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Introduction

Organisms are faced during their lives with an immense variety of problems, ranging from purely physical ones, such as changes in climate or geomorphic disturbances, to organism-specific problems related to food supply, predation, homeostasis, and reproduction. In order to enhance their chances of survival, organisms have to find adequate solutions for the problems with which they are confronted, for any of them could easily be fatal. Problem solving, in other words, is an essential dynamic survival mechanism, evolved to cope with disturbances in the ecological equilibrium. It can therefore be looked upon as an adaptive capacity enabling organisms to adjust themselves to one another and to their physical environment (see, e.g., Hodos and Campbell 1990; Macphail and Bolhuis 2001; Roth and Wullimann 2001; Reader et al. 2011; Shettleworth 2012a). The organism's adaptability, however, is but one aspect of fitness. Free-moving organisms, for example, can actively explore their environment

and thus generate new selection forces that can modify the structures involved. Mayr (1982, p. 612) even argues that “many if not most acquisitions of new structures in the course of evolution can be ascribed to selection forces by newly acquired behaviors.”

This suggests that in highly complex organisms, such as primates, behavior rather than environmental change may be the major driving force for evolution at the organismal level. However, this does not detract from the fact that all organisms, whether they are simple reflex automata or active and complex explorers, are above all concerned with keeping track of their local spatiotemporal environment, as part of their struggle for existence. Since sensory information processing and the ability to model reality (or certain parts of it) are essential components in this process, our idea of problem solving seems to correspond reasonably well to the notion of biological intelligence (Hofman 2003). In fact, with the evolution of sensory systems as adaptations to specialized environments, the capacity to process large amounts of sensory information increased and, with that, the power to create more complex physical realities.

In this chapter, some of the organizational principles and operational modes will be explored that underlie the information-processing capacity of the human brain, and it will be argued that the complexity of the cortical network circuitry is a measure of intelligence.

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Evolution of the Cerebral Cortex

If we assume that biological intelligence in higher organisms is the product of processes of complex sensory information processing and mental faculties, responsible for the planning, execution, and evaluation of intelligent behavior, variations among species in intelligence must in principle be observable in the neural substrate. In higher organisms, especially in primates, the complexity of the neural circuitry of the cerebral cortex is considered to be the neural correlate of the brain's coherence and predictive power and, thus, a measure of intelligence.

The evolutionary expansion of the cerebral cortex, indeed, is among the most distinctive morphological features of mammalian brains. Particularly in species with large brains, and most notably in great apes and marine mammals, the brain becomes disproportionately composed of this cortical structure (Welker 1990; Nieuwenhuys 1994a, b; Northcutt and Kaas 1995; Striedter 2004; Hofman and Falk 2012; Fig. 5.1). The volume of cortical gray matter, for example, expressed as a percentage of total brain volume increases from about 25 % for insectivores to 50 % for humans (Frahm et al. 1982; Hofman 1988), whereas the relative size of the entire cerebral cortex (including white matter) goes from 40 % in mice to about 80 % in humans (Hofman 1988, 2012; Azevedo et al. 2009; Herculano-Houzel 2009, 2012).

On the other hand, the relative size of the cerebellum remains constant across phylogenetic groups, occupying about 10–15 % of the total brain mass in different orders (Hofman 1988). Comparative studies among four mammalian orders, including primates, have recently revealed that the absolute neuronal composition in the cortex covaries significantly with that of the cerebellum (Herculano-Houzel et al. 2008; Lent et al. 2012), showing that these two brain structures display coordinated growth during phylogenesis in mammals (for reviews, see Herculano-Houzel 2012; Lent et al. 2012).

Such a coordinated evolution of the cerebral cortex and cerebellum fits well with the recent

clinical and experimental evidence suggesting an important role of the cerebellum in cognitive and affective functions, in close connection with cortical associative areas (reviewed by Schmahmann 2010). Although the cerebral cortex is not the only brain structure which was selected for in evolution for greater growth, as a result of growing environmental pressure for more sophisticated cognitive abilities, it has played a key role in the evolution of intelligence.

Scaling of the Primate Cerebral Cortex

During the past decades, considerable progress has been made in explaining the evolution of the cerebral cortex in terms of physical and adaptive principles (see, e.g., Macphail and Bolhuis 2001; Hofman 2003; Lefebvre et al. 2004; Lefebvre 2012; Roth and Dicke 2005, 2012). In addition, a quantitative approach to the comparative morphology of the brain has made it possible to identify and formalize empirical regularities in the diversity of brain design, especially in the geometry of the cortex (e.g., Hofman 1989, 2012; Changizi 2001, 2007; Clark et al. 2001).

Analysis of the cerebral cortex in anthropoid primates, for example, revealed that the volume of the neocortex is highly predictable from absolute brain size (Hofman 1989, 2007; Finlay and Darlington 1995; Zhang and Sejnowski 2000; Finlay et al. 2001; for recent reviews see Hofman and Falk 2012). The volume of the cortical gray matter, containing local networks of neurons that are wired by dendrites and mostly unmyelinated axons, is basically a linear function of brain volume, whereas the mass of long-range axons, forming the underlying white matter volume, increases disproportionately with brain size (Fig. 5.2). As a result, the volume of gray matter expressed as a percentage of total brain volume is about the same for all anthropoid primates.

The relative white matter volume, on the other hand, increases with brain size, from 9 % in pygmy marmosets (*Cebuella pygmaea*) to about 35 % in humans, the highest value in primates (Hofman 1989). The nonlinear nature of this

