Chapter 7
On the Matter of Mind: Neural Complexity and Functional Dynamics of the Human Brain

Michel A. Hofman

Abstract The evolutionary expansion of the brain is among the most distinctive morphological features of anthropoid primates. During the past decades, considerable progress has been made in explaining brain evolution in terms of physical and adaptive principles. The object of this review is to present current perspectives on primate brain evolution, especially in humans, and to examine some of the design principles and operational modes that underlie the information processing capacity of the cerebral cortex. It is shown that the development of the cortex coordinates folding with connectivity in a way that produces smaller and faster brains than otherwise would have been possible. It will be argued that in primates the complexity of the neural circuitry of the cerebral cortex is the neural correlate of higher cognitive functions, including mind-like properties and consciousness.

Keywords Brain evolution • Cerebral cortex • Cognition • Consciousness • Human mind • Information processing • Biological intelligence • Neural network • Primates

> *Evolution is a passage from the most automatic to the most voluntary.*
>
> John Hughlings Jackson (1884)

7.1 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. Problem-solving, in other words, is an essential dynamic survival mechanism, evolved to cope with disturbances in the ecological equilibrium. It can

M.A. Hofman, Ph.D.
Netherlands Institute for Neuroscience, Royal Netherlands Academy of Arts and Sciences, Meibergdreef 47, Amsterdam 1105 BA, The Netherlands
e-mail: M.Hofman@nin.knaw.nl

S. Watanabe et al. (eds.), *Evolution of the Brain, Cognition, and Emotion in Vertebrates*, Brain Science, DOI 10.1007/978-4-431-56559-8_7

therefore be looked upon as an adaptive capacity enabling organisms to adjust themselves to one another and to their physical environment (see, e.g., Macphail and Bolhuis 2001; Reader et al. 2011; Shettleworth 2012a). 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.

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 (Macphail and Bolhuis 2001; Roth and Dicke 2012; Hofman 2015). 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., Laughlin and Sejnowski 2003; Buzsáki et al. 2013). 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 the neural correlate of cognition.

7.2 Principles of Brain Evolution

If we assume that the cognitive capacity of complex organisms is the product of integrated sensory information processing and mental faculties, responsible for the planning, execution, and evaluation of intelligent behavior, variations among species in cognition must in principle be observable in the neural substrate. In mammals, especially in primates, the complexity of the neural circuitry of the cerebral cortex is considered to be the neural basis for the brain's coherence and predictive power and, thus, a correlate of higher cognitive and perceptual functions (Gazzaniga et al. 2008; Wang 2010; Chittka et al. 2012).

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 the cortical structure (Striedter 2005; Aboitiz and Montiel 2012; Smaers et al. 2012; Hofman 2014; Lewitus et al. 2014; Fig. 7.1). 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; 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

