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Extending mind, visuospatial integration, and the evolution of the parietal lobes in the human genus

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Abstract. Current theories in extended mind suggest that cognition is the result of an integrative process involving brain, body, and environment. The relationships between inner and outer components strictly depend on the functional interface, which is represented by the body. Posture and locomotion influence the sensorial and behavioral relationships between the body and the environment which, in Primates, are strongly dependent on the eye-hand system, and coordinated by processes of visuospatial integration. The upper and medial parietal areas (like the precuneus and the intraparietal sulcus) are crucial for such functions. These areas are associated with specific human cortical features, and have undergone relevant morphological changes in *Homo sapiens*. Therefore, it can be hypothesized that the visuospatial functions and the role of the body as an interface have experienced important evolutionary changes in our species. Neandertals did not display similar changes in terms of brain morphology, and at the same time they showed a different manipulative behavior: they needed their teeth and mouth to properly handle tools much more than any modern human group does. This may suggest a different (and probably less specialized) way to integrate inner and outer components through the body interface. Archaeology is essential to evaluate possible functional changes in extinct human species, by considering other kinds of visuospatial behaviors that are evident from human ecology and material culture. We suggest that changes in the visuospatial integration functions and in the parietal areas may have represented an essential component for enhancing embodiment capacity. What remains to be established is the role of genetic, epigenetic, and environmental factors, in generating anatomical and functional differences among human species and between human and non-human primates. Visuospatial integration, within the perspective of extended cognition, may have had a major influence in establishing current human intellectual abilities and social patterns.

Keywords: brain evolution; paleoneurology; precuneus; intraparietal sulcus; embodiment;

1. Beyond the braincase

René Descartes (1596-1650) was an influential supporter of the dichotomy between body and soul, introducing his dualistic philosophy based on a body component (*Res extensa*) and a soul component (*Res cogitans*). Following incomplete and incorrect neuroanatomical information integrated with some principles of symmetry and geometrical position within the body structure, he proposed the pineal gland as the point in which these two components interact (Berhouma, 2013). The symmetry issue was a little naïve: he stressed that the pineal gland was the only non-symmetrical element of the brain, and hence probably the point in which all the inputs must converge. The geometry issue was definitely structural: the pineal gland was at the center of the volume, namely the spatial core of the brain. Particularly, he proposed that the pineal gland was central in integrating eye movements and vision processes, with particular emphasis on the eye-hand system (Figure 1).

For long a time, the brain was interpreted as a self-sufficient machine. Many current reductionist approaches seem to continue following this perspective. Recently, we recognized the importance of the environment, its influence in shaping the brain structure and functions, and the incredible plasticity and sensitivity of the cerebral system. Nonetheless, despite the relevance of such influence, the “mind” was still interpreted as a product of the brain alone, which was thought to be simply influenced by external stimuli. A further epistemological step has been currently put forward following the theories on *extended mind*, which suggest that cognition is the integrative result of the outer and inner environments, bridged by the interface of the body (Clark, 2007, 2008).

The inner environment is represented by the network of organic structures characterizing the organisms as individual entities, as delimited by the body, by the actual cellular range of the nervous system, and by the processes associated with the neural responses. The outer environment is represented by the physical and cultural system forming the matrix in which the organism acts and perceives, composed by objects and processes which alter the organism’s structural and functional conditions, and integrating the organism’s reactions and responses.

According to perspectives in cognitive extension, the cognitive process is strongly based on the body experience (*embodiment*) and dependent on activations and regulations exerted by the physical interaction between body and objects (*body-artefact interface*)(Malafouris, 2010a). We can say that the body and the objects are the interfaces between brain, culture, and environment (Figure 2).

The body, intended as the structural and perceptual component of an organism, bridges the inner (neural) and outer (environmental) spaces. Objects, both natural and artificial, are intended as the material components of a culture, and represent a further (extra-corporal) interface, between the body and the environment. The interaction between the body and the objects is probably a dynamic process, which is part of the cognitive structure itself. The body is necessary to perform and decode the perceptive experience, while the material culture closes this loop to trigger and drive these neural processes. Objects can store information as external memories, support neural circuits through catalytic processes, and enhance our sensorial and computational capacities shaping our neural organization as active components of their functional networks. Objects, embedded as functional components of the environment, are incorporated within the neural and cognitive processes according to the principles of material engagement (Malafouris, 2008, 2010b). Our neural system is constantly trained and educated as to properly integrate the surrounding components, generating a network of dynamic relationships relying on organic and inorganic elements. Objects are formally implemented as the extended functional properties of the existing neural system, through processes which depends upon their physical distance from the body (Maravita & Iriki, 2004). Such a circuit is based on coordinated feedbacks and sensitive to reciprocal dynamics. These adaptive processes, represented as functional plasticity of the neural circuitry, are in addition shown to accompany structural modifications, not only at microscopic level (Hihara et al., 2006) but also at macroscopic level (Quallo et al., 2009). As a consequence, ecological, neural, and cognitive levels are part of an integrated system developed and evolved through mutual interactions (Iriki and Taoka, 2012).

There are several mechanical variables involved in this feedback, including the physical and spatial properties of the object, the way the hand touches the object, and the sensory input transmitted by the object when used to perceive or interact with the outer environment (see Turvey and Carello, 2011 for a detailed review). The body should be intended as a deformable interface receiving information from the external space, a perceptual system detecting information about internal and external inputs. It has properties typical of the tensional integrity (*tensegrity*) structures, namely mechanical systems which achieve a functional stability by continuous isometric tensions (Ingber, 2008). This condition generates a common tensile pre-stress condition able to synchronize mechanochemical transduction among its different components. This structural network can be hypothesized to act at organism, tissue, cellular, and subcellular level, and allows the perception of local forces on a global scale. Through the interface of body and objects, the brain and the environment shape each other (Malafouris, 2010b, 2013), giving the mind a historical perspective that goes beyond a strictly genetic and organic product. These external components could even supply "epigenetic"[1] or extra-genomic information that can be inherited over generations, contributing to the shaping of postnatal developmental patterns both in terms of bodily structures and cognitive capacities of offspring (descendants), to match such environmental conditions. Following this interaction, humans shape and are shaped by their ecological, cultural, and social niches, extending the cognitive processes through their extra-neural components (Iriki and Sakura, 2008; Iriki and Taoka, 2012).

Taking into account the hierarchical and reciprocal nature of these networks, it is clear that most of the elements commonly used to describe these systems must not be intended in terms of defined and fixed boundaries. If all these components are actively involved in the cognitive process, being part of it, a straight separation between brain, body, objects, environment, and culture is but an operational and conventional choice aimed at supplying a theoretical framework. Although these components may have specific different roles within the system, their distinction may be more a matter of functional coordination, and any attempt to localize boundaries or strict definitions may be ineffective and even misleading.

