1

Evolutionary aspects on the frontal lobes

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1 Introduction

The purpose of this chapter is to introduce you to the fascinating story about the evolution of the human brain and especially of its frontal lobes. The story begins in south east Africa some six million years ago and ends with the recent development of modern behavior and mental abilities like symbolic language and creative thinking. Some disadvantages linked to the dangers and demands of a large size brain will be dealt with. A discussion of the anatomical differences between the human brain and that of our close relatives, the African great apes, will follow. Evolutionary advantages linked to the big brain and its advanced frontal lobes will be described, with special focus on the evolution of language and abstract thinking. Our still very limited knowledge about what changes of the human genome, that made it possible to develop modern behavior, is then summarized. The chapter will end by discussing two very old and specifically human mental disturbances, schizophrenia and attention deficit hyperactivity disorder, from an evolutionary perspective.

2 Early history of human evolution and "the creative explosion"

The tremendous success of humanity, regarding population growth and ability to occupy practically all parts of the earth, is not due to any great bodily advantages of our species. Our main advantage is the possession of a brain that makes it possible for us to outsmart and control most of our competitors and enemies on the planet Earth and to change and use the environment to our (short-term) advantage. The chimpanzee is our closest living relative and the still unknown shared ancestor evolved into two lines of development around six million years ago. This separation took place in southeast Africa and was coincidental with marked climate changes – the eastern part of Africa turned into a more open landscape of savanna type including also plenty of wetlands

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and seashores. The upright position was advantageous for the different forms of hominids (different species of the *Australopithecus* family like *A. afarensis*; "Lucy") that were developed. It is a matter of debate whether the advantages of bipedalism (energy economic movements, easy spotting of food or predators), lack of fur, having sweat glands and body fat were that great on the savanna. There are many supporters of the *water ape* hypothesis claiming that the ancestors of humanity mainly populated the wetlands and the seashore (Leakey & Lewin, 1978). Here the availability of highly nutritious seafood should later be one of the prerequisites for the development of the large size brain. As is shown in Figure 1.1, the brain weight remained at about chimpanzee size for about three million years. Brain growth started with the appearance of the first representative of the *Homo* family, *Homo habilis*, about two-and-a-half million years ago. The first stone tools appear with the evolution of this line of species. No archeological findings indicate that the early hominids behaviorally were more advanced than present day chimpanzees. A steady increase in brain weight has taken place during the last two million years of evolution and peaking with *Homo neanderthalensis* and us, the *Homo sapiens sapiens*. A possible change of the genome responsible for this brain expansion is a successive inactivation of a gene (CMAH) that restricts brain development (Chou *et al.*, 2002). This gene is not active at all in modern humans.

A more precise answer to the question of whether the steady increase in brain weight was accompanied by a parallel development of higher mental functions is still lacking. We can only guess from archeological evidence, primarily from

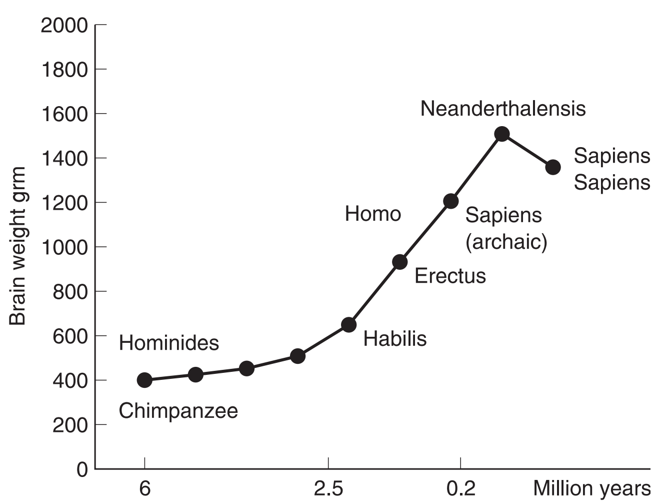

Figure 1.1. Increase of brain weight during the evolution of different hominid species. (Adapted from Jensen, 1996.)

the stone tools our ancestors left behind, what behavior they displayed. If advances in tool-making techniques are taken as indications of intellectual creativity, the progress was very slow during more than two million years (Calvin, 2004). Bilateral symmetric stone tools were invented about 1.6 million years ago, but after that an additional million years followed without much creative advances, at least regarding tool making. Other abilities, like more accurate throwing and better social and communicative skills might, however, have utilized the increasingly heavy brain. Calvin (2004) suggests that vocal communication skills have evolved from the primate one-call-one meaning to protolanguage abilities perhaps a million years ago. Protolanguage is considered to be close to the language of a normal two-year-old child talking with single words and short sentences (Bickerton, 1990). Protolanguage is not limited to a standard set of situation-dependent calls but can handle novel combinations of words. Calvin and Bickerton (2000) suggest that protolanguage developed gradually over a million years with an increase of vocabulary and mimicry, but still with short sentence length. General intelligence and creativity seem, however, not to have improved that much as indicated by the slow progress in tool-making technology. The simple rule that bigger is smarter might thus not be fully applicable to the evolutionary development of the brain.