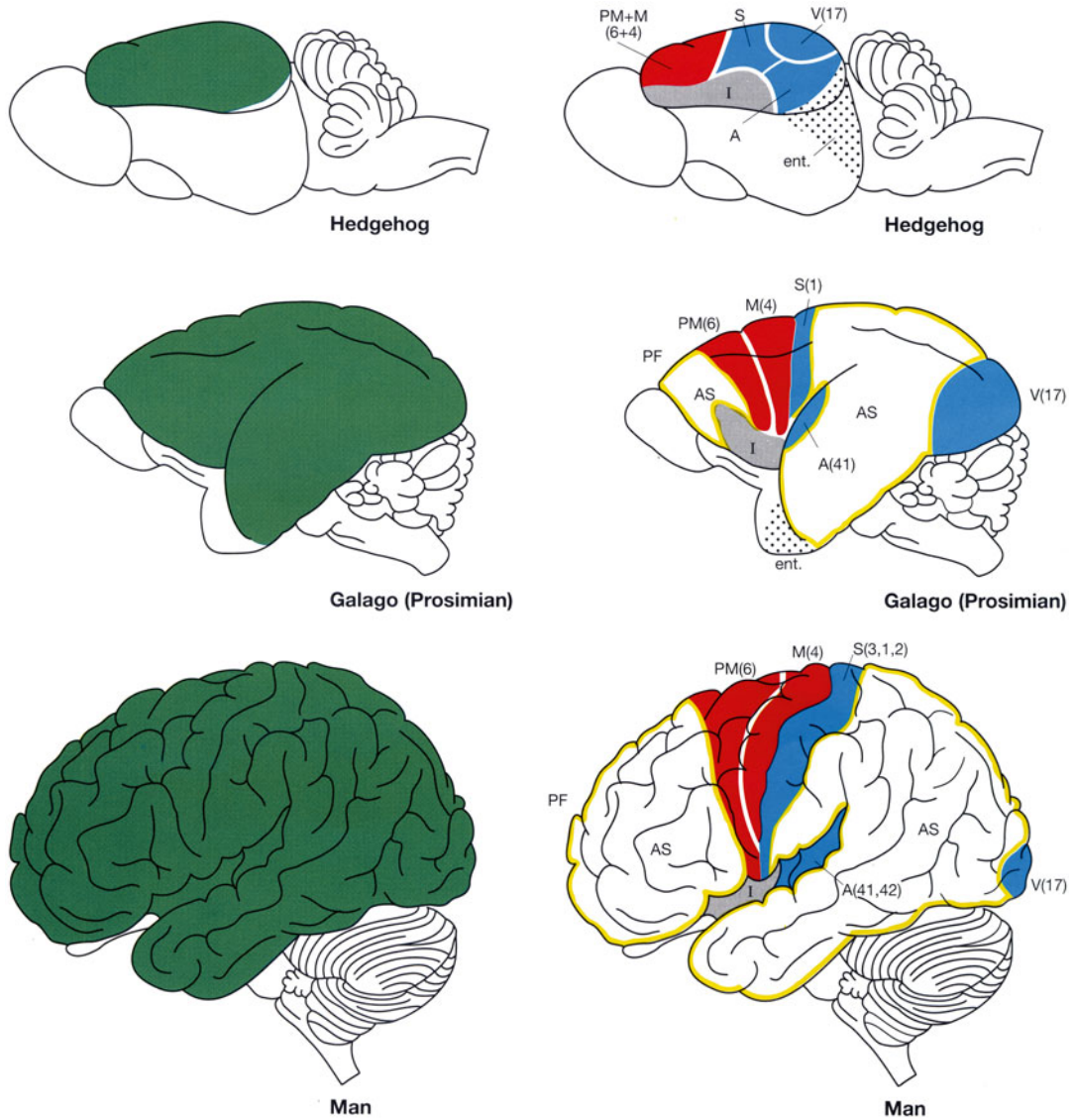


Fig. 5.1 Lateral views of the brains of some mammals to show the evolutionary development of the neocortex (green). In the hedgehog, almost the entire neocortex is occupied by sensory (blue) and motor (red) areas. In the prosimian *Galago*, the sensory cortical areas are separated by an area occupied by association cortex (outlined in yellow). A second area of association cortex is found in front

of the motor cortex. In man, these anterior and posterior association areas are strongly developed. A primary auditory cortex, *AS* association cortex, *Ent* entorhinal cortex, *I* insula, *M* primary motor cortex, *PF* prefrontal cortex, *PM* premotor cortex, *S* primary somatosensory cortex, *V* primary visual cortex (Reproduced with permission from Nieuwenhuys 1994b)

process is further emphasized by plotting the relative volume of white matter as a function of brain size (Fig. 5.3). The high correlation between both variables ensures that the curve, and its confidence limits, can be used for predictive purposes to estimate the volume of white matter

relative to brain volume for a hypothetical primate. The model, for example, predicts a white matter volume of about 1,470 cm³ for an anthropoid primate with a brain volume of 3,000 cm³ (Hofman 2001b, 2012). In other words, in such a large-brained primate, white matter would

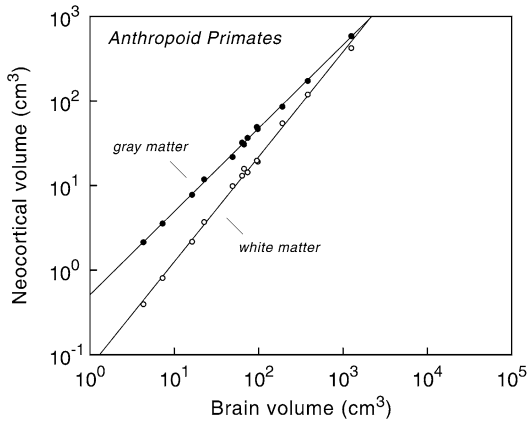


Fig. 5.2 Volumes of cerebral gray and white matter as a function of brain volume in anthropoid primates, including humans. Logarithmic scale. The slopes of the regression lines are 0.985 ± 0.009 (gray matter) and 1.241 ± 0.020 (white matter). Note the difference in the rate of change between gray matter (“neural elements”) and white matter (“neural connections”) as brain size increases (Reproduced with permission from Hofman 2001b)

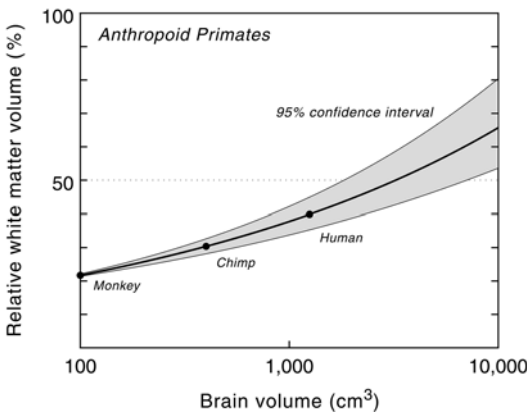


Fig. 5.3 Relative white matter volume as a function of brain volume in anthropoid primates. Semilogarithmic scale. The proportion of white matter increases with brain size, from 22 % in a monkey brain of 100 cm^3 to about 65 % in a hypothetical primate with a brain size of $10,000 \text{ cm}^3$ (Modified with permission from Hofman 2001b)

comprise about half of the entire brain volume, compared to one-third in modern man.