Two million years ago, the human genus introduced essential changes in the way the brain interacts with the environment, and in the way the body works as an interface. While some primates and birds can display *tool-assisted* foraging, humans become *tool-dependant* foragers (Plummer, 2004). Tool-dependence means that the whole foraging process (including its cognitive parts) strictly relies on the interaction between body and material culture, its properties and relationships being generated only through that interaction. Such a new level of integration between brain, hand, and tool required not only a change in some behavioral abilities, but probably also an important cognitive reorganization.

2. Parietal cortex as brain-environmental interface through eyes and hands

The relationships between body and environment and the neural organization underlying the visuospatial processes are a central issue in ecology, and have undergone profound changes at

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[1] Please note the term "epigenetic" is used in osteology for discrete traits associated with excesses or defects in ossification, or characters associated with presence/absence of specific anatomical features. Instead, here we refer to the molecular meaning of the term, namely specific factors, including environmental ones, generating changes of the chromatin structure, influencing expression of DNA sequences, or transcription of genomic codes (like nucleotide methylation or histone modifications).

macro and micro-evolutionary scales. In many multicellular organisms, there is a direct circuit between sensation (reception) and movement (response). In vertebrates, these two components are mediated by a complex central nervous system. Finally, in species with complex behaviors (like in many primates and cetaceans) inputs and outputs are integrated through higher functional centers computing selection and filtering, comparative simulations, decision making, and other high order cognitive managements. At the same time, the general spatial relationships between body and environment have changed radically, according to posture, locomotion, and to general somatosensory organization (Figure 3). Humans are a special case, in which bipedal locomotion was associated with increased dexterity and evolution of special handling capacities. Although the relationships between posture and praxis are not clear in terms of evolutionary sequences (e.g., Hashimoto et al., 2013), a full specialized bipedal structure and a patent capacity for complex tooling are strictly associated with the human genus.

Although the whole body represents the functional and structural interface between brain and environment, we can identify at least two main “ports” through which the flow is organized: the eye and the hand (see Bruner, 2010a, 2012). This condition is largely the result of our natural history which, in 70 million years, has characterized primates for their grip capacities and visual resources. Hand structure and function are well-known topics in human evolution, with a patent relevance especially in our genus (e.g., Susman, 1998; Tocheri et al., 2008). Vision too has a special meaning for primates, specifically for anthropoids, as mammals that changed from a night world made up of sounds and smells to a day-life based on colors and shapes (e.g., Jacobs, 1996; Heesy and Ross, 2001; Surridge et al., 2003). Primates importantly rely on their handling capacity, and relevant processes associated with human tool-using are rooted in the neural organization shared with non-human species (Iriki, 2006). There is no agreement on whether or not some specific hand anatomical features fundamental in humans are the result of selective pressure associated with tooling (Key and Dunmore, 2014) or else are based on the specialization of a generalized hominoid structure (Alba et al., 2003). Brachiation and suspensory behavior represented a relevant locomotor pattern in hominoids, with an important role in the life-style of the genus *Australopithecus*, and further specialization in living taxa like orangs and gibbons. Such an orthograde position (even more exaggerated in bipedalism) involved a new kind of relationship between hands and eyes: it generates an enhanced integration between the visual system (brain areas and sensory system) and the peripheral body as represented by the distal extremities (hands and fingers). This probably transformed “intransitive” actions into “transitive” actions, which may have represented a crucial node in the evolution of manual tool-use (Iriki and Taoka, 2012). In hominoids, investment in their eye-hand system is also visible in more frontated orbits and crossed optic fibers, with all these processes stressed further in humans after their specialization in bipedal locomotion associated with high precision grip.

We must evaluate what neural changes are associated with these adaptations, not only in terms of nervous system but also in a perspective of mind extension. The outer environment enters the neural system largely through visual inputs, and the neural system interacts with the outer environment largely through the hands. The body mediates this experience, and the brain coordinates the flow of information. The relationship between outer and inner environment is neurologically integrated in a set of functions we generally put under the name "visuospatial integration" (Figure 4).

In terms of functional neuroanatomy, the parietal areas are a central node for visuospatial integration, in particular their upper and inner cortical elements (Ebeling and Steinmetz, 1995). These areas have been scarcely investigated for several reasons. Firstly, their functions are integrative and complex, and hence difficult to simplify through experimental paradigms. Secondly, their position in the deep cortical volume makes functional damages infrequent, because protected by outer (superficial) cortex, and because a damage in these areas would be so invasive as to make the survival of the individual unlikely. Thirdly, the differences in gross anatomy among primates (most of all considering humans) are relevant, and therefore partially hamper comparative approaches based on homology. Fourthly, their boundaries are more blurred than other areas, making volumetric studies difficult to perform.

After decades of scarce consideration and the opinion that they were only secondary associative cortex, the upper and medial parietal cortex received more attention at the end of the past century (Mountcastle, 1995; Culham and Kanwisher, 2001). Their most patent functions are associated with visuospatial integration and attention (Andersen et al., 1997; Gottlieb et al., 1998; Rushworth et al., 2001; Andersen and Buneo, 2002; Wardak et al., 2005; Freedman and Assad, 2006), although recently different kinds of integrative processes have been discussed, such as those associated with numbering (Cantlon et al., 2006; Ansari, 2008; Nieder and Dehaene, 2009). Furthermore, these parietal areas are largely involved in many abstract cognitive processes which rely on spatial analogy and relational principles (Iriki and Taoka, 2012).

The intraparietal sulcus, a large cortical component hidden in the depths of the parasagittal cerebral volume, is specifically involved in the management of the eye-hand system (Sakata et al., 1997; Battaglia-Mayer et al., 2003; 2006; Orban and Caruana, 2014), integrating spatial information from the inside (organism) and the outside (environment). The coordinate systems from the inner (mostly proprioceptive) and outer (mostly visual) environments are integrated according to attention, saliency filters, and relational concepts, in order to simulate an "inner virtual space" (see Bruner, 2010a for a review). Interestingly, these areas present cytological differences between human and non-human primates (Vanduffel et al., 2002; Grefkes and Fink, 2005; Orban et al. 2006), with additional new elements (see section IV below for further details).

A second relevant deep parietal area is the precuneus, positioned midsagittaly between the two intraparietal sulci. It is particularly active in integrating visuospatial information with memory (Cavanna and Trimble, 2006; Margulies et al., 2009; Zhang and Li, 2012), representing the "eye of the self" (Freton et al., 2014). The precuneus contacts posteriorly with the occipital and visual areas, anteriorly with the somatosensory cortex, and inferiorly with the cingulate gyrus and retrosplenial cortex. Its position is essential to the general organization of the brain, being a principal node of the brain networks in terms of functional and structural relationships (Hagmann et al., 2008). It is at the same time a central node of the Default Mode Network (Buckner et al., 2008; Meunier et al., 2010). Finally, it is the geometrical core of the brain volume, and has an unusual high temperature and metabolic demand (Sotero and Iturria-Medina, 2011). Relevant extrinsic relationships between these deep parietal areas are formed by reciprocal and reentrant connections from and toward the frontal area (Battaglia-Mayer et al., 2003), and also in this case, humans display species-specific organization associating the fronto-parietal network with simulation capacity (Hecht et al., 2013). Although specific volumetric data are still lacking, in apes these elements are rather small when compared with the human values. Currently, the fronto-parietal system has been hypothesized to have a determinant role in the management of our complex cognitive levels (Jung and Haier, 2007).

