pointed out that the results of natural selection are not highly predictable. Gould (1989) made this argument when he declared that rewinding the tape of life on earth and playing it again would not lead to a repeat performance. Biological history is full of accidents, of happenstance. Therefore, Gould argued, evolutionary explanations must be crafted one event at a time, without recourse to general laws. On the other hand, Gould did grant that evolution is constrained by diverse physical principles, by rules of construction and good design, and by some scaling rules (Gould, 1986, 1989). In his view, “the question of questions boils down to the placement of the boundary between predictability under invariant law and the multifarious possibilities of historical contingency” (Gould, 1989, p. 290). Gould placed this boundary “so high that almost every interesting event of life’s history falls into the realm of contingency” (Gould, 1989, p. 290). This appears to be an extreme position, for many other evolutionary biologists place that same boundary lower. They tend to be far more impressed than Gould by the degree of convergent evolution in the history of life (Carroll, 2001; Willmer, 2003). They look, for example, at the convergent similarities of eyes in vertebrates and octopi and conclude that some design rules for eyes exist. In sum, disagreements persist about the importance of neural development or, for that matter, about the role that natural selection played in shaping brains. The developmental data used to support Finlay et al.’s (2001) hypothesis came from just 15 species and were collected by several different laboratories, using diverse methodologies. Moreover, the data are limited to dates of neurogenesis. We know virtually nothing about species differences (or similarities) in how large brain regions are prior to neurogenesis, how quickly the regions grow, or how much cell death they endure. Data on these other, relatively neglected aspects of brain development might reveal additional constraints, and they might clarify how regions can evolve mosaically even if neurogenic schedules are conserved.

Similarly lacking are data on natural selection and the brain. Although several analyses have shown that the size of some brain regions (relative to absolute brain size) correlates with aspects of a species’ behavior or ecology (e.g., Clark et al., 2001; de Winter and Oxnard, 2001; Iwaniuk et al., 2004), such correlations are only indirect evidence for natural selection. More direct data are difficult to gather, because direct demonstrations of natural selection at work require measurements of heritability and fitness functions. As it is, we know so little about how selection acts on brains that debates on its potency are bound to waxes and wanes in popularity (Kincaid, 1996; McIntyre, 1996), but it seems logical in principle. Naturally, one may debate whether human behavior is predictable enough to yield the kind of laws that are needed for nomological–deductive explanations (Beed and Beed, 2000).

Evolutionary biologists have likewise debated the role of general laws in explaining the past, which in their realm is phylogeny. Some have argued that natural selection is a universal law that can be used to explain the emergence of many, if not most, biological features. Others have countered that natural selection is a mathematical truth, rather than an empirically determined law (Sober, 2000). More importantly, many biologists have pointed out that the results of natural selection are not highly predictable. Gould (1989) made this argument when he declared that rewinding the tape of life on earth and playing it again would not lead to a repeat performance. Biological history is full of accidents, of happenstance. Therefore, Gould argued, evolutionary explanations must be crafted one event at a time, without recourse to general laws. On the other hand, Gould did grant that evolution is constrained by diverse physical principles, by rules of construction and good design, and by some scaling rules (Gould, 1986, 1989). In his view, “the question of questions boils down to the placement of the boundary between predictability under invariant law and the multifarious possibilities of historical contingency” (Gould, 1989, p. 290). Gould placed this boundary “so high that almost every interesting event of life’s history falls into the realm of contingency” (Gould, 1989, p. 290). This appears to be an extreme position, for many other evolutionary biologists place that same boundary lower. They tend to be far more impressed than Gould by the degree of convergent evolution in the history of life (Carroll, 2001; Willmer, 2003). They look, for example, at the convergent similarities of eyes in vertebrates and octopi and conclude that some design rules for eyes exist. In sum, disagreements persist about the importance of universal laws. This nomological–deductive methodology waxed and waned in popularity (Kincaid, 1996; McIntyre, 1996), but it seems logical in principle. Naturally, one may debate whether human behavior is predictable enough to yield the kind of laws that are needed for nomological–deductive explanations (Beed and Beed, 2000).