Volumetric measurements of gray and white matter in the neocortex of anthropoid primates have shown that the “universal scaling law” of neocortical gray to white matter applies separately for frontal and non-frontal lobes and that

changes in the frontal (but not non-frontal) white matter volume are associated with changes in other parts of the brain, including the basal ganglia, a group of subcortical nuclei functionally linked to executive control (Smaers et al. 2010). These comparative analyses indicate that the evolutionary process of neocorticalization in primates is mainly due to the progressive expansion of the axonal mass that implement global communication, rather than to the increase in the number of cortical neurons and the importance of high neural connectivity in the evolution of brain size in anthropoid primates.

Wen and Chklovskii (2005) have shown that the competing requirements for high connectivity and short conduction delay may lead naturally to the observed architecture of the mammalian neocortex. Obviously, the brain functionally benefits from high synaptic connectivity and short conduction delays. A magnetic resonance imaging study, furthermore, focusing specifically on the prefrontal cortex, has shown that the volume of the white matter underlying prefrontal areas is disproportionately larger in humans than in other primates (Schoenemann et al. 2005). It suggests that the connectional elaboration of the prefrontal cortex, which mediates such important behavioral domains as planning, aspects of language, attention, and social and temporal information processing, has played a key role in human brain evolution.

Design Principles of Neural Organization

Evolutionary changes in the cerebral cortex have occurred mainly parallel to the cortical surface (tangentially) and have been sharply constrained in the vertical (radial) dimension, which makes it especially well suited for the elaboration of multiple projections and mapping systems. A mosaic of functionally specialized areas has indeed been found in the mammalian cortex, some of the functions being remarkably diverse (Kaas 1993, 2008, 2012; Krubitzer 1995, 2007; Schoenemann 2006). At the lower processing levels of the cortex, these maps bear a fairly simple topographical

relationship to the world, but in higher areas, precise topography is sacrificed for the mapping of more abstract functions. Here, selected aspects of the sensory input are combined in ways that are likely to be relevant to the animal.

Using modern anatomical tracing methods, physiological recordings, and mapping studies, it has been established that each sensory modality is mapped several times in different areas, with about a dozen representations of the visual world and half a dozen each of auditory inputs and somatosensory sensations. In fact, the maps differ in the attributes of the stimulus represented, in how the field is emphasized, and in the types of computations performed. Clearly, the specifications of all these representations mean that functional maps can no longer be considered simply as hard-wired neural networks. They are much more flexible than previously thought and are continually modified by feedback and lateral interactions. These dynamic changes in maps, which seem likely to result from local interactions and modulations in the cortical circuits, provide the plasticity necessary for adaptive behavior and learning. Although species vary in the number of cortical areas they possess and in the patterns of connections within and between areas, the structural organization of the primate neocortex is remarkably similar.

The tremendous increase in the cortical surface without a comparable increase in its thickness during mammalian evolution has been explained in the context of the radial-unit hypothesis of cortical development (for reviews, see Rakic 2007, 2009). According to this model, neocortical expansion is the result of changes in proliferation kinetics that increase the number of radial columnar units without changing the number of neurons within each unit significantly. Therefore, the evolutionary expansion of the neocortex in primates is mainly the result of an increase in the number of radial columns.

The widespread occurrence of these neocortical columns, furthermore, qualifies them to be considered as fundamental building blocks in neural evolution (for reviews see Mountcastle 1997; Buxhoeveden and Casanova 2002b; Rockland 2010; Buxhoeveden 2012). It has

become evident that these cortical circuits integrate at higher levels of information processing, as a result of the hierarchical organization of the brain, thus enabling the system to combine dissimilar views of the world. It implies that if we seek the neural basis of biological intelligence, including mind-like properties and consciousness, we can hardly localize it in a specific region of the brain, but must suppose it to involve all those regions through whose activity an organism is able to construct an adequate model of its external world, perhaps it may even encompass the entire neo- and subcortical network.

It is evident that these neocortical columns are functional and morphological units whose architecture may have been under selective evolutionary pressure in different mammalian lineages in response to encephalization and specializations of cognitive abilities. We are beginning to understand some of the geometric, biophysical, and energy constraints that have governed the evolution of these neural networks (e.g., Felleman and Van Essen 1991; Chklovskii et al. 2002; 2004; Klyachko and Stevens 2003; Laughlin and Sejnowski 2003; Rockland 2010; Casanova et al. 2011). To operate efficiently within these constraints, nature has optimized the structure and function of these processing units with design principles similar to those used in electronic devices and communication networks. In fact, the basic structural uniformity of the cerebral cortex suggests that there are general architectural principles governing its growth and evolutionary development (Cherniak 1995, 2012; Hofman 1996, 2001a, 2007; Rakic 2009; Bullmore and Sporns 2012).

Comparative studies furthermore indicate that variability in subtle subcomponents of the columnar organization in human and nonhuman primates, such as the composition of the interneuron subtypes, are a primary source of interspecific differences in minicolumn morphology among species (Raghanti et al. 2010). Humans deviate from other primates in having a greater width of minicolumns in specific cortical areas, especially in the prefrontal cortex, owing to constituents of the peripheral neuropil space (Buxhoeveden and Casanova 2002a; Semendeferi et al. 2011).

These findings support the idea (Semendeferi et al. 2002; Allen 2009; Teffer and Semendeferi 2012) that human evolution, after the split from the common ancestor with chimpanzees, was accompanied by discrete modifications in local circuitry and interconnectivity of selected parts of the brain. The differences in columnar diameter among primates, however, are only minor compared to the dramatic variation in overall cortex size. Thus, it seems that the main cortical change during evolution has presumably been an increase in the number rather than the size of these neural circuits.