Archeological and genetic evidence from variations in mitochondrial DNA indicates that the species *Homo sapiens* (meaning the thinking human) has its origin in southeast Africa some 170 000 years ago (Ingman *et al*., 2000). This early (archaic) form of *Homo sapiens* had a slightly smaller brain than the Neanderthals and modern humans. Evidence of modern behavior, like symbolic thinking and creativity, is not present until about 80 000 years ago in Africa and about 40 000 years ago in Europe and other parts of the world that were populated by modern humans or *Homo sapiens sapiens* (meaning the human who knows that he/she knows). The rapid appearance of arts, gems, musical instruments, and advanced bone tools was called the *creative explosion* by Pfeiffer (1982) and is by others referred to as the *specialization event*. Recent excavations in the Blombos Cave in South Africa have revealed evidence of personal ornaments such as a sea shell bead and also ochre stones with engravings of most likely symbolic nature (Figure 1.2; Henshilwood *et al*., 2002, 2004). These artifacts together with advanced bone tools and musical instruments are interpreted as evidence of modern human behavior, including abstract and creative thinking and probably the use of some form of symbolic language with syntax and long and more complicated sentences. The creative explosion does not coincide with any increase in brain weight. The modern cognitive abilities have to be based on a functional reorganization that opened new ways of utilizing the old brain. It is likely that most of the key structures

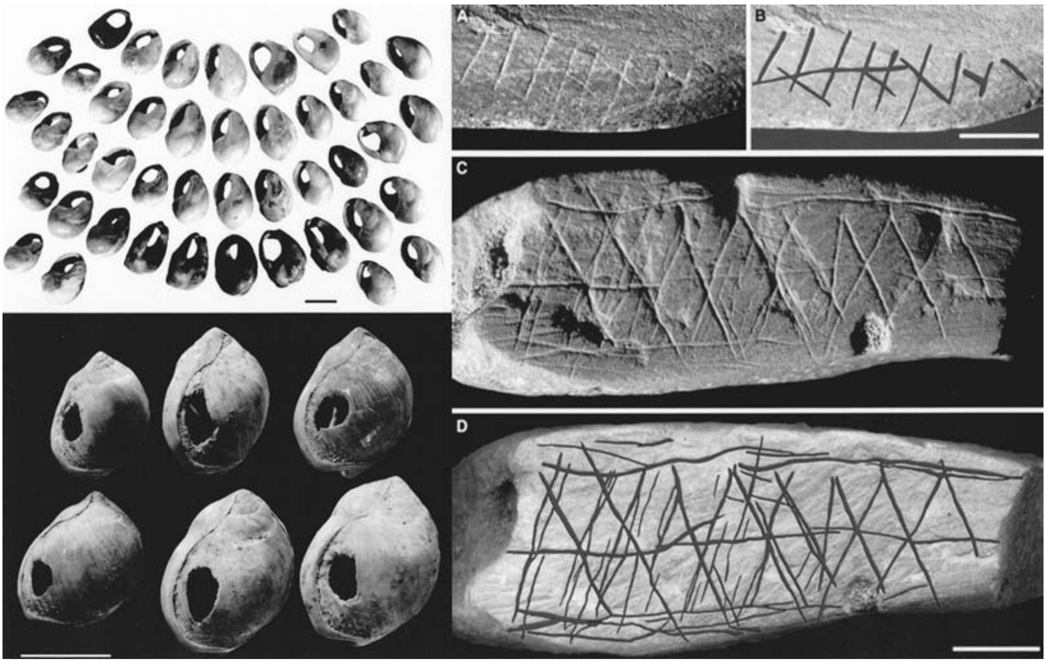

Figure 1.2. Evidence of modern human behavior from excavations in the Blombos cave in South Africa dated to about 77 000 years before present. A sea shell bead is seen to the left and ochre stones with engravings of probably symbolic nature are shown to the right. (From Henshilwood *et al*., 2002, 2004, reprinted with permission.)

linked to this new way of thinking were located in the frontal lobes. It has been suggested that the development of modern thinking and language was coincidental with the evolution of a more functionally lateralized brain (Crow, 1998). I will later return to the question of what functional changes that might have occurred during this recent period of human evolution. There are, however, also definite drawbacks and hazards linked to the possession of a big brain.

