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Brain Evolution, Innovation, and Endocranial Variations in Fossil Hominids

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ABSTRACT

The archaeological record provides compelling evidence that human artifacts became more and more sophisticated over time. The ability to innovate is therefore assumed to be a trait already present in our ancestors. Prehistoric artifacts give us some indirect insight into the cognitive capacities of their respective makers. Additionally, variations in endocranial morphology explain changes in the spatial organization of the neural mass. Neuropsychological research has significantly enhanced our understanding of how and where mental abilities are realized in our contemporary brains. Increasingly sensitive brain imaging techniques and adept experimental designs support the development and verification of biologically plausible models of cognitive processing for complex behavior such as creative thinking. In addition, primatology studies elucidate similarities and differences in the mental capacities between us and our closest living relatives. In combination, findings from the archaeological and the fossil record and our understanding of the capacities of present-day human and non-human primates allow us to detect and interpret gradual evolutionary changes in the human brain, which were potentially crucial for the development of specific mental processes. With regards to capacities associated with creativity, modifications within frontal, parietal, and cerebellar areas, as well as changes in the relationships between these areas and in hemispheric asymmetry are of particular interest. This article presents recent findings of this interdisciplinary approach and also draws attention to methodological limits and the many uncertainties that currently remain. Additionally, the possible link of innovative thought with changes in the human life-history pattern is discussed, namely the emergence of rather distinct stages of childhood and adolescence, which may play a major role for the surge of cultural transmission in our species.

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INTRODUCTION

One of the most fascinating human traits is the ability to innovate. Stone tool cultures can be dated back about 2.5 million years (Semaw et al. 1997), and the archaeological record provides a compelling account of the increasing sophistication of human artifacts. While some scholars interpret the archaeological relics as evidence for a gradual increase in sophistication in tool-making, many regard the transition from the Middle to the Upper Paleolithic as an important milestone in human evolution (Wurz 2002). In southern Africa this period, dated to around 80–70 ka, marked the onset of composite tools made from a combination of different components, the import of raw materials from distant sources (Minichillo 2006), and intentional ornamental work (Henshilwood et al. 2002).

This apparent rise in innovative abilities was almost certainly paralleled by an increase in cognitive capacities. Unfortunately, the mental abilities required to produce a certain artifact are rarely self-evident. Wynn and Coolidge (2009) pointed out that proposals concerning the nature and timing of the evolution of modern cognition must be both archaeologically credible as well as cognitively valid—found relics must be reliably identified and placed appropriately in time and space and the cognitive requirements ascribed to their making or use must be recognized or defined by the cognitive sciences.

Hypotheses on cognitive evolution should also be paleoneurologically plausible. Unfortunately, the fossil record is in many respects too scarce to allow for irrefutable verifications. Also, neural variations need not be associated with changes in the endocranial morphology, and conversely, morphological changes may merely reflect

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biomechanical adjustments of cranial architecture that do not coincide with functional neuroanatomic modifications (Bruner 2007). Nevertheless, paleoneurological findings can assist in the testing of cognitive hypotheses. Whenever possible, proposals concerning the evolution of cognitive processes should therefore rely upon the integration of evidence from comparative anatomy and the fossil record.

Cognitive neuroscience has begun to unravel the neural processes underlying mental achievements, which can be observed in present-day humans (and, to some extent, in other contemporary species). In our view, the integration between current neuroscientific approaches and archaeological evidences supplies intriguing directions for future research, providing tools for a "neuroarchaeology of mind" based on the reciprocal exchange between brain and culture (Malafouris and Renfrew 2008). The ever more sensitive brain imaging techniques and adept experimental designs allow us to observe the interplay of neural clusters in the brains of individuals performing a great variety of tasks. Such investigations have made possible the development and verification of models of cognitive processes involved in complex behaviors such as creative thinking. While there is no overall consensus in cognitive neuroscience about exactly how modular the brain really is, functional specialization of cortical and sub-cortical tissue is evident from a plethora of patient and neuroimaging studies. It is, for example, a well-established fact that executive functions such as the ability to plan, to choose between good and bad actions, or to determine similarities and differences between things or events are associated with activity of the prefrontal cortex (Ardila 2008). Only with this appreciation of what constitutes different aspects of thinking in a modern brain and what neural tissues are involved in their respective realization can we develop sound hypotheses about the phylogenetic history of mental capacities.

THE FRAMEWORK OF INNOVATIVE THINKING

NEUROPSYCHOLOGY AND NEUROANATOMY

In psychology, creative thinking is usually broken down into two major stages, which Guilford (1950) had labelled, respectively, divergent and convergent thinking—the former describes the generation of novel ideas from a given starting point, the latter the ability to bring together available information to solve a particular problem. Modern-day creativity techniques often base on this stage-two approach of linking previously unrelated ideas (Kyriacou 2009). De Beaune (2009) argues that also in the Neolithic new tools had resulted from a combination of pre-existing elements:

> "They were made possible by the fusion of two different technical actions, by the combination of a familiar action with a tool traditionally used for other purposes, or by the combination of a familiar tool with a new worked material."

Self-reports of contemporary thinkers support this notion, that recombination is a crucial feature in creative thinking, e.g., Albert Einstein argued that "combinatory play" was "the essential feature in creative thought generation" (West 1997).

The disentangling of creative processes in a laboratory setting allows researchers to overcome the methodological constraints of introspective reports—tasks can be designed to assess divergent or convergent thinking selectively and neuroimaging techniques can reveal the areas of the brain in which neural networks are recruited during these processes. Divergent thinking tasks are frequently designed in such a way that there is no pre-defined number of possible solutions. A well-established test is the Unusual Uses Task (Guilford et al. 1978; Torrance 1966) in which participants are requested to think of unusual uses for a common object such as a brick or a cardboard box. Answers can be assessed with respect to fluency (the number of suggested uses), cognitive flexibility (the number of different types of uses, e.g., using a cardboard box as a container versus as a platform) and originality (the infrequency of a suggested solution). Such ratings can be compared with personality traits and there are findings that suggest that divergent thinking correlates with openness to experience (McCrae 1987) but also with proneness to psychosis (Leonhard and Brugger 1998; Woody and Claridge 1977).