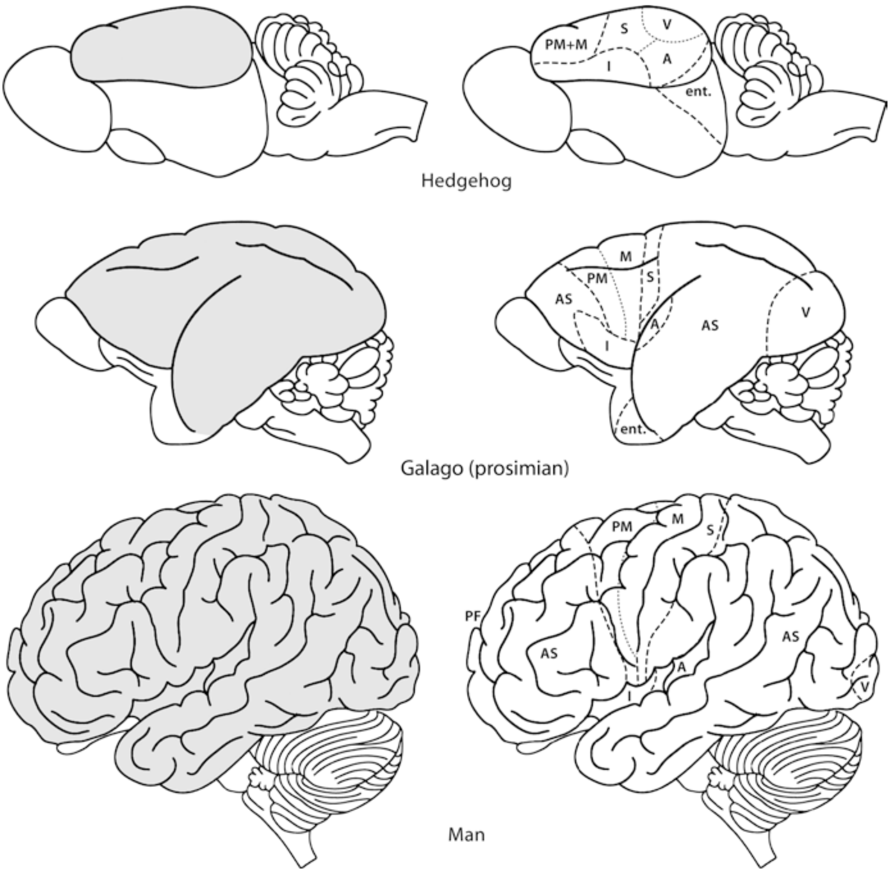

Fig. 7.1 Lateral views of the brains of some mammals to show the evolutionary development of the neocortex (*gray*). In the hedgehog almost the entire neocortex is occupied by sensory and motor areas. In the prosimian galago, the sensory cortical areas are separated by an area occupied by association cortex (AS). A second area of association cortex is found in front of the motor cortex. In human beings 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. Modified from Nieuwenhuys (1994)

orders (Stephan et al. 1981). Comparative studies among four mammalian orders, including primates, have revealed that the absolute neuronal composition in the cerebral 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.

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 (for reviews, see Schmahmann 2010; MacLeod 2012; Barton and

Venditti 2014). 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.

7.3 Organization and Evolution of the Cerebral Cortex

The cerebral cortex forms as a smooth sheet populated by neurons that proliferate at the ventricular surface and migrate outward along radial glial fibers (for reviews, see Cheung et al. 2007; Rakic 2009). Differences in the duration of neurogenesis, which increases more rapidly with brain size for the cerebral cortex than for subcortical areas (Charvet and Finlay 2014; Molnár et al. 2014; Suárez et al. 2014), lead to a systematic increase in the ratio of the cortical to subcortical regions. Whereas in small-brained species the cortical volume expands by virtue of a combined increase in surface area and cortical thickness, the increase of the cortical volume in species with a brain size of more than 3–4 cm^3 is almost entirely due to a disproportionate expansion of the cortical surface area (Hofman 1989, 2012). It is the increase of the cortical surface area beyond that expected for geometrically similar objects of different volumes that creates the need for cortical folding (Hofman 1989, 2016; Razavi et al. 2015; Striedter et al. 2015; Fig. 7.2).

Cortical folding is not a random process. Instead, the folds that develop reflect the functional organization of the cortex, and form patterns that are remarkably consistent across individuals and even among some species. How this happens is not well understood. Although many developmental features and evolutionary adaptations have been proposed as the primary cause of cortical folding, it is not evident that gyrification is reducible in this way (for a review, see Ronan and Fletcher 2015). There is now empirical evidence that suggests that the folding of the cerebral cortex is the product of a generalized mechanism, namely, the differential expansion of the

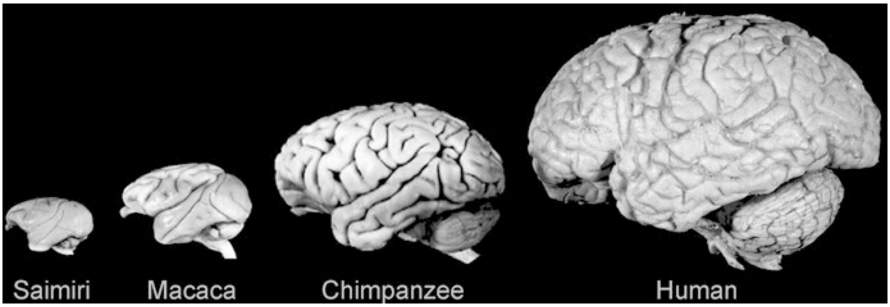

Fig. 7.2 Lateral views of the brains of some anthropoid primates showing the evolutionary expansion of the neocortex. Note the diverse configurations and gyral and sulcal patterns. *Saimiri sciureus*: E = 22 g; *Macaca mulatta*: E = 95 g; *Pan troglodytes*: E = 420 g; *Homo sapiens*: E = 1350 g. Reproduced with permission from Hofman (2007)

cortex. Mota and Herculano-Houzel (2012), for example, propose that cortical folding is driven by white matter connectivity. Specifically, they argue that the mechanical tension generated by the pattern of connectivity of fiber bundles traveling through white matter may account for the observed pattern of cortical surface convolutions. The authors propose the degree of tension, taken as directly proportional to the morphological characteristics of the fiber bundle (i.e., axonal length and average cross-sectional area and the proportion of efferent neurons), determines how much the cortical surface folds inward. This model is used to explain how surface convolutions vary with brain size and how gray matter thickness varies.