3 Disadvantages of possessing a big brain

Is the evolutionary development of the large size human brain a unique experiment by nature? Definitely not, we are all familiar with other big-brained species like the dolphins, and also some birds and fishes have relatively large brains (see Allman, 2000 for a review). The brain of one of them, the elephant-nosed fish, was by Nilsson (1996) found to consume 60% of the oxygen used by the entire body of the fish. This fish needed its big brain for an advanced ultrasound system used to locate the prey in muddy water. The very high nutritional demand of a large brain is one of its most significant disadvantages and regarding the human species it has certainly played a significant role for limiting population growth. In the adult human about 20% of the basal metabolism is used for feeding the brain and in the newborn this percentage is about 60 (Holliday, 1971). The brain is thus a very demanding organ that needs much energy for its development, maintenance, and function. The evolutionary change from a low-energy fruit and vegetables diet to one which is rich in energy and nutrients is considered to be a prerequisite for the development of the large brain. The inclusion of animal and fish meat in the diet, that took place several million years ago, has been linked to brain development (Leonard *et al.*, 2003) as well as the introduction of cooking (Wrangham & Conklin-Brittain, 2003). Raw meat and vegetables were not easy enough to chew and digest for the gracile hominids with their small jaws and digestive systems. Supporters of the water ape hypothesis also point to the advantages of seafood over animal meat regarding contents of essential fatty acids and other nutrients that the brain needs. The ability of humans to accumulate body fat during periods of good nutrition has been suggested to protect the brain from the negative effects of periods of starvation. The accumulation of body fat is likely to be of special importance in early childhood. No other land-living species has young ones who, during their first year, have a body fat percentage of about 25 (Leonard, 2002; Leonard *et al.*, 2003). In their review entitled *Survival of the fattest: fat babies were the key to evolution of the large human brain*, Cunnane and Crawford (2003) speculate about the brain protective value that the body fat of the baby has in periods of malnutrition.

A disadvantage of the large size brain is also a markedly increased risk for damage and disease. The population growth of humanity has until very recent times been strongly limited by a commonly brain-related high mortality during delivery, infancy, and childhood. Mortality during delivery is often directly related to the large head of the fetus with great risk for physical damage to mother and child as well as problems with perfusion and nutrition. Also, in adults, the brain is a very vulnerable organ, as is evident from the high prevalence of different forms of often mortal brain diseases, including disorders like Alzheimer's disease, linked to the expanded human life span.

These were some general facts about the big human brain. We will now focus on the subpart of the brain that is the topic of the present volume: the frontal lobes.

4 Do humans have larger frontal lobes than other primates?

The old "truth" that the frontal lobes of humans are exceptionally large and considerably larger than those of any nonhuman primate has recently been challenged by new investigations using modern brain imaging methods (Semendeferi *et al.*, 2002). The classical studies by Brodmann (1912) and Blinkov and Glezer (1968) seemed to show that the surface of the frontal cortex was 20–30% smaller in the chimpanzee (with a brain that is not considered to have changed much from that of our mutual ancestor). These studies used, however, much less precise methods for the delineation of the boundaries between the lobes than available when using present front-line brain imaging methodology. Semendeferi and coworkers (2002) found the following volume relations between the frontal cortex and the total cortex of the cerebral hemispheres: human 37.7%, chimpanzee 35.4%, gorilla 36.9%, orangutan 37.6%. They thus found no or very small differences between humans and the great African apes regarding the relative volume of the frontal lobes. According to these results the enlargement of the human brain has evolved with a generally preserved relationship between its major lobes.

Accepting that the relative size of the frontal lobes is about the same, some investigators have analyzed if any frontal subpart has been enlarged during human evolution. Another study by Semendeferi and collaborators (2001) focused on Brodmann's area 10, positioned in the most polar prefrontal part of the brain with a crucial role for many advanced human mental abilities, like self-control. This area was found to be of about double the relative size in humans compared to that of nonhuman primates. This opens up for speculations about what happened to the brain when modern behavior was developed. Changes of the functional organization and mode of operation are more likely than any major changes of brain anatomy. One such major organizational change is likely to be a relative enlargement of multimodal association areas in both anterior and posterior parts of the brain in combination with an increase of the relative amount of white matter.