3. The paleoneurological evidence for parietal expansion

Since the earliest paleoneurological studies, it was apparent that the parietal areas had undergone relevant changes during human evolution. Raymond Dart pointed at the parietal lobes when discussing the differences between humans and australopiths (1925), and Franz Weidenreich did the same studying the endocranial casts of *Homo erectus* (1936, 1941). The first available quantitative analysis on the evolution of the endocranial morphology evidenced a marked degree of parietal surface variation among hominoids and hominids (Holloway, 1981). Then, at the beginning of this century, shape analysis revealed that an actual bulging of the upper parietal surface was the main feature characterizing the globularity of the modern human brain, when compared with all the others extinct human species (Bruner et al., 2003, 2011; Bruner, 2004; Bruner et al., 2011b). Surface analyses evidenced that such bulging is associated with an early post-natal morphogenetic process (Neubauer et al., 2009), and confirmed that this stage is absent in chimpanzees and Neandertals (Neubauer et al., 2010; Gunz et al., 2010). Such direct evolutionary evidence is in agreement with the neuroanatomical evidence of specific additional parietal areas in humans when compared with other non-human primates (Van Essen, 2005; Zilles, 2005; Orban and Caruana, 2014), and it suggests that such changes are specific to our species, *Homo sapiens*, and not shared with other hominids.

In paleoneurology, all we have is the form of the brain, as molded and imprinted in the neurocranial morphology. Minor correlation between brain geometry and cognition has been recently evidenced, which may have been more relevant at evolutionary level when considering the largest differences between species (Bruner et al., 2011a). Nonetheless, inferences on brain functions from brain morphology alone are rather difficult to consider, and structural hypotheses are necessary to evaluate the complex relationships between cranial changes and brain variations.

Because of the morphogenetic relationships between brain and braincase, evolutionary shape changes in the upper vault elements are easier to interpret than changes in the lower endocranial districts (Bruner, 2015). In fact, during growth and development, the upper neurocranial bones are directly molded by the pressure of the underlying cortical surface, and changes are then correspondent among hard and soft tissues (Moss and Young, 1960; Enlow, 1990). We must also consider that the morphology of the human braincase is characterized by modest levels of large-scale integration: the three endocranial fossae are influenced by independent factors (Bruner and Ripani, 2008), the brain morphology is integrated only in terms of physical proximity and local effect (Bruner et al., 2010; Gómez Robles et al., 2014), and the sagittal elements are even scarcely integrated with the lateral elements (Bastir and Rosas, 2006, 2009). Because of this limited integration, it is unlikely that changes in one part will sensibly affect other distant districts. Hence, taking into consideration the direct morphological relationship between parietal lobes and bones, and the limited influence of extrinsic variations, morphological changes of the parietal bones are likely to be caused by specific morphological changes of the underlying cortical brain volumes.

Earliest inferences based on shape extrapolation pointed at the intraparietal sulcus as a possible source of difference between modern and non-modern parietal form (Bruner et al., 2010). However, a recent shape analysis of the midsagittal brain profile in adult humans revealed some important information: the main source of individual variability associated with the brain geometry is due to the proportions of the precuneus, with a pattern which is surprisingly similar to that observed in the distinction between modern and non-modern human species (Bruner et al., 2014a) (Figure 5). The resemblance between the two patterns suggests that the precuneus may be a major factor accounting for the morphological changes associated with the evolution of the modern human brain geometry (Bruner et al., 2014b). Although the exact nature of such "spatial dilation" of the parietal areas in modern humans is yet to be properly investigated, it is reasonable to think that these geometrical changes are associated with an actual expansion of the parietal cortex. In fact, the differences in the precuneal proportions in adult humans, paralleling the changes associated with the evolutionary origin of modern human brain form, are due to changes in its cortical surface area, dilating or reducing its longitudinal extension and generating the bulging of the parietal volume (Bruner et al., 2014c).

Functional and structural imaging suggests that humans and chimpanzees share similar organization of the default mode network, centered on the precuneus as a main hub supporting inter-areas communication (Rilling et al., 2007; Barks et al., 2015). If no qualitative difference will be found in this area among living hominoids, we should evaluate the possibility that differences could be more a matter of grade than of specific new-evolved structures or processes. Minor functional differences can generate important cognitive changes, and responses based on quantitative variations should be carefully considered, most of all when taking into account the possible existence of thresholds effects.

Interestingly, the same media parietal areas are also involved in early metabolic impairments observed in Alzheimer's disease (a neurodegenerative process which is mostly associated with *Homo sapiens*) and it was hypothesized that vulnerability to structural damages may be a secondary consequence of the anatomical and functional complexity of these cortical districts in our species (Bruner and Jacobs, 2013).

4. Primate parietal expansion by ecological, neural, cognitive interactions

Then, what could be the mechanisms that lead our parietal cortex to rapidly expand over the history of its evolution? Evolution involves at the same time changes based on variations of plesiomorph patterns expressing intrinsic plasticity of a given underlying scheme, reutilization of primitive traits for new structures and functions, and novel adaptations shaped through specific selective pressures. Taking into account the important cognitive changes associated with the human genus, this last component is probably relevant when dealing with manual ability and use of tools.

More than any other species, humans adjust their behavior by using any materials available in new environments. Any cognitive change in this sense must be in any case compatible with the operational stability of the other non-derived functions. A new balance between derived and plesiomorph neural functions, probably attained also through a certain redundancy, would result in the rapid construction of a new “neural-niche”, and leads to the exploration and exploitation of new “cognitive niches”. Such implemented functions would involve, consequently, changes in the human “ecological niche”, generating a feedback on the new brain requirements. In other words, ecological, cognitive and neural domains do interact, through a process of the “triadic niche construction” (Iriki & Taoka, 2012).