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; Lefebvre 2012; Roth and Dicke 2012; Isler and Van Schaik 2014). 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 (Hofman 1989, 2012, 2016; 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; Finlay and Darlington 1995; Zhang and Sejnowski 2000; Finlay et al. 2001; Hofman and Falk 2012). The volume of the cortical gray matter, containing local networks of neurons that are wired by dendrites and mostly nonmyelinated 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. 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 process is further emphasized by plotting the relative volume of white matter as a function of brain size (Fig. 7.3). 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 1470 cm^3 for an anthropoid primate with a brain volume of 3000 cm^3 (Hofman 2001, 2012). In other words, in such a large-brained primate, white matter would 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; Sherwood et al. 2012). These comparative analyses indicate that the evolutionary process of neocorticalization in primates is mainly due to the progressive expansion of the axonal mass that implements global communication, rather than to the increase in the number of

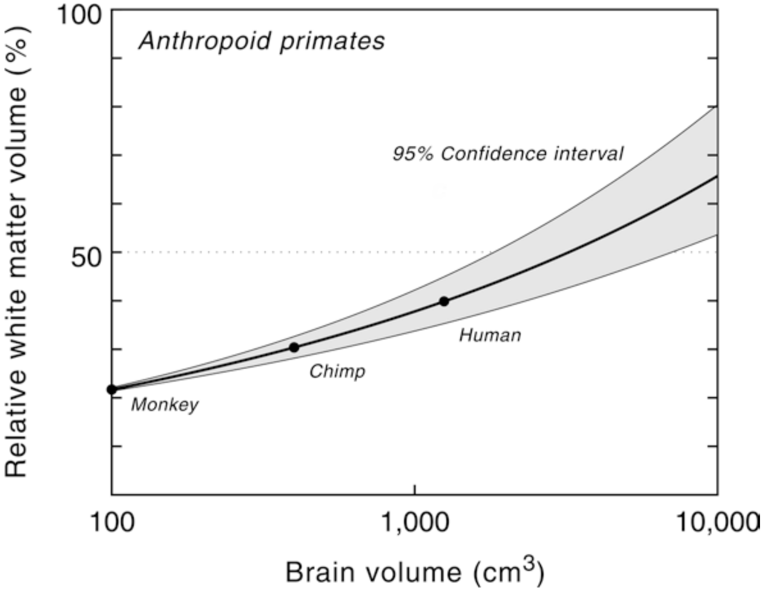

Fig. 7.3 Relative white matter volume as a function of brain volume in anthropoid primates. Semilogarithmic scale. The proportion of white matter increases with brain size, from 22% in a monkey brain of 100 cm^3 to about 65% in a hypothetical primate with a brain size of 10,000 cm^3. Modified from Hofman (2001)

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.

7.4 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 2000, 2012; Krubitzer 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 a 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 primate species vary in the number of cortical areas, and in the patterns of connections within and between these areas, the structural organization of their neocortex is remarkably similar (Young 1993; Hill et al. 2010; Preuss 2011; Papo et al. 2014a, b).

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 (Mountcastle 1997; Rockland 2010; Buxhoeveden 2012; Opris and Casanova 2014). 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. The grouping of neurons into clusters that interact over short distances has been found to be characteristic not only of the cerebral cortex but of subcortical structures as well, such as the thalamus and basal ganglia (Pay 1980; Mountcastle 1997). An important implication of this basic plan of brain organization is that functionally related subsets of cortical areas and subcortical nuclei could evolve independently of the development of other subsystems during evolution (Sherwood et al. 2008; Lefebvre 2012; Smaers and Soligo 2013). So if we seek the neural basis of cognition, 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.

7.5 Neural Network Wiring

Although the details of the interpretation of the columnar organization of the neocortex are still controversial (for critical reviews, see Da Costa and Martin 2010; Rockland 2010; Preuss 2001; DeFelipe 2015), 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. The human cerebral cortex, for example, contains about 20 billion neurons, which are interconnected via a massive yet highly organized network of axonal and dendritic wiring. This wiring enables both near and distant neurons to coordinate their responses to external stimulation. Understanding the organizing principles of cortical wiring, therefore, represents a central goal toward explaining human cognition and perception (see for example, Preuss 2011; Budd and Kisvárday 2013; De Reus et al. 2014; Wang and Liu 2014).