Mednick's (1958) Remote Associates Test is frequently used to assess convergent thinking. Participants are given three words which have no obvious relationship, e.g., board, magic, death. The task is to find a fourth word for which a link to every one of the given items can be made (here: black). The task naturally involves an initial phase of divergent thinking during which possible solutions are generated. In the subsequent convergent thinking phase, these candidate items then need to be checked against the task requirements. Typically, solving a problem involves iterations of divergent and convergent thinking as initially devised candidates will often need to be discarded.

Neural activity of individuals accomplishing tasks such as the Unusual Uses or the Remote Associates Test can be observed using imaging techniques. Typically, activation patterns between creative and non-creative tasks or between highly and less creative individuals are compared. For the Unusual Uses Task, Carlsson, Wendt, and Risberg (2000) had found that only highly creative individuals showed a bilateral increase of frontal activity. For less creative individuals, the activation was confined to the left hemisphere. A similar pattern was found by Howard-Jones et al. (2005) using a divergent thinking task in which participants were asked to generate stories from sets of three words. Half of these word triplets were semantically related (magician, trick, rabbit). In the other sets, the words bore no obvious relation to each other (e.g., flea, sing, sword). In addition, participants were asked to either be creative or be non-creative in their plot generation. The stories were later assessed for creativity by external examiners. Non-obviously related stimuli and the instruction to be creative both enhanced creativity ratings. Their measurements revealed that neural clusters in the middle frontal gyrus of the right hemisphere showed highest activation when participants were asked to invent creative stories based on non-related words.

Neural clusters in the right hemisphere also are recruited during convergent thinking tasks. Jung-Beeman et al. (2004) used the Remote Associates Test in conjunction with functional magnetic resonance imaging and electroencephalography in the search for neural correlates of insight. Problems such as those posed by the Remote Associates Test frequently trigger a "eureka moment" when participants find the correct solution. The researchers compared the signals of those items where participants perceived such a moment of insight to those items where this subjective feeling did not occur. Differences between the two conditions were most pronounced in the right anterior superior temporal gyrus, a fold in the upper part of the temporal lobe. The fact that these tests predominantly triggered networks located in the right side of the brain is in line with an increasing body of evidence, which suggests that the two hemispheres have adopted different strategies to meaningfully integrate novel information.

MacNeilage et al. (2009) propose that functional specialization of the hemispheres was already present in its basic form when vertebrates emerged about 500 million years ago and refer to a broad variety of only very remotely related species to back up their hypothesis. In their view, the left hemisphere was originally specialized for the control of well-established patterns of behavior under ordinary circumstances, whereas the right hemisphere became dominant in detecting and responding to unexpected environmental stimuli. The right hemisphere, they propose, took primary control in potentially dangerous situations and thus is the seat of environmentally driven bottom-up control. The left hemisphere on the other hand dominates in self-motivated behavior. Tucker and Williamson (1984) suggested that interhemispheric functional differences in humans can be explained by the fact that the two hemispheres are part of different neurotransmitter systems. According to their findings, the left hemisphere is under dopamine influence, resulting in superior motor control, whereas the right hemisphere is conditioned by adrenaline levels, which maintain alertness, and is thus more oriented towards novel information.

Rodel et al. (1992) demonstrated that participants recognized links between semantically closely related word pairs (fruit - apple) more easily if these were presented to the left hemisphere (via presentation to the right visual field). For semantically more distantly related concepts (sleep - death) however, performance was better when the stimuli were displayed in the left visual field (and hence projected to right hemisphere). Similarly, Kiefer et al. (1998) found that in a primed lexical decision task, effects of semantically distant primes could only be observed in the right hemisphere. Federmeier and Kutas (1999) found that the two hemispheres also differed in reacting to semantically anomalous sentences. They made subjects read sentences for which the last word met or did not meet expectations built up from the beginning of the sentence. They used three types of stimuli to finish a sentence—the expected word, an unexpected word of the same semantic category as the expected word, or a word of an unexpected category (The knight in shining armour drew his sword / blade / pay). The researchers analyzed the so-called N400 responses, a negative deflection in voltage at around 400 milliseconds after stimulus presentation, which has been established as a reliable marker of a surprise reaction. The researchers found that N400 signals were larger for words of an unexpected category than for unexpected words of an expected category in the left but not in the right hemisphere. Federmeier and Kutas concluded that the left hemisphere's processing of context is predictive, while right hemisphere processing is integrative. The right hemisphere thus seems superior in building new links between concepts and events.

The specialization of the two hemispheres may be not just advantageous but inevitable for a normal functioning of the human brain. Crow (1997, 2004) suggested that a failure to develop hemispheric dominance for language could be an underlying cause of schizophrenia. Distortions in interhemispheric processing have furthermore been linked to schizophrenia-like thought patterns in healthy individuals. Leonhard and Brugger (1998) proposed that thought disorder was triggered by a loosening of associations, which in turn was due to a lack of inhibition of right-hemispheric processing by the left hemisphere. Conversely, a healthy brain provides the necessary capacities to both creatively form novel links between existing concepts as well as to "reality-check" these ideas against the given context of the problem to solve. It is this combination of divergent and convergent thinking ability that presumably made us great tool-makers. These thinking styles are both presumably the result of widespread and diffused neural networks, and involve fine-tuning between perceptive and integrative areas.