Neural Network Wiring

Although the details of the interpretation of the columnar organization of the neocortex are still controversial (for recent reviews, see Da Costa and Martin 2010; Rockland 2010), it is evident that the potential for brain evolution results not from the unorganized aggregation of neurons but from cooperative association by the self-similar compartmentalization and hierarchical organization of neural circuits and the invention of fractal folding, which reduces the interconnective axonal distances.

Recent network studies, using diffusion tensor imaging (DTI), have demonstrated that the neurons in the neocortex are structurally and functionally highly organized and that this also holds for the wiring of the brain (Van den Heuvel and Sporns 2011; Wedeen et al. 2012). The interconnecting white matter axonal pathways are not a mass of tangled wires, as thought for a long time, but they form a rectilinear three-dimensional grid continuous with the three principal axes of development. The topology of the brain's long-range communication network looks like a 3-D chessboard with a number of highly connected neocortical and subcortical hub regions.

The competing requirements for high connectivity and short conduction delay may lead naturally to the observed architecture of the human neocortex. Obviously, the brain functionally benefits from high synaptic connectivity and short conduction delays. The design of the primate

brain is such that it may perform a great number of complex functions with a minimum expenditure of energy and material both in the performance of the functions and in the construction of the system. In general, there will be a number of adequate designs for an object, which, for practical purposes, will all be equivalent.

Recently, we have shown that in species with convoluted brains, the fraction of mass devoted to wiring seems to increase much slower than that needed to maintain a high degree of connectivity between the neural networks (Hofman 2003, 2007). These findings are in line with a model of neuronal connectivity (Deacon 1990; Ringo 1991) which says that as brain size increases, there must be a corresponding fall in the fraction of neurons with which any neuron communicates directly. The reason for this is that if a fixed percentage of interconnections is to be maintained in the face of increased neuron number, then a large fraction of any brain size increase would be spent maintaining such degree of wiring, while the increasing axon length would reduce neural computational speed (Ringo et al. 1994). The human brain, for example, has an estimated interconnectivity of the order of 10^3 , based on data about the number of modular units and myelinated nerve fibers (Hofman 2012). This implies that each cortical module is connected to a thousand other modules and that the mean number of processing steps, or synapses, in the path interconnecting these modules is about two.

Herculano-Houzel et al. (2010) have shown that in primates the mass of the white matter scales linearly across species with its number of nonneuronal cells, which is expected to be proportional to the total length of myelinated axons in the white matter. Decreased connectivity in the brain is compatible with previous suggestions that neurons in the cerebral cortex are connected as a small-world network and should slow down the increase in global conduction delay in cortices with larger numbers of neurons (Sporns et al. 2004, 2007; Wang et al. 2008; Fig. 5.4).

Once the brain has grown to a point where the bulk of its mass is in the form of connections, then further increases (as long as the same ratio in interconnectivity is maintained) will be unproductive.

Complex Neural Networks

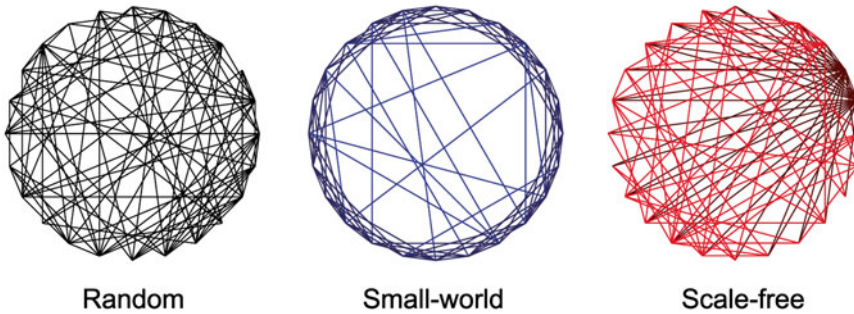


Fig. 5.4 Organizational principles of random, small-world, and scale-free networks. *Structural* cortical networks are neither completely connected with each other nor randomly linked; instead, their connections have small-world attributes with path lengths that are close to those of equivalent random networks but with signifi-

cantly higher degrees of local clustering. *Functional* cortical networks, on the other hand, exhibit both scale-free attributes with power law degree distributions as well as small-world attributes (Modified with permission from Sporns et al. 2004)

Increases in number of units will be balanced by decreased performance of those units due to the increased conduction time. This implies that large brains may tend to show more specialization in order to maintain processing capacity. Indeed, an increase in the number of distinct cortical areas with increasing brain size has been reported (Welker 1990; Kaas 2000, 2012; Striedter 2004). It may even explain why large-brained species may develop some degree of brain lateralization as a direct consequence of size. If there is evolutionary pressure on certain functions that require a high degree of local processing and sequential control, such as linguistic communication in human brains, these will have a strong tendency to develop in one hemisphere (Ringo et al. 1994; Aboitiz et al. 2003).

Biological Limits to Information Processing

The primate brain, as we have seen, has evolved from a set of underlying structures that constrain its size and the amount of information it can store and process. If the ability of an organism to process information about its environment is a driving force behind evolution, then the more information a system, such as the brain, receives and the faster it can process this information, the

more adequately it will be able to respond to environmental challenges and the better will be its chances of survival (Hofman 2003). The limit to any intelligent system therefore lies in its abilities to process and integrate large amounts of sensory information and to compare these signals with as many memory states as possible and all that in a minimum of time. It implies that the functional capacity of a neuronal structure is inherently limited by its neural architecture and signal processing time (see, e.g., Hofman 2001a; Laughlin and Sejnowski 2003; Changizi and Shimojo 2005).

The processing or transfer of information across cortical regions, rather than within regions, in large-brained primates can only be achieved by reducing the length and number of the interconnective axons in order to set limits to the axonal mass (Fig. 5.5). The *number* of interconnective fibers can be reduced, as we have seen, by compartmentalization of neurons into modular circuits in which each module, containing a large number of neurons, is connected to its neural environment by a small number of axons. The *length* of the interconnective fibers can be reduced by folding the cortical surface and thus shortening the radial and tangential distances between brain regions. Local wiring—preferential connectivity between nearby areas of the cortex—is a simple strategy that helps keep cortical connections short.