A given redundancy of the brain, initially necessary to stabilize the biological system against unexpected environmental noise, occasionally allowed the system to be reused for completely different functions, maybe through different combinations with other parts of the brain. In macaques, intraparietal neurons which normally code body image could be trained to code a tool in a way equivalent to the hand holding the tool itself (Iriki et al. 1996). The somatosensory and visual receptive fields converge in the parietal areas and share different neural references, like the location of the hand in the space, and any stimulus that can interact with this hand-centered space. The hand and the image of the hand are an integrated part of the body schemata. When a primate is trained to use a tool, the receptive fields of these neurons are expanded to include the tool itself, which is therefore incorporated into the body schemata (Iriki, 2006). Thus, the same neural network can represent the hand or the tool (*bistability*). This can be interpreted as the tool being included in the body, or else as the hand being interpreted as a tool (*polysemous* or *poly-semantic* interpretations). In fact, these two interpretations, in this sense, represent equivalent concepts from different perspectives, thus allow multiple meanings. It would be also worth noting that the body is prepared for a given “growth” of its structures, and such extension of the body schema can be integrated within this system which is already sensitive to ontogenetic size changes. That is, the extension of the body-schema through the extra-neural tool component can be biologically interpreted as a “sudden growth” of the body, and managed through the same mechanisms used to manage ontogenetic variations. This equivalence between body parts (hands) and tools leads to the externalization of the body (hand as tool) or, alternatively, internalization of external objects (tool as part of the body). Such “self-objectification” through eye-hand coordination processes is clearly influential in processes associated with embodiment and extending mind.

These neural responses are based on further complementary implications, including modification of the coordinate system of body-centered representations of the external world, transformation of external representation from body-centered coordinates to object (tool)-centered coordinate systems, and incorporation of tool-body relationships into different spatial attention control system. These polysemous mechanisms, emerged from alternative usages of extended/redundant existing machinery, would contribute to various aspects of control of the body to interact with the environment. Those functions that are most adaptive to body-environmental interactions would have been selected through evolutionary processes, and further enhanced/expanded through the mechanisms of the Triadic Niche Construction. In this sense, the implication of tool use-induced modification of the body schema has probably had a major role, in terms of adaptive changes, in the expansion of the parietal cortex in the human lineage. Non-human primates exhibited substantial expansion of the grey matter, also in the parietal areas, during a two-week tool-use training period (Quallo et al. 2009). Indeed, in the human archaeological context, the first neuroarchaeological attempts to associate brain imaging with stone tooling performance once more evidenced the role of the deep parietal areas (Stout and Chaminade, 2007), stressing further the possible relationships between biology and culture in terms of praxis and visuospatial integration processes.

Once a novel, alternative, and bistable state is associated with increased fitness, additional resources will be invested to stabilize the system, probably generating further redundancy. Humans can induce such a loop directly and actively, shaping a more comfortable environmental niche. Indeed, human-specific cognitive characteristics seem to be subserved mainly by these “expanded” parietal areas (Ogawa et al., 2009, 2014). Subsequently, triggered by extra-genetic or epigenetic factors embedded in such an environment, the corresponding neural niche in the brain could be reinforced further, generating a recursive intentional niche construction (Iriki & Sakura 2008). Some aspects of recently evolved cognitive functions resulting from such neural reuse could be found in processes associated with meta-self recognition, self-objectification processes (Iriki, 2006), or language and symbolic or abstract conceptual structures, all based on semantic inheritance most efficiently acquired during the unusually elongated human post-reproduction period. In these terms, human higher cognitive capacities should be viewed holistically as one specific component of the whole ecosystem. The brain’s functional characteristics seem to play a key role in this triadic interaction, and a crucial node for such integration seems to be the parietal cortex.

Humans have attained unusually long post-reproductive life spans, thus acquisition of cognitive functions, and resulting accumulation of knowledge, continues over the whole lifespan, tending to peak in middle to old age. Extra-genetic mechanisms seem necessary, to some extent, to support inheritance of such information over generations. In the second half of the 19th century, James Mark Baldwin proposed that specific expressions of phenotypic plasticity, induced by environmental factors, can orientate and influence following selective pressures, generating a situation in which evolutionary changes can be driven by the underlying variability potential and not by genetic adaptations (Baldwin effect; Baldwin, 1896; see Snajder et al., 2012 for a detailed analysis). Following this view, genetic changes will be then supported according to that direction of variation (genetic assimilation; Crispo, 2007).

Epigenetic factors associated with environmental conditions (including behavior and culture) and acting on the degree of sensitivity of phenotypic plasticity probably has an essential role in such kinds of mechanisms, linking Darwinian and the so-called "Lamarckian" evolutionary processes (Schlichting and Wund, 2014). Epigenetic factors can emerge through the "triadic niche construction" and become embedded in the environment as a result of the function of such a triadic network itself. Accordingly, post-reproductive inheritance can become a relevant factor in shaping and directing further cognitive changes. In this sense, biological factors orienting brain evolution would become directly intermingled with historical and cultural changes.

5. Praxis and body interface in Neandertals

At the end of the Middle Pleistocene, the skull Jebel Irhoud 1, in Morocco, displayed features which are specific to modern humans, but with no apparent bulging of the parietal morphology (Bruner and Pearson, 2013). If this specimen is actually a member of our lineage, we must conclude that the origin of our lineage did not necessarily match the origin of the modern brain morphology, the parietal enhancement being the result of a distinct and successive process.

A comparison between modern humans and Neandertals can be very informative when studying issues concerning the parietal lobe evolution. Both groups shared a similar cranial capacity, and a similar enlargement of the frontal lobes (Bruner and Holloway, 2010). Also the parietal area underwent form changes in both species, but to a different extent: Neandertals displayed a lateral bulging of the upper parietal surface, while modern humans displayed a whole dilation on the upper parietal volume, both laterally and longitudinally (Bruner et al., 2003; Bruner, 2004) (Figure 6). Interestingly, in non-modern humans (that is, all the human species except *Homo sapiens*), the parietal sagittal profile shows a negative allometry: larger brains have relatively shorter parietals. Neandertals shows the extreme of this pattern, being the most encephalized non-modern taxon, with a relatively shorter parietal lobe. At the same time, on the ectocranial area, they show, right at the parieto-occipital border, supernumerary ossicles, namely epigenetic osteological traits which may suggest a scarce integration within the growth and developmental patterns, with possible structural limits and constraints associated with a large brain and a plesiomorph neurocranial organization (see Bruner, 2014 for a review). A recent hypothesis, put forward by indirect correlation between cranial and brain structures, suggests that Neandertals could have had larger proportions of the occipital lobes (Pearce et al., 2013). Taking into account the fact that they had a cranial capacity similar to modern humans, larger occipital lobes are compatible with smaller parietal areas.

The first information we can have from these paleoneurological evidences is directly related to the brain elements involved: if endocranial morphology is directly influenced by the underlying brain mass, we must conclude that Neandertals experienced a lateral expansion in those brain areas associated with upper parietal lobes, and modern humans experienced a further and even more patent sagittal development of these elements. One may wonder whether the lateral expansion is related to the intraparietal sulcus, and the sagittal expansion to the precuneus. Nonetheless, this speculation is at present totally tentative.