In the mammalian cerebral cortex, reciprocal connections between excitatory and inhibitory neurons are distributed across multiple layers, encompassing modular, dynamical, and recurrent functional networks during information processing. These dynamical brain networks are often organized in neuronal assemblies interacting through rhythmic phase relationships. Accordingly, these oscillatory interactions are observed across multiple brain scale levels, and they are associated with several sensory, motor, and cognitive processes. Recently Bosman and Aboitiz (2015) argued that there are functional constraints in the evolution of brain circuits and that these constraints may be the result of advantages that oscillatory activity contributes to brain network processes, such as information transmission and code reliability.

Network studies, using diffusion tensor imaging (DTI), have demonstrated that not only the neurons in the cerebral cortex are structurally and functionally highly organized but that it also holds for the wiring of the entire brain (Van den Heuvel and Sporns 2011; Wedeen et al. 2012; Van den Heuvel et al. 2016). 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 development of new technologies for mapping structural and functional brain connectivity has led to the creation of comprehensive network maps of neuronal circuits and systems. The architecture of these brain networks can be examined and analyzed with a large variety of graph theory tools (for a review, see Sporns and Betzel 2016). It turns out that modularity is a key characteristic of brain networks across species and scales. Indeed, the modular organization of the primate neocortex may confer increased robustness and more flexible learning, help to conserve wiring cost, and promote functional specialization and complex brain dynamics (Gómez-Robles et al. 2014).

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 I have shown that in species with convoluted brains, the fraction of mass devoted to wiring seems to increase more slowly than that needed to maintain a high degree of connectivity between the neural networks (Hofman 2014, 2016). 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 neocortical columns and myelinated nerve fibers (Hofman 2012).

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, De Reus et al. 2014; Wang and Liu 2014).

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. 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 2005). 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; Rilling 2014).

7.6 Neural Correlates of Consciousness

That consciousness depends on the function of the brain has been known from ancient times. Although detailed understanding of the neural mechanisms of consciousness has not been achieved, correlations between states of consciousness and functions of the brain are possible. The emergence of computational theories of mind and advances in the understanding of neurophysiology have contributed to a renewal of interest in consciousness. Since the 1980s, there has been a great deal of investigation of the neural correlates of consciousness, which have led to a number of plausible suggestions about how such a theory might be developed. One such suggestion is that consciousness is an internal scanning or perception. Another is that it involves an explicit higher-order thought**,** i.e., a thought that one is in a specific mental state.

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, 2005; Baars 2005; Shettleworth 2012a).

The conscious representation of the world is likely to be widely distributed over many areas of the cerebral cortex and possibly over certain subcortical structures as well (Baars 2005; Fabbro et al. 2015). 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; Greenfield and Collins 2005). 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. Greenfield and Collins (2005) also argue that this raw, basic subjective state does not appear to be an exclusive property of the human brain. There is no obvious qualitative transformation in either the anatomy or the physiology of the central nervous system of human or nonhuman animals. Similarly, there is no clear ontogenetic line that is crossed as the brain grows in the womb, no single event or change in brain physiology, and certainly not at birth, when consciousness might be generated in an all-or-none fashion. A more plausible, and scientific, view of consciousness might be therefore that it is not a different property of the brain but that it is a consequence of a quantitative increase in the complexity of the human brain: consciousness will grow as brains grow. Hence, consciousness is most likely to be a continuously variable property of the brain, in both phylogenetic and ontogenetic terms.

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; Tononi and Koch 2015). 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. 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 the present essay.

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 spatiotemporal 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, 2005).

7.7 Evolutionary Models of 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 (Jerison 1991; Hofman 2003; Dicke and Roth 2016). 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; Isler and Van Schaik 2014). 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; Bouchard 2014).

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 (Macphail and Bolhuis 2001; Striedter 2005; Hofman 2007; Allen 2009; Reader et al. 2011). 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 (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 simple to more complex systems (Sherwood et al. 2008; Roth 2013).

According to John Hughlings Jackson, in his famous Croonian lectures on the evolution and dissolution of the nervous system in *The Lancet* in 1884, the highest level of nervous function is the most complex, the most integrated, and the most widely interconnected expansive network of coordination of sensorimotor functions (see Gillett and Franz 2013). Hughlings Jackson therefore distanced the higher centers from purely reflex functions, as the former showed the least automatic or stereotyped of nervous processes, continually reorganizing themselves throughout life, to become "the organ of mind," a dynamic and changing set of patterns of sensitivity and response.