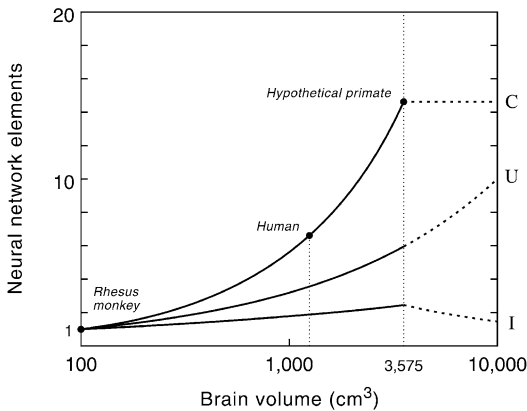


Fig. 5.5 The number of connections (C), cortical processing units (U), and level of interconnectivity (I) in the primate neocortex as a function of brain size. Semilogarithmic scale. Values are normalized to one at a brain volume of 100 cm^3 , the size of a monkey brain. Note that the number of myelinated axons increases much faster than the number of cortical processing units (see also Fig. 5.3). The human cerebrum, for example, contains six times more myelinated axons than that of a rhesus monkey, whereas the number of cortical processing units is only three times larger. *Dashed lines* show the potential evolutionary pathway of these neural network elements in primates with very large brains, that is, beyond the hypothetical upper limit of the brain's processing power (see text and Fig. 5.6). Note that a further exponential growth in the number of cortical processing units, without an increase in the number of connections, will lead to a decrease in connectivity between these units and thus to more local wiring (Reprinted with permission from Hofman 2012)

In principle, efficient cortical folding could further reduce connection length, in turn reducing white matter volume and conduction times (Young 1993; Scannell et al. 1995; Chklovskii et al. 2004). Thus, the development of the cortex does seem to coordinate folding with connectivity in a way that could produce smaller and faster brains.

Recently, Wang et al. (2008) have shown that there are functional trade-offs in white matter axonal scaling in mammals. They found that the composition of white matter shifts from compact, slow-conducting, and energetically expensive unmyelinated axons to large, fast-conducting, and energetically inexpensive myelinated axons. The fastest axons have conduction times of 1–5 ms across the neocortex and <1 ms from the eye to

the brain, suggesting that in select sets of communicating fibers, large brains reduce transmission delays and metabolic firing costs at the expense of increased volume. Delays and potential imprecision in cross-brain conduction times are especially great in unmyelinated axons, which may transmit information via firing rate rather than precise spike timing. In the neocortex, axon size distributions can account for the scaling of per-volume metabolic rate and suggest a maximum supportable firing rate, averaged across all axons, of $7 \pm 2 \text{ Hz}$. Clearly, the white matter architecture must follow a limited energy budget to optimize both volume and conduction time.

Another way to keep the aggregate length of axonal and dendritic wiring low, and with that the conduction time and metabolic costs, is to increase the degree of cortical folding. A major disadvantage of this evolutionary strategy, however, is that an increase in the relative number of gyri can only be achieved by reducing the gyral width. At the limit, the neurons in the gyri would be isolated from the remainder of the nervous system, since there would no longer be any opening for direct contact with the underlying white matter. Prothero and Sundsten (1984) therefore introduced the concept of the gyral “window,” which represents the hypothetical plane between a gyrus and the underlying white matter through which nerve fibers running to and from the gyral folds must pass. According to this hypothesis, there would be a brain size where the gyral “window” area has an absolute maximum. A further increase in the size of the brain beyond that point, that is, at $2,800 \text{ cm}^3$, would increase the cortical surface area, but the “window” would decrease, leading to a lower degree of neuronal integration and an increase in response time.

The remarkably high correlation between gray matter, white matter, and brain size in anthropoid primates ensures that the proposed model can be used for predictive purposes to estimate the volume of white matter relative to brain volume for a hypothetical primate (Hofman 2001b). Model studies of the growth of the neocortex at different brain sizes, using a conservative scenario, revealed that with a brain size of about $3,500 \text{ cm}^3$, the total volume of the subcortical areas (i.e., cerebellum,

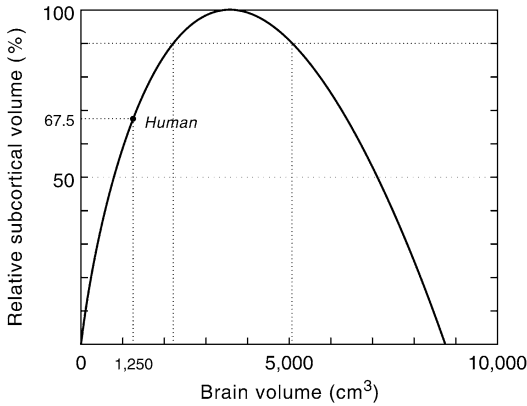


Fig. 5.6 Relative subcortical volume as a function of brain volume. The predicted subcortical volume (i.e., brain volume—predicted neocortex volume) must be zero at zero brain size. Likewise, the subcortical volume will be zero when the brain is exclusively composed of cortical gray and white matter. At a brain size of 3,575 cm³, the subcortical volume has a maximum (see also Fig. 5.5). The maximum simulated value for the subcortical volume (366 cm³) is then taken as 100%. The larger the brain grows beyond this critical size, the less efficient it will become. Assuming constant design, it follows that this model predicts an upper limit to the brain’s processing power. Modern humans are at about two-thirds of that maximum (Modified with permission from Hofman 2001b)

brain stem, diencephalon, etc.) reaches a maximum value (Fig. 5.6). Increasing the size of the brain beyond that point, following the same design principle, would lead to a further increase in the size of the neocortex, but to a reduction of the subcortical volume. Consequently, primates with very large brains (e.g., over 5 kg) may have a declining capability for neuronal integration despite their larger number of cortical neurons.