Evolutionary biologists have likewise debated the role of general laws in explaining the past, which in their realm is phylogeny. Some have argued that natural selection is a universal law that can be used to explain the emergence of many, if not most, biological features. Others have countered that natural selection is a mathematical truth, rather than an empirically determined law (Sober, 2000). More importantly, many biologists have pointed out that the results of natural selection are not highly predictable. Gould (1989) made this argument when he declared that rewinding the tape of life on earth and playing it again would not lead to a repeat performance. Biological history is full of accidents, of happenstance. Therefore, Gould argued, evolutionary explanations must be crafted one event at a time, without recourse to general laws. On the other hand, Gould did grant that evolution is constrained by diverse physical principles, by rules of construction and good design, and by some scaling rules (Gould, 1986, 1989). In his view, “the question of questions boils down to the placement of the boundary between predictability under invariant law and the multifarious possibilities of historical contingency” (Gould, 1989, p. 290). Gould placed this boundary “so high that almost every interesting event of life’s history falls into the realm of contingency” (Gould, 1989, p. 290). This appears to be an extreme position, for many other evolutionary biologists place that same boundary lower. They tend to be far more impressed than Gould by the degree of convergent evolution in the history of life (Carroll, 2001; Willmer, 2003). They look, for example, at the convergent similarities of eyes in vertebrates and octopi and conclude that some design rules for eyes exist. In sum, disagreements persist about the importance of general laws. This nomological–deductive methodology waxed and wanes in popularity (Kincaid, 1996; McIntyre, 1996), but it seems logical in principle. Naturally, one may debate whether human behavior is predictable enough to yield the kind of laws that are needed for nomological–deductive explanations (Beed and Beed, 2000).

Evolutionary biologists have likewise debated the role of general laws in explaining the past, which in their realm is phylogeny. Some have argued that natural selection is a universal law that can be used to explain the emergence of many, if not most, biological features. Others have countered that natural selection is a mathematical truth, rather than an empirically determined law (Sober, 2000). More importantly, many biologists have pointed out that the results of natural selection are not highly predictable. Gould (1989) made this argument when he declared that rewinding the tape of life on earth and playing it again would not lead to a repeat performance. Biological history is full of accidents, of happenstance. Therefore, Gould argued, evolutionary explanations must be crafted one event at a time, without recourse to general laws. On the other hand, Gould did grant that evolution is constrained by diverse physical principles, by rules of construction and good design, and by some scaling rules (Gould, 1986, 1989). In his view, “the question of questions boils down to the placement of the boundary between predictability under invariant law and the multifarious possibilities of historical contingency” (Gould, 1989, p. 290). Gould placed this boundary “so high that almost every interesting event of life’s history falls into the realm of contingency” (Gould, 1989, p. 290). This appears to be an extreme position, for many other evolutionary biologists place that same boundary lower. They tend to be far more impressed than Gould by the degree of convergent evolution in the history of life (Carroll, 2001; Willmer, 2003). They look, for example, at the convergent similarities of eyes in vertebrates and octopi and conclude that some design rules for eyes exist. In sum, disagreements persist about the importance of
general laws for explaining the evolutionary history of brains. Marsh (1886) had proposed that brains consistently increase in size over evolutionary time, but later authors vehemently disagreed (see Jerison, 1973; Buchholtz and Seyfarth, 1999). Personally, I think that Marsh did have a point, for brain and body size have both increased, at least on average, in several vertebrate lineages (see Striedter, 2005). Still, Marsh’s laws were merely descriptions of phylogenetic trends, not causal laws. The first explicitly causal law of brain evolution was Arie¨ns Kappers’ (1921) law of neurobiotaxis, which states that cell groups in evolution tend to move toward their principal inputs. Unfortunately for Arie¨ns Kappers, later studies showed that cell groups do not move quite so predictably and called into question some of the mechanisms that supposedly produced neurobiotaxis. The next major putative law of brain evolution was Ebbesson’s (1980) parcellation principle, which states that brains become more complex by the division of ancestrally uniform cell groups into daughter aggregates that selectively lose some of their ancestral connections. This principle was strenuously criticized by most comparative neuroanatomists, mainly because its empirical foundation was shaky (see Ebbesson, 1984). Although a weak version of Ebbesson’s theory, stating merely that brains become less densely connected as they increase in size, is probably defensible (Deacon, 1990a; Striedter, 2005), the strong version of Ebbesson’s original idea has failed the test of time: plenty of data now show that brains evolve not only by the loss of connections, but also by creating novel projections.