Beyond changes in the brain gross morphology, cognition in extinct species can be only investigated by means of behavioral correlates. Interestingly, in this case we have a peculiar clue: dental anthropology. On the front teeth of Neandertals and their ancestors (*H. heidelbergensis*) we can observe surface marks left by a non-alimentary use of the mouth (Bermudez de Castro et al., 1988; Lozano et al., 2008). These taxa generally used their mouth as a “third hand”, supporting praxis and handling. Marks have been left by the physical contact with handled objects, scratching the dental surface. In Neandertals and their ancestors, these marks are rather numerous and, more importantly, they are present in all the individuals.

Also modern populations use the mouth as a third hand, and the situation is rather heterogeneous (Clement et al., 2012). Nonetheless, most modern hunter-gatherers do not use teeth in handling, or they do only to a limited extent, for secondary and occasional behavior. Those groups using the mouth as a third hand do not harm it hitting the dental surface and generating scratches. In those few groups that have scratches on the dental surface, such scratches are few, and limited to a minor percentage of individuals (40%). Hence, we must conclude that using the mouth in handling is not necessary in developing complex cultures, and furthermore that such activity is not necessarily associated with damages on the labial surface of the teeth.

If we consider that Neandertals had a complex culture, that the eye-hand system is the main body interface between brain and environment, that this system is integrated in the parietal areas, and that Neandertals lack the parietal dilation observed in modern humans, we can wonder whether this extreme use of the teeth as a third hand may denote some difficulties in the visuospatial neurosomatic system of this human group. It has been therefore hypothesized that the use of the mouth as a third hand is evidence of an underlying process of mismatch between cultural and biological complexity, with constraints in the visuospatial integration capacity (Bruner and Lozano, 2014). In Neandertals, the eye-hand system, as an interface, could have been inadequate in integrating the visuospatial processes required by the complex culture, needing additional body elements (the mouth) to interact with the material culture. According to this perspective, the feedback between cognition and culture may have generated a loop in which the visuospatial integration system (in terms of body and/or corresponding neural organization) of Neandertals failed to keep pace appropriately with the increasing complexity of their culture. As a consequence, the eye-hand system was not enough to integrate the body-artefact relationships, so requiring a different supplementary interface (the mouth).

Because the mouth is used in every primate species as additional support to praxis, differences between modern humans and Neandertals may have not been the result of a discrete change, but more a matter of grade: common use versus infrequent or null use, methods harming teeth versus safer techniques. Interestingly, it has been hypothesized that also early modern humans relied much more on tooth-tool use, but with a different pattern when compared with Neandertals, more based on posterior than frontal teeth (Fiorenza and Kullmer, 2013). Posterior teeth are generally used for strength operations, while front teeth are generally used for precision handling, and this difference between Neandertals and early modern humans hence suggests a very different necessity behind these different behaviors. This could be particularly relevant, because those early modern humans shared with Neandertals also a very similar culture (Richter et al., 2012). Precise data on their endocranial morphology is still lacking, but at least one specimen (Skhul 5) shows a parietal bulging which is not so marked as in later modern human specimens (Bruner, 2010b). In the available reconstruction of its endocasts, some damage may prevent a conclusive quantification, but the bulging of the parietal areas seems not so pronounced as to give a typical globular brain shape.

It is worth noting that in the cortical somatosensory representation (the “homunculus”), the mouth is the most represented structure after the hands. Therefore, in cases where hands are not sufficient to correctly attend the interface functions of the body, the mouth is automatically the next element in importance. As mentioned previously, such hierarchy can be easily recognized in the reaching patterns, in which hand reaching follows, in terms of behavioral complexity, neck and head reaching (Iriki and Taoka, 2012). Needless to say, the use of mouth for praxis breaks also one of the main rules of the evolution of manipulation: the coordination between eye and the effectors, a visual contact which is considered to be fundamental in tooling and associate cognitive processing.

It has been stated that the use of the mouth, instead of a forced and inadequate solution associated with limits of the praxis system, may represent a kind of enhancement of the body as an interface, or even the sign of a complex sensorial integration (Malafouris, 2014;

Langbroek, 2014). However, the mouth is of fundamental ecological importance, and its involvement in handling is a very risky investment, which is apparently inappropriate for such a redirection of functions. Taking into account the biological background of primates' evolution, this alternative interpretation is at least improbable. Because of the evolutionary framework presented here, the extremely high prevalence of marks in the front teeth of Neandertals could be the behavioral witness of an eye-hand system which was inadequate for manipulation in such a complex cultural context, and which therefore needed additional support.

Interestingly, similar limits in the spatial abilities in Neandertals have been also hypothesized to interpret their patterns of land use and territory managements (Burke, 2012). Neandertals and modern humans may have displayed some relevant differences in the use of the landscape strategies, suggesting different capacities and abilities in their cognitive maps and cognitive representations. Imagery and memory are the integrated components of neural processes underlying egocentric and allocentric representations, mostly relying on a network formed by the medial temporal and medial parietal areas (Burgess, 2008; Freton et al., 2014). Both parietal and temporal areas have been hypothesized to show specific traits in modern humans. Hence, we have at least two indirect indications of probable differences in visuospatial functions between modern humans and Neandertals, namely the specific behavior associated with the dental marks and the ecological evidence associated with their different hunter-gatherers lifestyle. This is pretty attractive taking into account that the major brain morphological differences between them can be detected in areas involved in visuospatial integration.

Necessarily, hypotheses in cognitive archaeology are speculative. However, integrated evidence from paleoneurology, dental anthropology, archaeology, and cognitive science, suggest that the handling procedures in the two human species with largest cranial capacity, namely Neandertals and modern humans, were different, as were also different their brain morphology. To evaluate the hypothesis of a relationship between dental marks, visuospatial integration, and parietal evolution, we should consider the actual behavioral differences among those populations currently using tooth-tooling in some aspects, in terms of efficiency, cultural transmission, and visuospatial performances. This can be done by traditional functional imaging and neurometrics, but also through traditional psychometric approaches, and it can seriously add to this issue. A developmental perspective, which includes considerations on the use of the mouth during ontogeny, may probably also supply further information on the relationships between visuospatial performance and body resources.

6. Testing visuospatial integration and the evolution of embodying capacity

Within the variation of the human genus, a clear correlation between brain morphology and tool culture cannot probably be tested, because of the non-linear nature of cultural changes, and because of the limited variations available to support statistical approaches. Nonetheless, it must be noted that in large-brained hominids, lateral bulging of the parietal areas is generally associated with the use of "Mousterian-like" tools, and the overall dilation of the upper parietal volumes is associated with Aurignacian tools. Both upper and deeper parietal areas are involved in visuospatial integration processes, so such association merits further attention. Interestingly, according to hand anatomy, it has been hypothesized that early modern humans had different handling behaviors when compared with Neandertals, despite the similar industry they shared (Churchill, 2001; Niewoehner, 2001). Hand differences may supply direct structural and functional information on the evolution of the interface. In this sense, it is worth noting that the hand is the ultimate component of a corticospinal chain, which must be carefully considered when dealing with evolution and embodiment (Martín-Loeches, 2014). It is also worth nothing that the hand mediates a large set of cognitive responses which are self-sufficient to explore the affordance of an object by dynamic touching (Turvey and Carello, 2011), allowing a direct body (non-visual) control of the brain-artefact interface.