Limits to Human Brain Evolution

A progressive enlargement of the hominid brain started by about 2–2.5 million years ago, probably from a bipedal australopithecine form with a brain size comparable to that of a modern chimpanzee (see, e.g., Falk 2004, 2007, 2012; Robson and Wood 2008; De Sousa and Cunha 2012). The linear scaling law determined for primates allowed Lent et al. (2012) to estimate the number of neurons in the brains of hominins, using brain vol-

umes as inferred from fossil cranial endocasts (Klein 2009). It shows that ancestral primates living between 35 and 20 million years ago—arboricole and quadruped—did not have more than 20 billion neurons in their brains. In the Pliocene period, between 5.3 and 2.5 million years ago, neuronal numbers may have increased to about 40 billion in *Australopithecus*, just above the estimated 30 billion neurons of chimpanzees. These hominins became bipedal and produced the first flaked stone tools. Another increase took place in the early Pleistocene, about 2.5 million years ago, with the appearance of the genus *Homo*. The number of neurons in the brain grew to about 50 billion in *Homo habilis*, reaching about 70 billion in *Homo erectus*, and finally about 90 billion in modern man. With such a large number of neurons, bipedal locomotion consolidated, and hand-finger movements acquired sophisticated abilities, which allowed *Homo* to produce more and more elaborate tools, dominate fire, and improve social interactions. It means that over the past 2–2.5 million years, more than a doubling in the number of neurons has taken place, leading to one of the most complex and efficient structures in the animated universe, the human brain.

In view of the central importance placed on brain evolution in explaining the success of our species, one may wonder whether there are physical limits that constrain its processing power and evolutionary potential. The human brain has evolved from a set of underlying structures that constrain its size and the amount of information it can store and process. In fact, there are a number of related factors that interact to limit brain size, factors that can be divided into two categories: (1) energetic constraints and (2) neural processing constraints (see, e.g., Wang et al. 2008; Herculano-Houzel 2009).

Energetic Limits

The human brain generates about 15 watts (W) in a well-insulated cavity of about 1,500 cm³. From an engineering point of view, the removal of sufficient heat to prevent thermal overload could be a significant problem. But the brain is

actively cooled by blood and not simply by heat conduction from the surface of the head. So the limiting factor is how fast the heat can be removed from the brain by blood flow. It has been suggested by Falk (1990) and others that the evolution of a “cranial radiator” in hominids helped provide additional cooling to delicate and metabolically expensive parts of the brain, such as the cerebral cortex. This vascular cooling mechanism would have served as a “prime releaser” that permitted the brain size to increase dramatically during human evolution. So to increase cooling efficiency in a larger brain, either the blood must be cooler when it first enters the structure or the flow rate must be increased above current levels.

Another factor related to blood flow has to do with the increasing energy requirements of a larger brain, a problem that is exacerbated by the high metabolic cost of this organ. It is unlikely, however, that the rate of blood flow or the increasing volume used by the blood vessels in the brain—in humans about 4 %—constrain its potential size. A bigger brain is metabolically possible because our cardiovascular system could evolve to transport more blood at greater pressure to meet the increased demand. This should not be taken to imply that thermal and metabolic mechanisms play no role at all in setting limits to brain size. Ultimately, energetic considerations will dictate and restrict the size of any neuron-based system, but as theoretical analyses indicate, thermal and metabolic factors alone are unlikely to constrain the potential size of our brain until it has increased to at least ten times its present size (Cochrane et al. 1995).

Neural Processing Limits

The limit to any neural system lies in its ability to process and integrate large amounts of information in a minimum of time, and therefore, its functional capacity is inherently limited by its neural architecture and signal processing time. The scaling model of the geometry of the neocortex, for example, predicts an absolute upper limit

to primate brain size (Hofman 2001b; Fig. 5.6). Without a radical change in the macroscopic organization of the brain, however, this hypothetical limit will never be approached, since at that point (ca. 8,750 cm³), the brain would consist entirely of cortical neurons and their interconnections, leaving no space for any other brain structure.

Cochrane and his colleagues (1995) looked at the different ways in which the brain could evolve to process more information or work more efficiently. They argue that the human brain has (almost) reached the limits of information processing that a neuron-based system allows and that our evolutionary potential is constrained by the delicate balance maintained between conduction speed, pulse width, synaptic processing time, and neuron density. By modeling the information-processing capability per unit time of a human-type brain as a function of interconnectivity and axonal conduction speed, they found that the human brain lies about 20–30 % below the optimal, with the optimal processing ability corresponding to a brain about twice the current volume. Any further enhancement of human brainpower would require a simultaneous improvement of neural organization, signal processing, and thermodynamics. Such a scenario, however, is an unrealistic biological option and must be discarded because of the trade-off that exists between these factors.

Of course, extrapolations based on brain models, such as the ones used in the present study, implicitly assume a continuation of brain developments that are on a par with growth rates in the past. One cannot exclude the possibility of new structures evolving in the brain, or a higher degree of specialization of existing brain areas, but within the limits of the existing “Bauplan,” there does not seem to be an incremental improvement path available to the human brain. At a brain size of about 3,500 cm³, corresponding to a brain volume two to three times that of modern man, the brain seems to reach its maximum processing capacity. The larger the brain grows beyond this critical size, the less efficient it will become, thus limiting any improvement in cognitive power.

Neural Correlates of Consciousness

Consciousness and affective experience may have arisen concurrently in the evolution of the nervous system, as a way to elaborate and extend the potential reach of instinctual urges, while new levels of cortical information processing and cognition promoted the ability of organisms to efficiently pursue goals essential to survival. In fact, affective experience, being an intrinsic brain function, cannot exist independent of consciousness, since in essence it is something that exists as part and parcel of conscious perception (Zeman 2001; Shettleworth 2012a).

In approaching the problem of consciousness, Crick and Koch made the tentative assumption that all the different aspects of consciousness employ a basic mechanism or perhaps a few such mechanisms (Crick and Koch 1990, 1998). In the case of visual consciousness, for example, they have suggested that its biological usefulness in humans is to produce a single but complex interpretation of the visual scene in the light of past experience, either of ourselves or of our ancestors (embodied in our genes), and to make this interpretation directly available, for a sufficient time, to parts of the brain that make a choice among many different but possible plans of action (Crick and Koch 1995). Exactly how this works in detail is unclear.

To be aware of an object or event, Crick and Koch (1995) have argued that the brain has to construct a multilevel, explicit, symbolic interpretation of parts of the visual scene. It means that there are specific groups of neurons at all levels of the visual hierarchy which employ coarse coding to represent some *aspect* of the visual scene. In the case of a particular face, all of these neurons can fire to somewhat face-like objects (Young and Yamane 1992). Notice that while the *information* needed to represent a face is contained in the firing of the ganglion cells in the retina, there is no explicit representation of the face there. A representation of an object or an event will usually consist of representations of many of the relevant aspects of it, and these are likely to be distributed, to some degree, over different parts of the visual system.