The white matter of the brain has been in the focus of some recent studies of differences in brain anatomy between humans and other primates. Schoenemann and collaborators (2005) used magnetic resonance imaging (MRI) in their study of the brains of 11 primate species measuring gray, white, and total volumes of prefrontal regions as well as the entire brain. They found that the prefrontal white matter shows the largest differences between human and nonhuman primates in contrast to a lack of differences regarding gray matter. These results have, however, been questioned by Sherwood and collaborators (2005) based on problems with the method used to delineate the prefrontal part of the brain. The disputed question is whether the frontal white matter is enlarged more than expected from the well-established relationship between total brain size and relative amount of white matter. A larger brain needs more white matter to support the connectivity between its increased number of neurons.

In a recent study, Schenker *et al.* (2005) subdivided the white matter in gyral and core white matter and found that the human gyral white matter was larger than expected in proportion to the core white matter as well as to the cortex. This might indicate that one of the evolutionary changes in humans is a difference in the way information is processed. An elevated proportion of white to gray matter may facilitate neural transmission with positive effects on, for example, fast learning while an increased ratio of gyral to core white matter might facilitate fast and efficient intrahemispheric processing of information. An increased number of axons and dendrites, together with an increased myelination, might thus provide the advanced connectivity needed for human higher cognitive functions. As discussed above, the absolute size of the brain is not the sole factor that determines its functional efficiency. The reorganization of the brain without enlargement seems to be a very important evolutionary mechanism. Within a constant total brain size have some areas been relatively smaller in humans, like the olfactory bulb and the primary visual cortex (Semendeferi *et al.*, 1998), while others have been enlarged with strengthened connectivity like area 10 and Broca's and Wernicke's areas. That the qualitative features of a brain are more important than its size is further illustrated by the fact that Einstein had a rather small brain (Witelson *et al.*, 1999) and that the recently discovered possibly new human species, *Homo floresiensis*, in spite of a small size brain, shows signs of advanced intelligence, like skillful hunting. The main anatomical feature, that is likely to have made this small brain that bright, is its highly convoluted frontal lobes, with a remarkably large Brodmann area 10 (Falk *et al.*, 2005).

At the cellular level there are findings of recently evolved new types of cells like the spindle neurons. These cells are narrow and elongated and mainly present in the anterior cingulate cortex (Nimchinsky *et al.*, 1995). They are unique to humans and the great apes, but much less common in the latter species (Nimchinsky *et al.*, 1999). Allman and collaborators (2002) suggest that the spindle neurons relay to other parts of the brain, especially to area 10, known to be involved in the retrieval of episodic memories and the planning of adaptive responses. The authors suggest that the evolutionary development of a close interaction between the new spindle neurons and area 10 is crucial for the ability to adapt to changing conditions.

5 Evolutionary advantages of the big brain with its advanced frontal lobes

The evolutionary advantages of a big brain have been debated for several decades. There is a general agreement that changes of the behavior of the hominids have been the force beyond brain development. The fossils do not tell us about behavior – behavior can be studied only indirectly by what our ancestors left behind, for example stone tools and signs of culture like burial graves and cave paintings. The earliest theory, popular until the 1950s, suggested that the expanding brain was needed for tool-making. The fact that the progress in tool-making technology was rather slow during millions of years in spite of an increasing brain weight, led, however, to questioning of the theory. In the 1960s the *Man the Tool Maker* theory was replaced by the *Man the Hunter* theory. Successful hunting of game that is physically larger and stronger than a human, does certainly require a bright mind for planning to outsmart the prey in collaboration with fellow hunters. Calvin (2004) has pointed out the fact that killing by throwing a weapon from a distance is a highly demanding activity, not seen in other species. The synchronized ballistic movements when throwing the spear only take about one eighth of a second to complete with no possibility for correction after the initiation of the throw. During the preparation of such a program of movements hundreds of muscles are engaged and their activity released like preprogrammed fireworks. A large and creative brain is likely to be needed, especially for the frequently novel ballistic movements needed for successful hunting.

Others, like Foley (1987), have argued for the importance of nutritional strategy as a force for the development of the brain. The use of tools and cooking increased the amount of energy that was derived from the nutrition-rich meat needed to support the development of the demanding big brain. Food sharing within the group was an important factor for securing nutritional requirements. Such social abilities are today considered to be the main evolutionary force beyond brain development.