Confronted with this abundance of failed brain evolution laws, most evolutionary neuroscientists have emphasized only a single, undisputed regularity of brain evolution, namely, that numerous aspects of brain structure and function are highly conserved across species. Specifically, they focused, à la Geoffroy St. Hilaire, on the existence of common plans of construction and highlighted molecular homologies between invertebrates and vertebrates (see above). This has been productive. It is important to note, however, that the principle of phylogenetic conservation predicts stability and does not deal explicitly with change. Is brain phylogeny subject to just a single law, which states that brains change little over time? Or are there also laws of evolutionary change in brains? I affirmed the second possibility (Striedter, 2005), but laws of evolutionary change in brains are no doubt difficult to find. C. J. Herrick, a founding father of evolutionary neuroscience, put it well:

Most scientific research has been directed to the discovery of the uniformities of nature and the codification of these in a system of generalizations. This must be done before the changes can be interpreted. The time has come to devote more attention to the processes and mechanisms of these changes... but it is much more difficult to find and describe the mechanisms of... [the] apparently miraculous production of novelties than it is to discover the mechanical principles of those repetitive processes that yield uniform products (Herrick, 1956, p. 43).

The last few years have seen an uptick in the number of studies that address evolutionary change and novelty in brains (Aboitiz, 1995; Catania et al., 1999; Rosa and Tweedale, 2005), and modern research on brain scaling and developmental constraints (see above) has advanced our understanding of the regularities that lurk within brain variability. In addition, a rapidly increasing number of studies is beginning to reveal genomic changes that are probably linked to changes in brain size and/or structure (e.g., Dorus et al., 2004; Mekel-Bobrov et al., 2005). Therefore, the time Herrick discussed, when evolutionary change becomes a focus of analysis (see also Gans, 1969), is probably at hand.

Thus, I envision a future in which most evolutionary neuroscientists will embrace many different laws, some dealing with constancy and some with change. A few philosophers of science (e.g., Beatty, 1995) might decry such a vision, because they think that any natural law deserving of its name must apply universally, in all contexts and without room for other, countervailing laws. I have no training in philosophy, but think that all scientific laws apply only in specified domains and given assumptions (Striedter, 2005). In the real world, particularly in the complex world of biological systems, most laws or principles are sometimes excepted. This does not make them useless but, instead, prompts us to ask what causes the observed exceptional cases (West and Brown, 2005). If we understand the causal basis of our laws, then the exceptions should, with further work, become explicable. In other words, I think that evolutionary neuroscientists can fruitfully avail themselves of Hempel’s nomological–deductive approach to history. To some extent, they always have.

1.01.6 Conclusions and Prospects

In summary, the history of evolutionary neuroscience features some serious missteps, such as the idea that brains evolved in a phylogenetic series and Arie¨ns Kappers’ law of neurobiotaxis, but it also reveals considerable progress. The scala naturae has ceased to guide the research of evolutionary neuroscientists...
and the idea of neurobiotaxis has quietly disappeared. The once stagnant field of brain allometry is showing signs of revival, largely because of new statistical techniques and a new emphasis on absolute brain size. The debate about concerted versus mosaic evolution persists, but directions for rapprochement are emerging. In general, the field has flirted with a broad variety of theoretical ideas and found some of them wanting and others promising. In terms of theory, the field is still quite young, but it is poised to mature now.