In this context, investigations regarding the gross anatomy and morphometrics of specific, localized brain areas are of particular interest. Dorsolateral and orbital prefrontal areas are associated with executive functions including metacognitive as well as emotional/motivational processes and have been extensively researched (Ardila 2008). Somewhat less attention has been paid in neuroanatomy to the posterior parietal areas, which are indeed associated with functions supporting creative processes. The upper parietal lobules are associated with integration of external (mostly visual) and proprioceptive signals (Andersen et al. 1997; Mountcastle 1995; Wardak et al. 2005). They recruit different co-ordinate frames, filter the recognized spatial environment by ranking its components, and interact between attentional and intentional responses (Andersen and Buneo 2002; Freedman and Assad 2006; Gottlieb et al. 1998; Rushworth et al. 2001). Consequently, the upper parietal areas (including the intraparietal sulcus) provide an inner image of the perceived reality, and of the relationships between its components. This image is context-dependent, associated with conceptual representations of the objects, of the neighbouring spatial environment, and of the presence/integration of the own body within it. These parietal representations of the immediate environment provide an inner virtual reality, in which objects can be mentally manipulated and thereby potentially brought to new use. Such processes link the potential to generate a spatial model directly with the concept of simulation. Notably, the parietal lobes also are deeply involved in hand-eye coordination (Battaglia-Mayer et al. 2006), and the intraparietal area has been demonstrated to be directly involved in tool manipulation (Stout and Chaminade 2007). This recruiting of networks involved in motor actions presumably reflects a crucial aspect of our evolutionary development. In early human species innovation was most probably firmly grounded in the material world (for discussions see Boivin 2004; Iriki and Osamu 2008), and early tool use was presumably a crucial trigger for the explosion of human intellectual abilities. It is worth noting that recently the same cortical areas also have been related to the perception and assessment of beauty (Cela-Conde et al. 2009) and to numerical processing (Ansari 2008; Cantlon et al. 2006) again suggesting involvement beyond the realms of simple spatial tasks.

Another area involved in our versatile ability to merely imagine the manipulation of objects is the cerebellum. The human cerebellum has been found to display pronounced functional modularity (Imamizu et al. 2003) and it plays a crucial role in a network that acts as a simulator of motor actions. It anticipates the result of signals to muscles without actual input from the motor system and, through training, is able to fine-tune itself by comparing predictions to actual outcomes of motor actions. This ability is a prerequisite for precision throwing, a skill which is far more advanced in humans than in the other primate species. Knapping and throwing are both high-precision actions, which led Gärdenfors (2003) to suggest that hominids needed to master throwing before they were able to form stone tools. In part, our advanced throwing skills can be explained by evolutionary changes in the shoulder section. However, neural reorganization also must have been a prerequisite.

We interpret evidence in the fossil record for gradual changes over time in the relationships between the frontal, parietal, and cerebellar areas as a strong indication for changes in the mental capacities associated with creativity.

COMPARATIVE APPROACHES

In primates, innovation is more frequent in males, adults, low rank individuals, and mostly associated with foraging (Reader and Laland 2001). At least one captivity-born bonobo is said to have developed individual flaking techniques (Schick et al. 1999) and an orang-utan has been successfully trained to detach a flake from a pre-shaped flint core (Wright 1972). Furthermore, it is known that chimpanzees in the wild prepare leaves or small branches to catch termites or to fish for honey (Boesch and Boesch 1990; Goodall 2000). Using stones to crack open nuts has been observed in numerous wild populations and one group observed by Boesch and Boesch (1990) used clubs and sticks in combination. Recent findings by archaeologists investigating primate artifacts suggest that such behavior dates back at least several millennia (Mercader et al. 2007). Moreover, chimpanzees can be trained to retrieve food rewards from devices that provide two different dispensing mechanisms and an animal who detects either solution to obtain food is likely to pass the principle on to conspecifics (Whiten et al. 2005), thus providing evidence of social learning in an innovative context. Despite of all these examples, which indicate that tool use is not at all foreign to our closest cousins, they do not seem to have developed more than marginal capacities to use tools in novel contexts or to further develop the characteristics of an artifact through any form of recombination. Importantly, there is no compelling evidence that they use tools to make tools. The available data indicate that such second-order tool use to be a uniquely human capability. Kitahara-Frisch (1993) suggested two reasons for this—a lack of necessity in other primate species to obtain food by complex means and a limitation in planning to the immediate presence. Wild chimpanzees do prepare twigs to use them as rods to fish for ants, extract sap from oil-palm trees using parts of leaves as, respectively, pestles and sponges, or crack open panda nuts using stones. Tool-making and use however seems restricted to a context with a prompt dietary reward (note however the report by Orvath 2009, of a zoo chimpanzee who would pile stones to throw them at visitors at a later point in time; importantly, the individual does not seem to be in an overt state of arousal while gathering missiles). Conversely, early hominids seemed to have profited from an apparent ability to foresee non-immediate rewards. Producing stone flakes allowed them to later sharpen the ends of sticks to dig up roots or to detach meat from animal carcasses.

These differences in innovative abilities are almost certainly linked to anatomic differences of the brain. It is well established that the human cerebral cortex is much larger in relation to body size than that of other primates. Furthermore, in absolute terms, the frontal lobes of humans are about twice the size of those of orang-utans and about five to six times the size of those of chimpanzees (Deacon 1997). However, the volume of the frontal lobes in modern humans corresponds to that expected for an ape of similar brain size (Semendeferi et al. 2002). Nevertheless, spatial differences between modern humans and apes can be recognized in many different cerebral areas (Aldridge 2010). Ontogenetically, the most striking dissimilarity is the marked bulging of the parietal surface in the early postnatal period in *Homo sapiens* (Neubauer et al. 2010).

Conversely, hemispheric asymmetry is not an entirely human trait. Indeed, a certain degree of dissimilarity between the hemispheres has been observed in a number of vertebrates and even invertebrates (Levin 2005). Support for evidence of hemispheric specialization in our closest relatives, the great apes, has been suggested with considerable consistency. They show gross anterior and posterior brain asymmetry to a certain extent, even if rarely in combination, like in the human brain (Holloway and De La Costelareymondie 1982). There also is some evidence of hemispheric specialization in the equivalent of Broca's area (Cantalupo and Hopkins 2001) and at the temporal plane (Geschwind and Galaburda 1985) in the great apes.