Socializing is a very important part of the behavior of primates in general but has reached exceptionally high levels of complexity in humans. Archeological evidence indicates that the change of social activities with work and food sharing is coincidental with the appearance of the *Homo* lineage (Isaac, 1978). This new behavioral pattern could work only in conjunction with the use of tools. The slaughtering of big animals was made possible by the use of proper tools with collaborative efforts also including the transportation of the meat to the homestead for safe sharing. The social demands that are linked to work and food sharing are by Glynn Isaac and others considered to be the most essential factor beyond the development of the human brain and its intelligence. It created a nutritional dependence within the group, a dependence that might have caused a selective pressure favoring collaborative abilities and empathic and altruistic actions. Such abilities strengthened the social bands within the group. There was most likely also a strong selective pressure that favored the ability to plan and calculate and not the least to communicate. Exchanges of experiences are of much more importance for a collaborating group of hominids than for species with more individual methods for providing nutrition. The smoothly collaborating and communicating group had thus a very significant advantage. The strong selective pressure for efficient communication made us develop oral speech.

6 Language evolution

Many mental abilities may be listed when discussing the factors that make us different from other species but our symbolic language stands out as the most important. In its oral and written forms, language is the main tool for exchange and accumulation of knowledge within and in between individuals and generations. The child's innate capacity to learn the sounds, words, sentences, and syntax of the language spoken in its environment is strikingly different from the total inability of a young chimpanzee, even when fostered in a human family, to imitate or utter anything but the simple sounds and calls of wild chimpanzees (Arcadi, 2000). Interestingly, chimpanzees raised in a human environment might learn sign language and both initiate and maintain conversations with their interlocutor using hand movements (Jensvold & Gardner, 2000; Bodamer & Gardner, 2002). The lack of voluntary control of the facial muscles makes it, however, impossible for the chimpanzee to accompany the hand signs with mimicry, which is an important companion of human sign language.

Premack (2004) points out that many species are able to copy someone's choice of an object. A second and more advanced level of imitation is for the observer to copy the model's motor action. To do this a mental representation of the visually perceived action has to be formed and an action conforming to the perceived one must be produced. This is an easy task for young humans but impossible for other species. The unique ability of humans to imitate sounds and motor acts is probably one of the frontally based abilities required for language. The mirror neurons are the likely neuronal basis for this ability. These neurons are active during watching someone moving as well as during the performance (imitation) of the same movement (Rizzolatti & Arbib, 1998). Their presence in the area that is homologous to the Broca's area in nonhuman primates has made these neurons very likely to be linked to the development of human language. There is also evidence that this area is involved in a gestural mirror neuron system in humans (Nishitani & Hari, 2000).

Another unique human ability that Premark (2004) points out is teaching. Teaching is the reverse of imitation. In imitation the novice observes the expert while in teaching the expert observes the novice and also judges the performance and tries to modify it (Premack & Premack, 2003). Imitation thus produces a rough copy, which is subsequently modified and smoothed by the teacher. A chimpanzee mother never teaches her infant anything. The infant observes and imitates but the mother never returns any response to the failure or success of the imitation. This uniquely human ability to teach, likely based on frontal lobe processes, helps to explain why it might take several years for an animal to acquire a new technology, learned by a human child in a short time. When it comes to learning the mother tongue language, adults teach the children words, but not grammar. The evolution of language has thus most likely required the development of the teaching ability.

Human communication is intentional with the goal to inform the listener and to correct the receiver if the information does not result in the action intended. There is no evidence indicating that any nonhuman primates are able to correct errant listeners. Their communication is thus not intentional. Only one-way information is given about, for example, a threat in the immediate environment. Language-trained chimpanzees can learn a few hundred words but all words are based on their sensory experiences. Metaphors or abstract words, like time, cannot be sensed, and cannot be learned by a chimpanzee (Premack, 2004). Human language is thus recursive while other species use nonrecursive ways of communication. Recursive communication requires the frontally based ability to get insight into the mental life of others. Social abilities like mentalizing or theory of mind are thus closely linked to the development of the human language.

7 When and how did human higher intellectual functions evolve?

Traditionally it is assumed that syntax and other features of our ability to communicate evolved through an interaction between culture and genes. Syntax made long and complicated thoughts possible, which were the basis for creativity and innovations appearing at the time of the creative explosion some 50 000 years ago. It made it possible for us to structure our experiences. As pointed out by Calvin (2004) we have a remarkable ability to discover patterns and rules embedded in what we experience, to see hidden patterns in seeming chaos. This is most likely one of the keystone abilities that makes the child able to grasp the words and syntax of the language spoken in its environment. Structuring made it possible to think a long train of connected thoughts, to think about the past and to speculate about the future. How was the mental life of *Homo sapiens* before the creative explosion? It is very difficult for us to imagine a less rich mental life than what we have. We can, however, learn a lot from cases like the 11-year-old boy described by Oliver Sacks (1989), who was considered to be mentally retarded but turned out to be deaf. He was able to learn sign language, which made it possible for Sacks to interview and test him. The boy had no problems with perceptual categorizations or generalizations but seemed unable to hold