According to the general evolutionary framework presented here, we should be able to localize three different components in the human eye-brain-hand system. First, some structural and functional elements, at both neural and somatic levels, are deeply rooted in the primate phylogenetic history, their adaptations to diurnal activity patterns, vision enhancement, shape and color detection, and hand-reaching specialization influenced by suspensory locomotion and orthograde posture. Second, some structures and processes should be intended as adjustments and departure from the primate schemes, to avoid constraints or loss of functionality. The relevant encephalization in the genus *Homo* may actually involve drawbacks and limits both in terms of functional and structural interactions, between skull and brain and among their elements (Bruner et al., 2014b). In general, allometric rules can facilitate evolution with a given size range, but they impose functional limits at the extremes of the general ranges of a taxon. Third, some species-specific features must be intended as new specific adaptations to environmental, cultural, or social pressures. In this sense, the evolution or enhancement of specific parietal medial areas to increase visuospatial complexity (and possibly embodiment capacities) may have represented a fundamental change.

It is clear that evolutionary changes based on selective processes can occur at different levels of this network. More importantly, the efficiency of the embodying capacity can be altered (and specifically enhanced) by modification of its components or of the relationships among the components. In the first case, changes of a specific functional area (of the central nervous system as well as of the body) can improve or demote the ability to integrate inner and outer information. In the second case, the components do not change, but their relationships do, by virtue of modifications in the underlying mechanisms of communication and integration. Of course, these two kinds of changes are not mutually exclusive. Although visuospatial abilities are integrated in similar and shared functions, they are likely supported by processes at least partially modularized through distinct pathways. For example, it is interesting to observe that the perception of the shape of an object may rely on processes which are functionally distinct by the processes associated with its manipulation and grasping (Goodale et al., 1994). Hence, it is likely that these two components may undergo integrated but independent evolutionary modifications.

Needless to say, although evolutionary changes can concern specific components or their relationships, then selection will act on the whole system (brain-body-environment), being sensitive to consequent changes of the overall fitness and reproductive potential associated with any genetic, physiological, or cultural, modifications. In this context, any change influencing the embodying ability can increase or decrease the capacity of the organism to rely on extended cognitive schemes. This is of course valid at interspecific (phylogenetic) or intraspecific (individual) level.

To evaluate this scenario, we should consider two main analytical limits. At neontological levels, there is no reason why we should think that living non-human primates may be good proxies for hominid ancestral conditions. Macaques and chimps have evolved millions of years after the divergence with our lineage, and we ignore the directions of such changes. Although we can assume that non-human primates may have changed to a lesser degree from our common ancestor than our own species, such an assumption cannot be strictly tested nor quantified. Primates can supply relevant information for all the shared components (see Iriki and Taoka, 2012), but not for our derived processes. At paleontological levels, information is fragmentary, incomplete, and associated with limited statistical samples. Beyond paleoneurology, the anatomy of the hand can supply further perspectives. It is also worth noting that, within the human genus and most of all in the Neandertal lineage, the inner ear underwent minor but significant changes (Spoor et al., 2003). Although a parsimonious hypothesis can interpret such changes in terms of cranial structural adjustments, these structures are important in body coordination, gaze adjustments, and head motion (Spoor et al., 2007). It is then tempting to include the inner ear morphology within the evolutionary perspective on the visuospatial integration system, through the eye-head-body sensory feedback.

Probably the most relevant test to analyze visuospatial capacities can be provided by archaeology. If visuospatial functions underwent a recent enhancement in the human genus, and if the body has improved (or even changed) its role as an interface between brain and environment, the archaeological record may be able to reveal such differences in terms of operational output. Namely, other visuospatial behaviors can be investigated to evaluate possible phylogenetic changes in this sense. Tool use, tool making, land use, territory management, or hunting techniques can reveal subtle cognitive changes which go beyond the evidence of gross anatomical brain variation.

7. Extending mind, cognitive archaeology, and the social context

In the last decade, integration between cognitive sciences and evolutionary biology is supplying new perspectives in the interpretation of the behavioral evidence associated with paleontological and archaeological information. In cognitive archaeology, one of the first of these attempts was put forward by F. Coolidge and T. Wynn, focusing on possible changes in the working memory processes (Coolidge and Wynn, 2005; Wynn and Coolidge 2003). Following the model introduced by Baddely and Hitch (1974), they proposed that changes in the phonological capacities and executive functions may explain an important enhancement of working memory in modern humans. The frontal areas are a central node for executive functions, and the lower parietal areas are essential for phonological processes. In fact, current theories on intelligence evidence the importance of the fronto-parietal system (Jung and Haier, 2007). The separation in “lobes” is a matter or nomenclature, useful to communicate and share information. In practical terms, we know that the frontal and parietal areas work in tandem, through constant feedbacks (Battaglia-Mayer et al., 2003). The third component of Baddeley’s model is the visuospatial sketchpad, which keeps the spatial and relational coordinates between the parts. Processes associated with visuospatial integration largely rely on crucial nodes of the deep parietal element, like the intraparietal sulcus and the precuneus. Taking into consideration that these areas are central in the coordination between inner and outer environments through the interface of the body, we suggest that they could be relevant when dealing with cognitive extension and body-artifact interface. The intraparietal cortex specifically coordinates the eye-hand functions. The precuneus integrates information from vision, body, and memory. This allows a proper coordination between inner and outer information, so generating a “virtual” or “imagined” space in which we can “think about doing” something. This means a proper management of the interface (the body), and simulation capacity.

Of course, such imagined space may not be a necessary prerequisite to extend the mind, if interpreted as a unidirectional representation of the outer reality. However, it becomes essential in the moment that the cognition does extend, allowing a constant synchronization and interchange between inner and outer worlds, and coordinating a proper use of the body interface. Although the importance of body and perception has been always emphasized in the theories of distributed cognition, the concept of internal or mental "representation" has been generally associated with neurocentric and disembodied cognitivism, based on a strict separation between mind and body (Malafouris, 2013). Such reaction against a rigid dualistic approach has probably generated excessive cautions toward the concept of representation itself. A representation is not necessarily disembodied, and the fact that traditional approaches employed representation in a different way, should not lead to a rejection of the whole perspective (Prinz and Barsalou, 2000). Being an inner and dynamic biological condition, a "representation" would be better considered in the present context as inevitably structured on and within the constant interaction with body components and with external components. Such a "representation" may appear simply as neural configuration, or else a proper spatial scheme based on stimulated imagery and visual processes. Nonetheless, in any case it is generated, influenced, and structured, on elements of the body and of the environment, representing an essential organic component of the cognitive process. The fact that the circuits involved in "representation" and imagery are intra-cranial, does not mean that this involves a neurocentric perspective. We totally agree with the necessity to "look for forms of representation that are more intimately connected to sensory-motor system, which mediate our interaction with the world" (Prinz and Barsalou, 2000; p. 66).