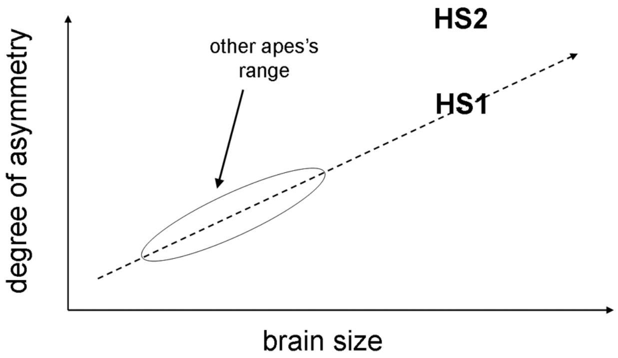

Figure 1. For cerebral asymmetry associated with Homo sapiens *we cannot currently ascertain whether its degree of expression is expected considering the group-specific allometric trajectories (HS1), or if modern humans exceed the figure expected for their large brain size (HS2).*

However, such findings may have to be treated with some caution, as a recent large-scale study questions the rigidity of former claims of volumetric asymmetries in the human Broca's area (Keller et al. 2009). The authors argue that "asymmetry of Broca's area has not been reproducibly demonstrated, particularly on a gross morphological level." On the cytoarchitectural level, findings of observable asymmetries seem less controversial and appear to be uniquely human, specifically radial cell structures of the temporal lobes are more densely packed in the right hemisphere (Buxhoeveden and Casanova 2000).

As mentioned, Tucker and Williamson (1984) explained interhemispheric functional differences by differences in the respective neurotransmitter systems of the hemispheres. To our knowledge, there are unfortunately no directly comparable data on neurotransmitter metabolism in apes available. However, the respective neurobiological systems must share properties at large as no receptors or proteins have been found in the human brain that do not also exist in the chimpanzee brain and many key neurotransmitter receptors are sequenced similarly in humans and chimps (Previc 1999).

THE PALEONEUROLOGICAL EVIDENCE

Considering the cerebral districts involved in functions related to innovation, the paleoneurological record provides information for at least three areas of interest—the cerebral asymmetries, the morphology of the frontal lobe, and the evolution of the parietal cortex. Information about cerebellar morphology, another area of interest, is unfortunately hardly available from the fossil record.

The early paleoneurological approaches have been historically biased by two main factors. The first is intrinsic to paleontology—the scarce and fragmented fossil record always hampers the recognition of the actual extinct variability, and even more the application of robust statistical procedures. The second is associated with the epistemological linearity of many past morphometric approaches—analyses often were restricted to the absence/presence or measure of single features, without taking into account the relationships between and within anatomical components. Supported by computer modelling and multivariate statistical tools, concepts like allometry, morphological integration, and modularity, are becoming increasingly important for advancing inferences on the evolutionary variations (Bruner 2007).

The neurocranial morphology is the result of several different structural and functional interactions between soft and hard tissue, which complicate (or even render useless) the distinction between causes and consequences. In this context, the main aim of paleoneurological studies should be the separation of those morphological variations associated with adjustments of the anatomical system (like constraints and consequences secondarily involving neutral brain changes) from those directly related to neural adaptations. Following the criterion of parsimony, only when explanations based on structural cranial rearrangements can be excluded, may the possibility of adaptive neural changes be seriously considered. With regards to neural systems, such adaptive changes may involve cognition.

HEMISPHERIC ASYMMETRY

The cerebral torque has been hypothesized to be a hallmark of modern humans, associated with the evolution of language and with the genesis of psychotic disorders (e.g., Chance and Crow 2007). As mentioned, although volumetric asymmetries at the frontal and occipital areas also can be frequently detected in chimps and gorillas (Holloway and De La Costelareymondie 1982), it seems that their prevalence, degree, and, most of all, their antero-posterior combination, are very limited when compared to modern humans. The fossil record is too fragmented to support robust statistical models, but it can be affirmed that a certain degree of endocranial asymmetry is displayed in almost every extinct species of the genus *Homo* (Grimaud-Hervé 1997; Holloway 1980, 1981). Unfortunately, the fossil data also are blurred by diagenetic distortions of the specimens, which often make the interpretation of minor asymmetries impossible or unreliable. In any case, the most limiting factor associated with paleontological inference on the evolution of hemispheric specialization is the scarce knowledge about the allometric patterns of variation associated with endocranial asymmetries—the larger the brain, the more evident the asymmetries, and we presently lack data available on the allometric expression of these traits (Figure 1). That is, we cannot know whether or not humans have a predicted degree of asymmetry on the basis of their cranial capacity, which is three times larger than that of the other great apes, and three times larger than the figure predicted by their body size. In this case, the quantitative gap between the extant taxa (chimps and gorillas versus modern humans) makes any hypothesis even more speculative, considering the very small metric differences and the problems in applying statistical regression approaches to discontinuous ranges of variation. Consequently, any com-