Predicting directions of growth for any science is problematic, but I believe that most future developments in evolutionary neuroscience will parallel developments in other, non-neural domains of evolutionary biology. After all, the history of evolutionary neuroscience is full of ideas that originated in non-neural areas of biology. For example, the methodology of phylogenetic reconstruction or cladistics (which I did not discuss in this article but have treated elsewhere; see Striedter, 2005) was originally developed by an entomologist (Hennig, 1950; see also Northcutt, 2001). Similarly, evolutionary developmental biology was burgeoning before it turned to brains (Hall, 1999). Therefore, I think it likely that the future of evolutionary neuroscience has already begun in some non-neural field. Maybe molecular genetics, with its new emphasis on evolutionary change (Dorus et al., 2004), will soon take center stage. Maybe the excitement about linking physiological allometries to metabolic parameters (West and Brown, 2005) will infect some mathematically inclined evolutionary neuroscientists. Or perhaps the next big thing in evolutionary neuroscience will be microevolutionary studies that integrate across the behavioral, physiological, and molecular levels (Lim et al., 2004). Maybe the future lies with computational studies that model in silico how changes in neuronal circuitry impact behavior (e.g., Treves, 2003). It is hoped that all of these new directions – and more – will bloom. If so, the field is headed for exciting times.

On the other hand, evolutionary neuroscientists are still struggling to make their findings relevant to other neuroscientists, other biologists, and other taxpayers (see Relevance of Understanding Brain Evolution). It may be interesting to contemplate the evolution of our brains, or even the brains of other animals, but can that knowledge be applied? Does understanding how or why a brain evolved help to decipher how that same brain works or, if it does not work, how it can be repaired? Are advances in evolutionary neuroscience likely to advance some general aspects of evolutionary theory? All of these questions remain underexplored (see Bullock, 1990).

Near the end of the nineteenth century, Jackson (1958) attempted to apply evolutionary ideas to clinical neurology, but his efforts failed. It has been pointed out that some species are far more capable than others at regenerating damaged brain regions (e.g., Kirsch and Kirsch, 1964) and that nonhuman apes tend not to suffer from neurodegenerative diseases such as Alzheimer’s (Erwin, 2001). Such species differences in brain vulnerability and healing capacity might well help us elucidate some disease etiologies or lead to novel therapies. Unfortunately, this research strategy has not yet succeeded. Thus far, evolutionary neuroscience’s most important contribution has been the discovery that human brains differ substantially from other brains, particularly nonprimate brains, which means that cross-species extrapolations must be conducted cautiously (Preuss, 1995). This is an important message, but it can be construed as negative in tone. Hopefully, the future holds more positive discoveries.

Work on justifying evolutionary science is especially important in the United States, where anti-evolutionary sentiment is on the rise. Many conservative Christians believe that evolution is a dangerous, insidious idea because it makes life meaningless (Dennett, 1995). Add to this fear the notion that our thoughts and feelings are mere products of our brains (e.g., Dennett, 1991) and evolutionary neuroscience seems like a serious threat to God’s supremacy. Although this line of argument is well entrenched, Darwin and most of his immediate followers were hardly atheists (Young, 1985). Instead, they either distinguished clearly between God’s words and God’s works, as Francis Bacon put it, or argued that God’s creative act was limited to setting up the laws that control history. Either way, God was seen as quite compatible with evolutionary theory. Moreover, Darwin’s view of life need not produce a meaningless void. Instead, it helps to clarify our relationships with other humans, other species, and our environment. Those relationships, in turn, give meaning to our lives, just as linguistic relationships give meaning to our words. Thus, Darwin knew – and we would do well to recall – that evolutionary biology can be useful even if it yields no direct medical or technological applications. Even Huxley (1863), who was a very pragmatic Darwinian and coined the word ‘agnostic’, knew that the uniquely human quest to comprehend our place in nature is not driven by mere curiosity or technological imperatives, but by a profound need to understand ourselves, our purpose, our existence. Within that larger and enduring enterprise, evolutionary neuroscience will continue to play a crucial role.
References


**Further Reading**