The conscious representation of the world is likely to be widely distributed over many areas of the cerebral cortex and possibly over certain sub-cortical structures as well (Baars 1997). Crick and Koch (1998) postulated that only some types of specific neurons will express the neural correlate(s) of consciousness and that these neurons will probably be fairly close together and will all project roughly to the same place. An alternative hypothesis is that the neural correlate of consciousness is necessarily global (Greenfield 1995). In its most extreme form, this would mean that at one time or another, any neuron in the cortex and associated structures could be part of the neural correlate of consciousness.

The neural correlate of consciousness is defined as the minimal set of neuronal events that gives rise to a specific aspect of a conscious percept (Crick and Koch 2003). The cerebral cortex is probably the most suited part of the brain to look for this neural substrate, as it has very highly and specifically interconnected neuronal networks, many types of excitatory and inhibitory interneurons, and acts by forming transient coalitions of neurons, that is, assemblies of nerve cells, the members of which support one another. The dynamics of coalitions are not simple, as Crick and Koch (1990, 2003) have pointed out. In general, at any moment the winning coalition is somewhat sustained and embodies what an animal is conscious of. On the basis of experimental results in the macaque, Desimone and Duncan (1995) suggest that selective attention biases the competition among competing cell assemblies, but they do not explicitly relate this idea to consciousness.

Coalitions can vary both in size and in character. For example, a coalition produced by visual imagination (with one's eyes closed) may be less widespread than a coalition produced by a vivid and sustained visual input from the environment. These cortical neuronal networks (at least for perception) can be thought of as having nodes. Each node is needed to express one aspect of one percept or another. An aspect cannot become conscious unless there is an essential node for it. For consciousness, there may be other necessary conditions, such as projecting to the frontal

cortical areas. Thus, a particular coalition is an active network, consisting of the relevant set of interacting nodes that temporarily sustain itself (Crick and Koch 2003). The smallest useful node may be a cortical column (Mountcastle 1997) or, perhaps, a portion of a cortical column. The feature which that node represents is (broadly) its columnar property. Edelman and Tononi (2000) presented a theory of consciousness, based on the idea of a “dynamic core,” which resembles the coalition concept to a large extent. The dynamic core hypothesis, however, rejects the idea that there is a special subset of neurons that alone expresses the neural correlate of consciousness, a view which is also defended in this chapter.

Most of the theories of consciousness have the idea of competing assemblies of neurons in common. Consciousness depends on certain coalitions that rest on the properties of very elaborate neuronal networks. It is suggested that attention consists of mechanisms that bias the competition among coalitions, especially during their formation. Furthermore, the idea that the spatio-temporal dimensions of these nodes represent the neural correlates of mind is most appealing, as it suggests that consciousness, being an integral part of the species’ problem-solving capacity, correlates to some extent with the degree of complexity of a nervous system. Therefore, the search for the neural correlates of consciousness should be complemented by a search for its computational correlates (see, e.g., Atkinson et al. 2000; Zeman 2001).

Evolutionary Models of the Mind

Considering biological intelligence as the problem-solving capacity of an organism makes it possible to speak of degrees of intelligence and of its evolution from amoeba to man (Hofman 2003). But what does it mean precisely when one says that species differ in intelligence or that vertebrates are in general more intelligent than invertebrates? It means that there are differences in the abilities of organisms to perceive and interpret the physical world. Biological intelligence can thus be conceived as to reflect the temporal

and spatial complexity of the species’ niche, without referring, however, to the kinds of situations organisms encounter in everyday life (Reader et al. 2011; Roth and Dicke 2012). It is, in fact, a measure of capacity, independent of the way the capacity is used, and it may be treated as a trait for “anagenetic” rather than “cladistic” analysis (Gould 1976; Jerison 1985). It implies that when distantly related species are comparable in their problem-solving capacity, we should consider the species to be comparable in biological intelligence. Yet the near equality in intelligence may be based upon radically different adaptations. Since neural mechanisms and action patterns evolve in the contexts of the environments in which they are effective, and since species never occupy identical niches, many and various intelligences (in the plural) must have evolved in conjunction with evolving environments (Jerison 1985).

In theory, each ecological niche requires its own degree of biological intelligence. That means that specific neural and sensorimotor adaptations always occur in relation to particular environments. A striking example is the mammalian brain, where the evolutionary changes in the balance of the sensory systems are the result of the adaptive radiation of species into many different ecological niches (Pirlot 1987; Macphail 1993; Macphail and Bolhuis 2001; for reviews, see Roth and Wullimann 2001). These sensory systems, like any other biological feature, could evolve as a result of natural selection, because any subject that forms inadequate representations of outside reality will be doomed by natural selection.

In this view, cognitive systems and emotional phenomena can also be considered to be the result of interactions between genetic aptitude and natural environment, as they have a number of biologically useful functions: one is to keep track of the individual’s whereabouts in the world by constructing a schematic model of reality (Popper 1982; Churchland and Churchland 2002; Premack 2007). It is evident that the mind, as an emergent property of sufficiently complex living systems, has its evolutionary history like any other trait that increases adaptation to the environment and that its functions have increased

with the evolution from lower to higher organisms (Popper 1982). It might explain the dramatic evolutionary expansion of the human neocortex, being the region where both perception and instruction take place, where the external world is interpreted and modeled, where concepts are formed and hypotheses tested, in short, where the physical world interacts with the mind.

Evolutionary psychology seeks to explain these evolved functional characteristics of the human mind through the lens of an explanatory framework where special adaptive mechanisms are postulated to have been critical for hominid survival and reproductive success (see Panksepp et al. 2002). These “adaptive modules” are theoretical constructs unique to the hominid lineage and should be clearly distinguished from the spatiotemporally defined neural processing units (or modules) of the cerebral cortex discussed in the previous sections (for a review, see Shettleworth 2012b). The existence of a variety of genetically inherited “adaptive modules” is dubious at best when considered simultaneously with our current understanding of mammalian brain organization. Indeed, the organization of the cerebral cortex, which is commonly assumed to be a prime anatomical substrate for unique cognitive functions, exhibits no robust signs of localized anatomical specialization above and beyond specific sensory and motor connections and their polymodal interactions.