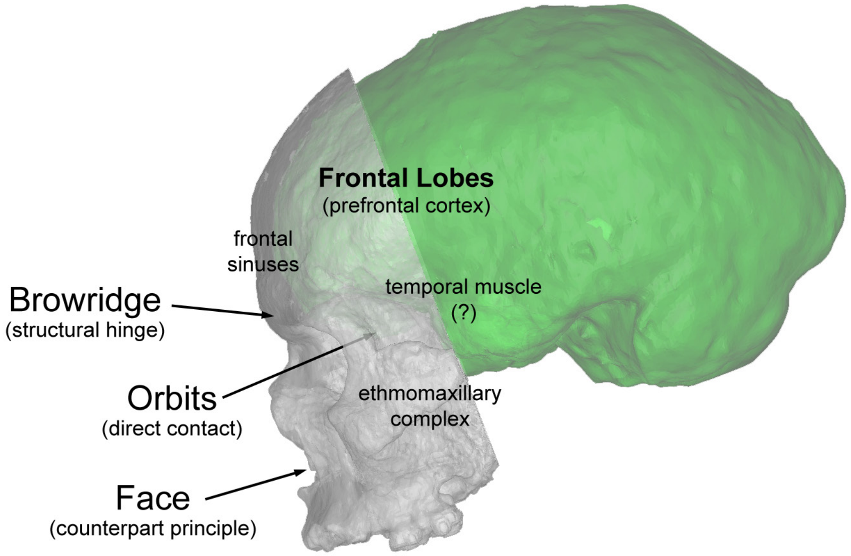

Figure 2. The frontal lobes (in particular, the prefrontal areas) are housed in the anterior cranial fossa, which morphogenesis is associated with a complex functional and structural system formed by hard and soft tissues. Morphological changes must be interpreted within these relationships, which are far from being adequately described even for modern human populations. Here, some non-neural components which may have some influence on the morphology of the anterior cranial fossa, shown on the digital reconstruction of Mladeč 1 skull and endocast. Morphological integration is the result of reciprocal relationships, in which each component may directly or indirectly influence each other.

ment on the degree of cerebral asymmetries in extant or extinct humans is useless if this basic information is ignored. So, at present we may just recognize that some morphological differences between right and left hemispheres can be observed in the extant apes, and that the human fossil record does not show marked differences from the modern human variation.

It is worth noting that the crude concept of morphological asymmetry may even be misleading. Asymmetry in histology, biochemistry, or metabolism is well definable. On the other hand "asymmetry" in the hemispheric gross anatomy is a very general concept, which lacks a generally accepted definition. Morphological asymmetries are caused by differential growth and development of the two hemispheres. In terms of biomechanics, this involves a redistribution of the strains along the neurons, and most of all against the falx cerebri, the sickle-like fold of dura mater which descends vertically in the fissure between the cerebral hemispheres. Neural biomechanics are a very recent area of investigation (e.g., Hilgetag and Barbas 2005; Toro and Burnod 2005; Van Essen 1997), and we presently ignore the factors leading to the differential spatial allocation of the neural masses, such as cellular proliferation, cellular growth, tissue density, and biomechanical interaction with the surrounding hard and soft endocranial elements.

THE FRONTAL LOBES

The frontal lobes have always received much attention because of their hypothesized association with "higher" cognitive functions. There is a general agreement that the current gross morphology of Broca's area can be described in fossils possibly associated with the earliest human species, about two million years ago (Holloway 1995). Such specimens (like KNM-ER1470, formerly included in the hypodigm of *H. habilis*) are, however, not unambiguously recognized as belonging to the human lineage (Wood and Collard 1999).

The prefrontal areas are encapsulated in the anterior cranial fossa, the morphogenesis of which is fairly passive for its upper components (associated with brain pressure and connective tensors), but more complex at its base (Enlow 1990; Moss and Young 1960). The structural and functional network influencing the morphology of the anterior fossa (both in terms of ontogeny and phylogeny) includes the browridge, the orbits, the middle face, and possibly the temporal muscle (Figure 2). Accordingly, the morphological variations of the frontal lobes are the result of a mixture of different components, reciprocally influencing each other (Figure 3). Some changes are merely topological, changing the spatial relationship between the neurocranial and the facial structures without affecting the morphology of the single components (e.g., Bruner and Manzi 2005). Other variations are structural adjustments to maintain the biomechanical balance (such as those at the browridge; Lieberman 2000; Shea 1985; Weidenreich 1941). Some differences are size-related, being the results of the allometric relationships within the anatomical system. Additionally, some differences can be associated with actual changes of the neural organization. Of course, this complex morphogenetic system demands caution when dealing with infer-

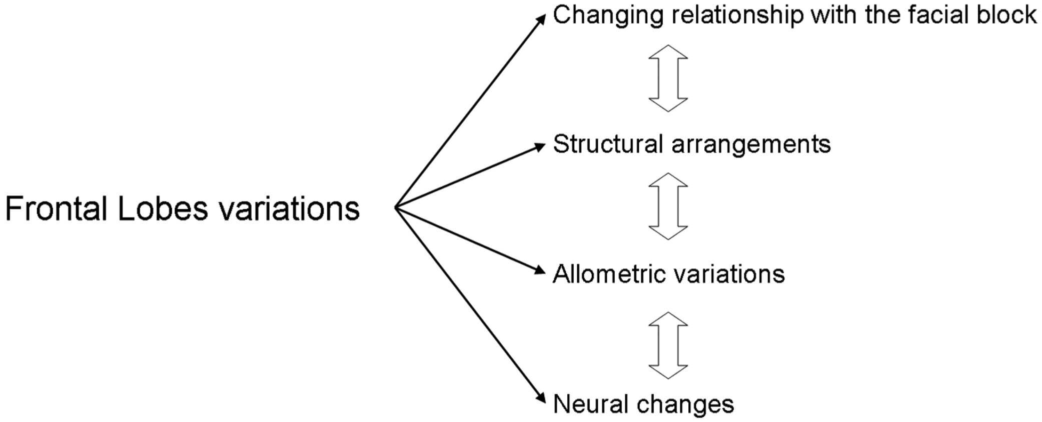

Figure 3. The morphological changes of the anterior cranial fossa are the final results of different factors including spatial variations, functional adaptations, and structural consequences. Of course, within the anatomical systems causes and consequences are confused into a biological network based on feedbacks and reciprocal influences, making any linear interpretation of these processes rather useless, if not misleading.

ences on single traits or on specific and localized anatomical variations at the anterior cranial fossa.