Such "representation" is embodied if it is constituted and structured on body elements, constituted and structured on environmental elements, and physiologically sustained by activation and storage processes which require non-neural elements. A "representation", in this sense, is such because it reproduces relationships, allowing simulations and virtual handling of external elements. Recognizing the importance of the body, of the sensorimotor experience, and of the spatial structure in extended cognition (even when dealing with concepts related to chronological aspects and self awareness – Malafouris, 2013), the role of visuospatial integration in embodying capacity should not be undervalued. This is particularly reasonable when recognizing specific evolutionary changes in those parietal areas which are crucial for the management of the body interface, the management of the body schemata, and the management of the relationships between outer and inner environments.

Taking into consideration the anatomical and evolutionary variability of the parietal areas, at least four potential scenarios can be tentatively discussed to explain the intra- and inter-specific evolutionary changes:

1. Environmental account: the anatomical differences were due to physiological response to training and environmental influences, including cultural ones, and to autocatalytic processes between brain complexity and cultural complexity.
2. Enhanced metaplasticity account: genetic changes involved changes in the sensitivity to training, and selection promoted an increase in the training capacity and neural plasticity.
3. Epigenetic account: environmental influences (including cultural factors) on the molecular structure of the genes altered their expression patterns and generated feedbacks between cultural and biological changes.
4. Genetic account: genetic variations influencing specific parietal functions were positively selected because of cognitive advantages.

These four potential scenarios are of course not mutually exclusive, and all merit future attention with multidisciplinary studies integrating evolutionary neuroanatomy, psychometrics, genetics, and neurophysiology.

It is worth noting that the possibility itself of the mind to extend does not tell anything about the actual efficiency of the cognitive performance. Terms like “intelligence”, “talent”, or “creativity” depend on process capacities but also on the context and the targets. In evolution, the goodness of a behavior is simply measured through the fitness increase/decrease associated with that phenotype. That is, biological (Darwinian) adaptations can be evaluated according to their direct influence on the reproduction rates (the influence on the number of offsprings). In contrast, cultural and social success is less easy to evaluate and quantify. In fact, we currently ignore if “intelligence”, “talent”, and “creativity” may be associated with an increased capacity of extending mind and interaction with the environment, or else with its opposite, namely a minor necessity to do it and a larger independence from contexts and objects.

There are many issues still open in this sense, and probably we are merely scratching the surface. Despite the fact our common feeling suggests that technology is amazingly increasing our possibility of extension (cybertools, internet …), Marco Langbroek wonders whether culture may instead limit our necessity to use the body as a proper interface, by-passing the actual process of mental extension (pers. comm.). It is worth noting that, conversely, it seems that the digital era is just changing the processes of visuospatial integration, and the way our bodies connect. Visuospatial ability is one of the cognitive functions more influenced by videogames, changing asymmetry patterns or sexual differences in short time ranges (Feng et al., 2007). Our neural circuits are currently being shaped by new kinds of extensions, like hand-mouse-cursor, hand-touchpad, hand-screen, hand-keyboards and so on. Maybe it is no coincidence that we have defined this era as “digital”, according to the Latin word *digitus*, which means *finger*.

Theories on extended mind emphasize once more that, because of the feedback between inner and outer components, brain and mind are not only the results of a biological process, but also of a historical process. A mind needs a brain, objects, and a context. Biology provides the brain, culture provides the objects, and society provides the context. In this sense, intelligence and knowledge are relative to the interaction among these three components. Therefore, a special note should be devoted to social networks.

Herbert Spencer, in his book The Study of Sociology (1873), evidenced that “the human being is at once the terminal problem of Biology and the initial factor of Sociology”. In primates, brain evolution and social structure are deeply related by reciprocal influences and limits, brain size and group parameters being strictly associated (Dunbar, 1998, 2008; Dunbar and Shultz, 2007).

Although the precuneus is a main hub of the default mode network, it is also especially active during social tasks and responses (Barks et al., 2015). As a bridge between the sensorial world (visuospatial integration), memory, and inner levels of consciousness, it has been frequently hypothesized to be associated with empathy and autonoesis, both prerequisites for structuring the social context. This is even more intriguing when considering that limits in spatial abilities, influencing the landscape management, can also seriously constrain the social organization according to both neural and ecological parameters (Burke, 2012). The processes involved in internal and external spatial perception and exploration rely on shared neural factors, influencing search strategies, resource exploitation, and the dynamics of the social structure (Hills et al., 2015). Apart from many indirect relationships between spatial management and social cognition, the body is essential to the perception and understanding of others, being the physical entity that experiences and compares the interaction among the social elements (Maister et al., 2015). Interestingly, the complexity of the relationships within groups and between individuals show a strong correlation with behaviors associated with touch, like grooming (Dunbar, 2010). Such contact is essential to stimulate and support networking, probably by direct involvement of opiod endogenous neurotransmitters like the endorphins, through biochemical induction and rewards (Machin and Dunbar, 2011). Therefore it seems that the hand, beyond material culture, has a special role as a functional port also when dealing with social inter-personal interactions. Finger-pointing represents an important cognitive step in infants and, since “The Creation of Adam” of Michelangelo to the lighting finger of Spielberg's E.T., hand contact has always represented something more than a simple mechanical act. M.C. Hescher's famous self-portrait in a spherical mirror (Hand with reflecting sphere – 1935) depicts the circularity of the eye-hand system, where his hand supports the sphere in which he stares at himself. His picture "Drawing hands" (1948) well depicts the complexity that can arise when the object handled by a hand is another hand. We must admit that, if embodiment represents a fundamental process when integrating material culture, it should be even more complex when integrating different minds. Recently, internet has represented an amazing enhancement in this sense, further extending our effective and receptive systems through technological implementations. According to the Gaia Theory proposed by James Lovelock, the analogy between our species and the neural system is, in this sense, striking. Many decades before, Santiago Ramón y Cajal evidenced that, like the desert palms, human heads "fertilize each other by distance" (Reglas y consejos sobre investigación científica - 1897).

If we accept mind extension as a possible mechanism of interaction between brain and environment, between body and objects, we must agree that simulation capacity, the eye-hand system, and the generation of an imaged space as a result of integration between inner and outer environment, must have an interesting role in such process. The fact that *Homo sapiens* display anatomical differences in those areas crucial for these functions is fascinating. The pineal gland of Descartes, which he believed could integrate much of this information, was positioned close to the core of the brain volume. Also the precuneus has a similar pivotal spatial position, in the deep parietal area. And it is interesting that, because of its central role in visual imagery, it was described twenty years ago as "the mind's eye" (Fletcher et al., 1995).