Although the adaptation of an organism to its environment is the chief process directing biological evolution, with the evolution of intelligence, organisms became more and more independent of their environments, by modifying the environments according to their needs. This process culminated in the evolution of mankind, which can be understood only as a result of the interaction of two kinds of evolution: the biological and the cultural (Ayala 1986; Herrmann et al. 2007; Premack 2007). Such considerations have led various authors to argue that the human brain can acquire a large variety of epigenetically derived functions via interactions of a limited number of evolutionary conserved affective/motivational systems (situated largely in subcortical areas) with a set of plastic general-purpose

learning mechanisms in the cerebral cortex (see Panksepp and Panksepp 2000; Adolphs 2009). It does not mean that there are no special-purpose learning systems in the brain, such as fear learning, but the human cerebral cortex includes much more than a conglomeration of special-purpose learning mechanisms. It contains a neural architecture that can generate flexible features which may be best conceptualized as *rewritable*.

Cultural evolution, however, being the emergent result of the evolution of mind, cannot dispense with biological preconditions; it builds on biological facts and faculties. Though cultural evolution indeed presupposes biological evolution, it is not fully explicable in terms of theories and methods of the latter. In fact, cultural evolution has transgressed organic evolution and shows a certain autonomy (see Hofman 2003). The special status of cultural heredity can be derived from the fact that most cultural innovations are devised precisely in order to meet the environmental challenges or to improve our models of reality, whereas biological evolution has a mindless random character. It is appropriate, therefore, to distinguish adaptations to the environment due to cultural selection from those that take place by the selection of genotypes. Cultural inheritance, furthermore, is an infinitely faster process than genetic inheritance, since it is based on the transmission of information through direct communication and through books, the arts, and the media, which makes that a new scientific discovery, or technical achievement can be transmitted to the whole of mankind in less than one generation (Ayala 1986).

Human Language and Intelligence

It is evident that the role of human language in the transmission of knowledge is extremely important, even so prominent and pervasive that it is hardly possible to estimate human general intellectual capacity independent of linguistic capacity (Macphail 1982; Schoenemann 2012). Its manifestations and, in particular, that of its newly acquired functions—description and argumentation—are the most peculiar phenomena in

human problem solving. While animals can communicate by expressing their inner state by means of their behavior and by signaling to conspecifics (e.g., in case of danger), man is the only creature that is able to make true and false statements and to produce valid and invalid arguments.

The progressive accumulation of interactions between environment (both physical and social), “conserved” subcortical systems, and the “general-purpose” cerebral cortex gave rise to a qualitatively different shade of mind—one that could communicate not merely with signs, but in symbolic terms. On the other hand, we have seen that a language system—of the type found in humans—is not essential for consciousness. It is plausible that organisms that do not possess a sophisticated language system are aware of the external world. This is not to say, however, that language does not enrich consciousness or that it does not contribute to our model of reality.

If we assume that part of the basis of human speech is inherited in the DNA and that language is as much a biological as a cultural adaptation, then changes in the brain that permit the advantageous supplement of language acquisition to perception and communication would have had obvious selective advantages throughout the period of hominid evolution (Deacon 1998; Schoenemann 2012). We may conceive human language, therefore, as a superorganic form of adaptation, having evolved not only as a cognitive adaptation contributing to the knowledge of reality of each individual but also as a means of sharing and, even more importantly, influencing states of mind among conspecifics. Indeed, because of language, human beings are not only able to construct individual representations of the external world, but they can also contribute to and learn from *collective* models of reality, that is, the cumulative experience of the whole of mankind. With its cognitive and linguistic skills, *Homo sapiens* tries to know its world and even exerts itself to the utmost to control it.

It is obvious that by virtue of language, human beings tend to have highly organized informational states of mind and, consequently, are excellent problem solvers. But although knowledge of reality may be a necessary condition for survival,

it is surely not enough: the degree of intelligence reached by a species does not determine the propensity of its reproductive success. This may be inferred from the indiscriminate elimination of millions of species through the eras, from ammonites to australopithecines. It means that though adaptability increases with the evolution of biological intelligence, environmental catastrophes can always be fatal to a species. But not only external factors can threaten the existence of organisms; *Homo sapiens*, despite its impressive intellectual capacities, might in the end become the victim of its own mind by, paradoxically, creating problems that it is then unable to solve.

Concluding Remarks

All organisms are constantly engaged in solving problems and must therefore have fitting and relevant models of their specific environments in order to enhance their chances of survival. Consequently, the problem-solving capacity of a species is assumed to reflect the temporal and spatial complexity of its ecological niche.

The thesis presented here is that biological intelligence can be considered to be a correlate of the problem-solving capacity of a species, manifesting itself in the complexity of the species’ model of reality. With the evolution of sensory systems as adaptations to specialized environments, the capacity to process large amounts of sensory information increased and, with that, the power to create more complex physical realities. The processing of large amounts of information originating from the various sense organs and the construction of complex models of reality require a neural system that selects, integrates, stores, and models—in other words, a system with mind-like properties that enables the organism to make sense of an otherwise chaotic world. But once we allow mind-like properties to come in, such as motivation, emotion, preference, and anticipation, we must allow that it is not only the hostile environment which plays an organizing or designing role in the evolution of biological intelligence but also the active search of an organism for a new ecological niche, a new mode of living.

Since the mind, prehuman and human, takes a most active part in evolution and especially in its own evolution, hominization and the evolution of our linguistic world may have begun as a cultural adaptation to new ecological niches. The process probably started at the time of hominid divergence a few million years ago, as part of the cognitive and manipulative adaptation to what was in essence a more complex physical reality. In other words, some of the seemingly unique higher functions of the human brain, such as language and other neuro-symbolic capacities, were not necessarily due to genetic selection and may have emerged epigenetically through learning and cultural experiences because of the dramatic expansion of the neocortex and its increased tendency to neural plasticity. It seems that the time is finally ripe to begin to building an evolutionary viewpoint of the mind based on comparative concepts that incorporate the intrinsic systems found in all primate brains.

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