Nonetheless, some raw and naïve metrics do provide interesting cues. A general observation of *Homo* endocasts provides a basic conclusion—larger brains have relatively wider frontal lobes (i.e., a more squared appearance in the dorsal view), while smaller specimens have relatively narrower frontal lobes (i.e., more convergent lateral walls of the anterior fossa). This dichotomy allows us to separate *Homo ergaster/erectus* (relatively narrow frontal lobes) from *H. sapiens* and *H. neanderthalensis* (relatively wider frontal lobes) (Bruner 2004).

A preferential lateral allocation of the frontal neural mass in the most encephalized human species can be interpreted as the result of the cranial functional matrix. On one side, the orbit frontation and the reduction of the temporal muscle in hominids produced a lateral opportunity for the expansion of the anterior brain volumes, at least in terms of space availability. At the same time the frontal lobes lie directly behind or right on top of the orbital roof in humans, and, in any case, the morphogenesis of the anterior fossa is strongly constrained by structural relationships with the facial block (Enlow 1990). This anatomical constraint limits the vertical development of the frontal brain mass (accordingly, the anterior mid-sagittal endocranial profile has been rather stable since the Middle Pleistocene; Bookstein et al. 1999). Together, these two factors may explain the relative widening of the frontal lobes in large-brained human species—increasing brain size and neural mass is better accommodated laterally at the anterior fossa than superiorly.

Although this may be interpreted as a general allometric trend of the human cranial architecture, the alternative hypothesis must also be considered—a phylogenetic non-allometric influence on the frontal lobe morphology, associated with some specific neural adaptation. Evidence supporting this hypothesis exists—brain size in the Ceprano skull (European Early/Middle Pleistocene) and in Saccopastore 1 (European Middle/Late Pleistocene) is similar, but the first specimen shows a clear frontal narrowing similar to the small-brained taxa (Bruner and Manzi 2005, 2007) and the second specimen shows a definite frontal widening similar to the largest Neandertals (Bruner and Manzi 2008). Hence, although sharing a similar cranial capacity, the first endocast exhibits an "archaic" frontal narrowing, the second a "derived" frontal enlargement. Because they represent different phylogenetic contexts (*H. antecessor/heidelbergensis* vs *H. neanderthalensis*), it must be assumed that the differences at the frontal lobes are not strictly allometric, but associated with specific evolutionary changes. Needless to say, two specimens alone do not provide sufficient statistical robustness for such inferences. However, recent allometric analyses support this hypothesis on a quantitative ground (Bruner and Holloway 2010)—both modern humans and Neandertals display wider frontal lobes than expected according to the pattern described for archaic and less encephalized human species.

A final remark has to be provided regarding the difference between allometric and non allometric changes (see Gould 1966). A departure from the expected allometric trend may be associated with a specific adaptation or with a structural arrangement to avoid functional constraints. Alternatively, allometric changes could represent passive consequences, but also brand-new evolutionary potentiality (exaptations). In the case of the frontal lobes, for example, even a "simple" allometric enlargement can be involved in threshold effects and emergent functions associated with the geometrical properties of the neural connectivity. In this sense, the interpretation of allometry as an opposite to adaptation is too strict, and scarcely useful in the context of the functional and structural network leading to selection and evolution.

It must, however, be stressed that neural variations do not necessarily match gross morphological changes, and it is clear that the frontal lobes also underwent evolutionary changes in white/grey matter proportions and gyrification (Rilling 2006) which cannot be revealed by the endocranial morphology alone.

THE FRONTO-PARIETAL NETWORK

The upper parietal areas have been hypothesised to have undergone a species-specific enlargement in large-brained human species (Bruner 2004, 2008; Bruner et al. 2003). Neandertals show only a lateral widening of the parietal surfaces when compared to more archaic human species, while modern humans display a general enlargement of the whole parietal volumes. Although such variations can be related to general rearrangements of the cranial architecture, there is evidence suggesting that the upper parietal lobule and the intraparietal sulcus may be directly involved in these differences (Bruner 2010). Such bulging of the parietal surface is achieved in the early post-natal period in modern humans (Neubauer et al. 2009), through a morphogenetic process which is absent in chimps (Neubauer et al. 2010) and Neandertals (Gunz et al. 2010). The upper parietal cortex is involved in selecting saliency information from the environment, generating an outer reference of coordinates with these data, matching this outer reality with an inner reference of coordinates (the self, mainly based onto the head, eyes, and shoulder position), and providing interactions between the inner and outer perception (mainly through the eye-hand coordination; see Bruner 2010 for a review on these topics). As already evidenced, this may allow mental experiments, including those cognitive steps necessary to plan a tool, which is necessary to construct another tool. This higher-order tool use also involves the capability to mentally decompose an object into components, or conversely to combine different components from different contexts to form a novel object.

The intraparietal sulcus is an interesting area of evolutionary and cytological discontinuity (Orban et al. 2005; Vanduffel et al. 2002). In contrast, the upper parietal areas show a certain continuity with the occipital lobes (see Ebeling and Steinmetz 1995; Eidelberg and Galaburda 1984), in accordance with the importance of vision in processing environmental information. But most of all the upper parietal areas are characterized by a very developed system of cortico-cortical connections with the dorsal prefrontal volumes (Battaglia-Mayer and Caminiti 2002; Battaglia-Mayer et al. 2006; Wise et al. 1997), linking the functional and volumetric evolution of the parietal and frontal districts. This is particularly interesting when considering the role of the prefrontal cortex in the management of the executive functions associated with the evolution of working memory (Wynn and Coolidge 2003, 2006), and the direct involvement of the parietal areas in the working memory processes (Chafee and Goldman-Rakic 1998). General features of intelligence may be associated with the fronto-parietal network (Jung and Haier 2007) and it is therefore quite intriguing that the two most encephalized humans species (modern humans and Neandertals) both display changes in the frontal and parietal morphology.