The notion of evolution as passage from the most simple and automatic to the most complex and voluntary implies 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 (Hofman 2003, 2015). 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." 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, and where concepts are formed and hypotheses tested, in short, where the physical world interacts with the mind.

One of the basic assumptions according to this hypothesis of the evolution of perceptual worlds is that each new system is modeled after a pre-existing one. Thus, human perceptual worlds involve some new developments beyond those of any other species, and these developments are logical extensions of those which evolved previously. The evolution of increasingly complex perceptual worlds may have reduced stereotyped behavior, thus enabling an animal to modify its behavior according to its experience. Jerison in fact writes (Jerison 1973, p. 23) that "if the nature of the perceptual world defines a dimension of intelligence, the evolution of intelligence is to be sought in the changes among species with respect to their perceptual worlds." However, one should be aware, when defining intelligence, of the extent to which particular sensory capacities have been developed as species-specific traits for life in a specialized niche. The implication is that integrative functions of the brain, rather than the sensory modalities themselves, may best define intelligence. In particular the enlargement of the brain in mammals beyond the basal somatic requirements may be associated with the tendency to integrate all information coming from different sensory systems by special intracortical networks.

Evolutionary psychology seeks to explain these evolved, functional characteristics of the human mind through the lense of an explanatory framework where special adaptive mechanisms are postulated to have been critical for hominin survival and reproductive success (Panksepp et al. 2002). These "adaptive modules" are theoretical constructs unique to the human lineage and should be clearly distinguished from the spatiotemporally defined neural processing units 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 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 (Herrmann et al. 2007; Premack 2007; Hofman 2015). 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 (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, Donald 1991; Hofman 2003, 2015). 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.

7.8 Human Language and Cognition

The most peculiar phenomenon in human problem-solving is the manifestation of language and, in particular, that of its newly acquired functions (Macphail 1982; Deacon 1998, 2006; Roth 2013; Hauser et al. 2014; Lieberman 2015). While animals can communicate by expressing their inner state by means of their behavior and by signaling to congeners, (e.g., in case of danger), human beings are the only animals that are able to make true and false statements and to produce valid and invalid arguments. Some of these higher functions, however, have been ascribed to some nonhuman primates as well. It is evident that the role of human language is so important and pervasive that it is not possible to estimate human general intellectual capacity independent of linguistic capacity (Macphail 1982; Passingham 2008; Schoenemann 2012; Bolhuis et al. 2014; Hauser et al. 2014; Corballis 2015).

Despite its important role in human cognition the evolutionary history of language still remains an enigma. Until recently it was widely held that language, and its left-hemispheric representation in the brain, were uniquely human, emerging quite recently in evolutionary terms after the emergence of *Homo sapiens*, some 70,000–100,000 years ago (e.g., Berwick et al. 2013; Bolhuis et al. 2014). Changing views of language, however, suggest that it was not a recent and sudden development in human evolution but that modern language is the product of a gradual coevolution of neurobiological and cultural-linguistic conditions, which took place since the genus *Pan* was separated from the hominin lineage about 4–6 million years ago (e.g., Deacon 1998; Falk 2004; Christiansen and Chater 2008, 2015; Pagel et al. 2013; Levinson 2016). New genetic evidence and the interpretation in context of fossil and artifact discoveries shed light on this controversy (see, e.g., Hillert 2015). The data indicate that premodern language might have been already spoken by *Homo erectus*. However, the protolanguage that was used by these early hominins may have been different from modern language. In fact, the complex properties of modern language require not only cortical wiring for language-specific operations, “a language-ready brain,” but also a linguistic code related to complex concept formation. There are now strong indications that these cultural-linguistic features coevolved along with genetic changes over a period of several million years.

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 hominin evolution. It has hypothesized, therefore, that the large size of the modern human brain results from demands made on the retrieval systems owing to the evolution of language (Popper and Eccles 1977; Macphail 1982; Rilling 2014; Dicke and Roth 2016). 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 (Chomsky 2007; Bouchard 2013). 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, who 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 hominin evolution (Deacon 1998; Schoenemann 2012; Bouchard 2013; Bolhuis et al. 2014). We may conceive human language, therefore, as a super-organic form of adaptation, 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 (Premack 2004; Bouchard 2013). 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.

7.9 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 cognition 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 higher cognitive functions 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 hominin 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.

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