THE ELEMENTS OF THE ENDOCRANIAL BASE

Although there are some volumetric cerebellar changes described among human species (Weaver 2005), the most visible difference is related to the position of the cerebellar lobes with respect to the cerebral ones (Grimaud-Hervé 1997). The posterior fossa (housing the cerebellar volumes) is more posterior in Asian *H. erectus*, and more anterior in *H. sapiens*. Nevertheless, taking into account the complex structural organization of the endocranial base (Bruner and Ripani 2008; Lieberman et al. 2000), such differences are more likely to be the results of the spatial arrangements of the basicranial architecture. Even if the anterior position in *H. sapiens* involves the shortening of the average connection distance between the cerebellar and cerebral areas, it is quite difficult to provide robust cognitive inferences on this ground. Neontological data suggest that the cerebellum gained less in size than the brain overall during hominid evolution (Rilling and Insel 1998). Nevertheless, the human cerebellum has more than twice the volume of the gorilla cerebellum and more than three times the volume of that of the other great apes. This growth in absolute terms may have been a prerequisite for the pronounced functional modularity found in the modern human cerebellum and the high level of sophistication in human motor movement simulation.

Another cerebral component which is difficult to analyze in paleoneurology is the temporal area. Temporal lobes are known to be highly relevant for cognition, and have been hypothesized to present spatial changes among hominoids (Aldridge 2010) and among human species (Bastir et al. 2008). Unfortunately, the contiguity and geometrical correspondence between temporal lobes and middle cranial fossa is limited to a small antero-lateral portion of the former. Additionally, even more than the posterior (cerebellar) fossa, the middle cranial fossa (housing the anterior and lateral portions of the temporal lobes) is largely involved in the functional and structural dynamics of the cranial base (Bastir and Rosas 2009; Bruner and Ripani 2008; Lieberman et al. 2000). Therefore, its morphology is influenced by many non-neural factors. Considering both the limited correspondence between neural mass and cranial bones and the multifactorial morphogenesis of the endocranial base, morphological and evolutionary inferences on the temporal lobes base onto the endocranial form are hence very tentative.

We can synthesize the paleoneurological evidence as follows. The information on raw hemispheric morphological asymmetries is not sufficient to evidence marked differences between apes and hominids, or between extant and extinct human species. Hypotheses require proper quantitative postulates and a robust theoretical framework. Evolutionary morphological changes in the frontal lobes volumes are debated, but changes at least in the frontal lobe proportions have been quantitatively demonstrated. In this sense, modern humans and Neandertals show relatively wider frontal lobes than their ancestors. Although this is not the result of a general human allometric pattern, it can be discussed whether or not such frontal widening is a structural spatial consequence or a specific neural adaptation. Of course, the boundaries between these two hypotheses are blurred. Concerning the parietal areas, Neandertals display a certain widening of the upper volumes compared to more archaic human species, while modern humans show a definite and remarkable relative enlargement of the whole parietal surface. The intraparietal areas may be involved in such differences. Because of these variations, the relationships between the frontal and parietal networks lend themselves more easily to interpretation than their specific and localized changes. Information on the cerebellar areas is currently too restricted to allow for any robust hypothesizing.

INNOVATION, BRAIN EVOLUTION, AND CULTURAL TRANSMISSION

A final consideration should also be provided concerning the atypical configuration of the *H. sapiens* life-history. In a very original paper, Bogin and Smith (1996) applied a comparative approach to extrapolate the life-history pattern in extinct hominids. Among primates, modern humans are characterized by having two additional stages—childhood and adolescence. Bogin and Smith hypothesized that the first evolved in the earliest human forms ("*H. habilis*"), while the second evolved in later archaic species (advanced "*H. erectus*"). Their proposal is guided by the not necessarily correct assumption that the evolutionary onset and development of these stages is gradual and linear. Also, they assume that chimps display the original and primitive pattern from which humans evolved. Nevertheless, the paper is a very good example of comparative analysis in paleontology and illustrates how the examination of life histories can aid to enhance our understanding of human speciation. Lorenz (1974) had described adolescence as a stage of "physiological neophily," in which traditional relationships are rejected. While some scholars regard creativity primarily as the result of private, inner thoughts (Gardner 1993), we suggest that social aspects should not be entirely disregarded. Creative achievements often emerge through interactions with other people and artifacts that embody collective knowledge (Coward and Grove 2011; Csikszentmihalyi 1996; Fischer 2005). Such interactions need not always be collaborative—the refusal of existing conventions, a behavior which is probably most pronounced during adolescence, may indeed be an important trigger for innovative thought. This has been found to be true on population levels—younger members of rural communities have been found to be more dissatisfied with their status quo than older individuals (McGlade and McGlade 1989). However, in a review of chimpanzee innovation, Reader and Laland (2001) found no age effect, but a higher propensity of innovation by low-ranking individuals.

In a sketch of a model of triggers for a creative mind we include not only the assumed neuroanatomic changes but also our species' particular life-history (Figure 4), with its possibly species-specific ontogenetic stages and an increase in life span, which enhances opportunities for cultural transmission of innovations (for a broad overview of these variables in hominid evolution see Coward and Grove 2011). In this sense it is important to keep in mind the scarce current knowledge on the reciprocal influence between brain and culture (Mithen and Parsons 2008).

Evidently, innovative thinking is abundant in humans long before adolescence. This has been demonstrated for very different domains (see Wallach and Kogan 1965, for a general overview; Russ et al. 1999, for creativity in pretend play; Sak and Maker 2005, for mathematical problem solving; Järvinen, et al. 2007, for technical innovation). However, the adolescent brain does undergo significant changes—the volume of frontal grey matter peaks at the age of 11 to 12, whereas temporal grey matter reaches its volume peak four to five years later (Giedd 2004). Measures of creative thinking and creative leisure activities in adolescents have been found to be more reliable predictors of creative attainments in adults than school-oriented measures of intelligence (Milgram and Hong 1993).

Recognizing the evident cultural differences displayed by modern humans when compared with non-modern human species, and assuming adolescence to regulate innovation rates, it may be speculated that this stage evolved as a specific and discrete feature in *H. sapiens*, rather than being a character which evolved gradually along the human phylogeny. Hawcroft and Dennell (2000) argue that childhood and development patterns in Neanderthals were different to those of modern humans. Encephalization, longevity, and trans-generational flow of information are tightly related topics (Allen et al. 2005), and the unique rate of cultural change in modern humans possibly required changes in the structure of our species' life-history. Culture is a system based onto super-organic adaptations requiring a post-reproductive ontogenetic stage (e.g., Hawkes et al. 1998, but see Kachel et al. 2010 questioning the "grandmothering hypothesis"). If this post-reproductive period acts as a stable reservoir of information, we may hypothesize that the life-history changes associated with adolescence are the counter-part needed to provide a productive rate of innovation.

CONCLUSIONS

It is more and more evident that topics in brain evolution can be developed only through the proper integration of different perspectives. The archaeological evidence, the fossil record, and neuropsychological data must be combined with information from ecology and the social sciences to provide reliable scenarios and useful hypotheses. At 120 ka, compared to their ancestors, in Europe Neandertals displayed at the same time relative widening of the frontal lobes, a certain latero-lateral bulging of the upper parietal surface, and a patent cultural change (Bruner and Manzi 2008). More or less in the same period, in Africa, modern humans evolved a relative widening of the frontal lobes and a marked overall bulging of the upper parietal surface, followed by a further cultural shift. It is therefore worth noting that the more the fronto-parietal changes, the higher the cultural complexity. Until recently, the most striking evidence of the early cultural evolution in modern humans were cave paintings and body ornaments. More recently, flutes have been recovered from early Aurignacian sites dated to 35 ka (Conard et al. 2009). Music—part of the

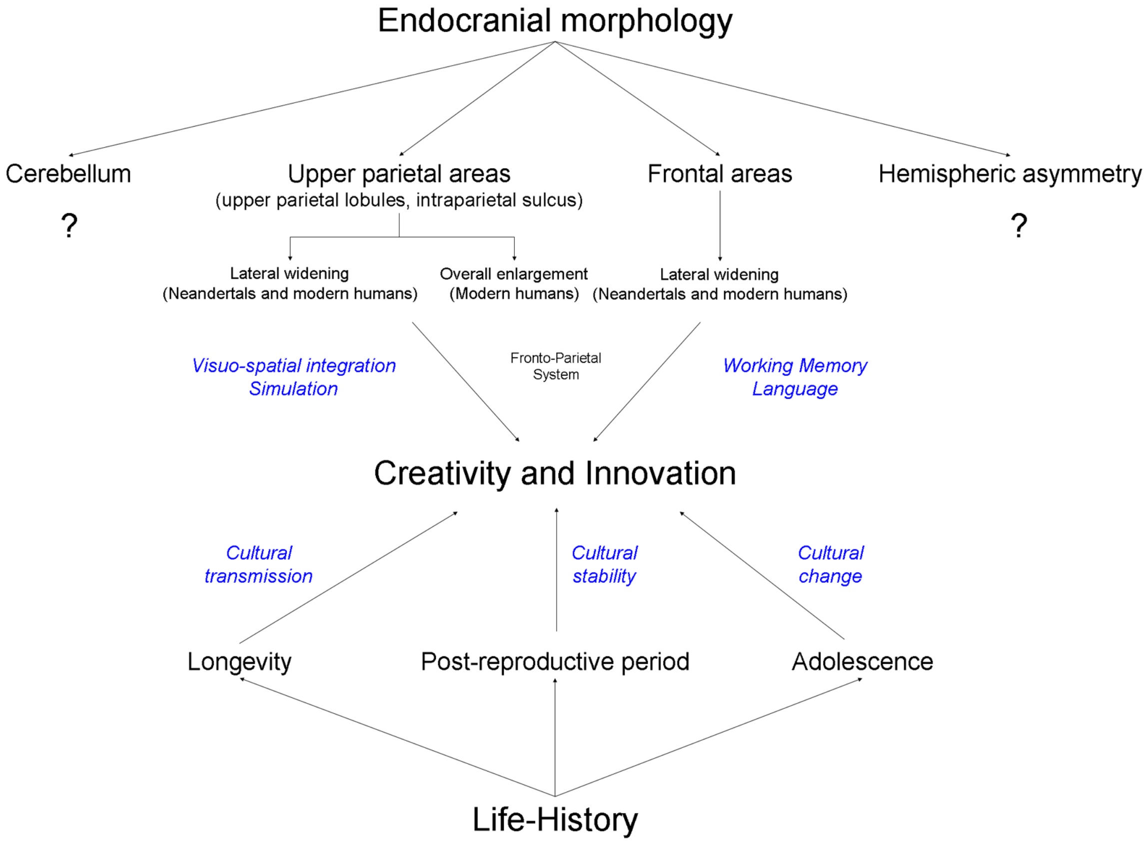

Figure 4. Changes in cognitive processes associated with creativity and innovation may be influenced by neurological variations as well as by differences in the life-history. The formers can be investigated in fossils species taking into consideration the endocranial morphology. There is evidence in modern humans (and partially in Neandertals) suggesting that the evolution of the fronto-parietal network could have been associated with relevant cognitive changes. Similar relationships are considered also in the framework of the evolution of the enhanced working memory and language (Wynn and Coolidge 2006). Variations in the life-history deal with brain metabolism and energy requirements, the evolution of a post-reproductive period, and possibly with the appearance of a new ontogenetic stage (adolescence).

"modern cognition package" of our species—recruits neural capacities for perception and integration, coordination between emotional and metacognitive functions, complex planning, communication, and requires creative abilities. Multidisciplinary approaches are most likely to increase our insight—apart from understanding the actual neurobiological factors behind the history of human brain evolution, we also must learn to comprehend the relationships between brain, mind, and culture (Malafouris 2010).

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