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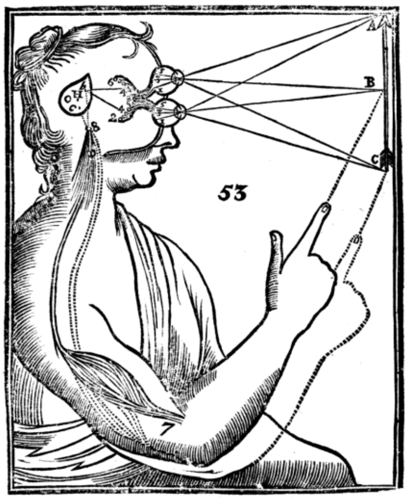

Figure 1. Discussing the dichotomy between body and soul, Descartes gave much importance to the role of the eye-hand system in integrating the outer and inner environments, with the pineal gland being the pivotal structure able to coordinate the process (Meditations metaphysiques, 1641).

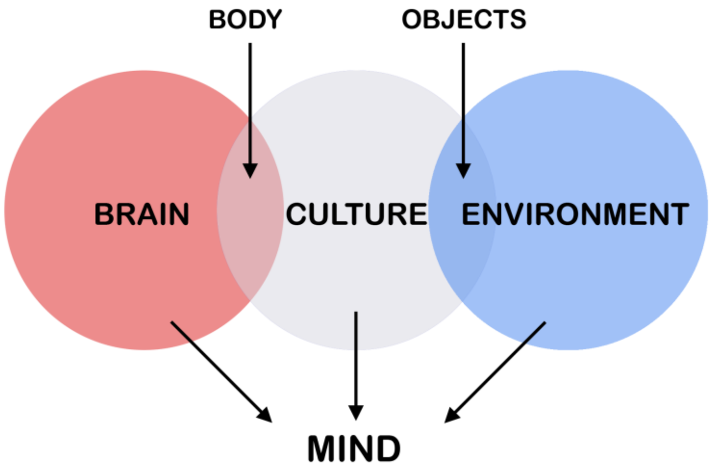

Figure 2. The integration between brain, culture, and environment is a basic principle in human ecology. According to the theory of extended mind, these three systems are all necessary to generate our cognitive levels, these levels being grounded in the body experience and its interactions with the material component of culture.

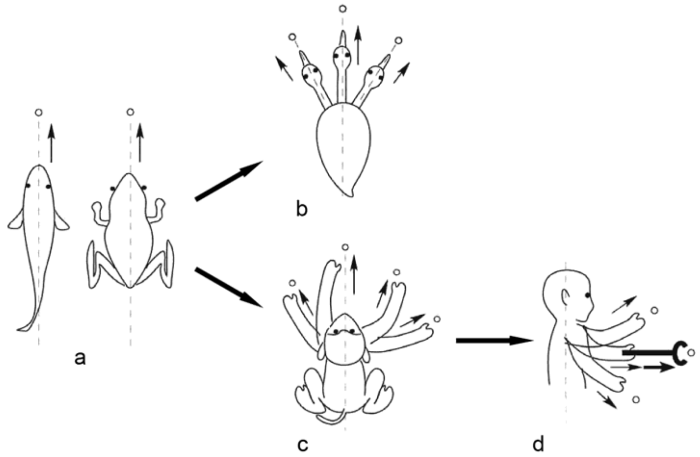

Figure 3. Reaching-and-grasping movements depend on the relationships between body and environment, and by the structural organization of the neurosomatic system. In the simplest process, vertebrates move toward a target with the whole body (a). Birds orientate and redirect their head and neck (b), while primates use their arms (c). In bipedal, brachiator, and leaping primates, the axis of the interaction between body and objects is vertical, due to the orthograde posture. In humans such change is more complex because of handling capacities and use of tools (d). Redrawn after Iriki and Taoka, 2012.

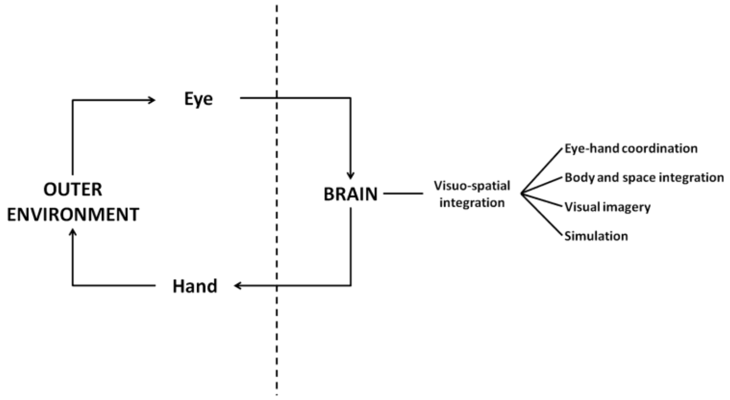

Figure 4. In primates (and most of all in humans), the outer environment enters the nervous system largely through visual inputs, and the nervous system is in contact with the outer environment largely though the hand. The parietal areas are essential nodes of the processes of visuospatial integration coordinating the eye-hand system and the outer and inner environments.

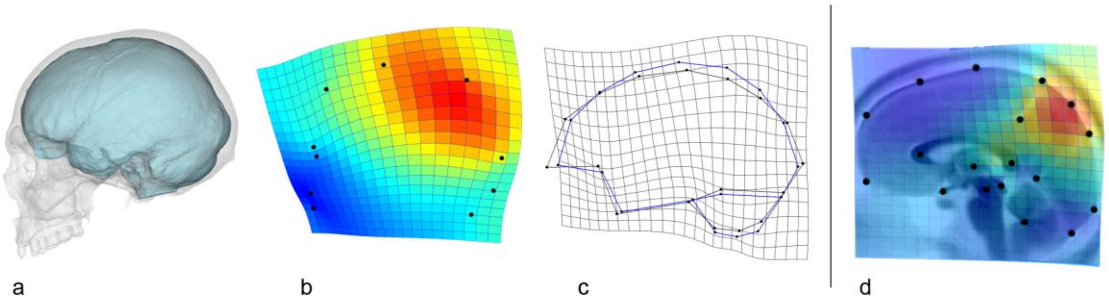

Figure 5. Changes in the parietal areas can be quantified and visualized through geometric approaches: a) tomographic reconstruction of a modern human skull and endocast; b) cranial outline, showing the geometric deformation associated with modern human skull form, that is facial flattening and parietal bulging; c) endocranial outline, showing the spatial deformation associated with modern human brain form, mostly due to parietal bulging; d) the main pattern of intra-specific adult brain form variation in modern humans is due to parietal bulging associated with expansion of the precuneus (data and images after Bruner, 2004; Bruner et al., 2004; Bruner et al., 2014a,b). The inter-specific and intra-specific patterns are very similar, with the former displaying a larger magnitude.

From: Bruner E. & Iriki A. 2016. Extending mind, visuospatial integration, and the evolution of the parietal lobes in the human genus. Quat. Int. (early view).

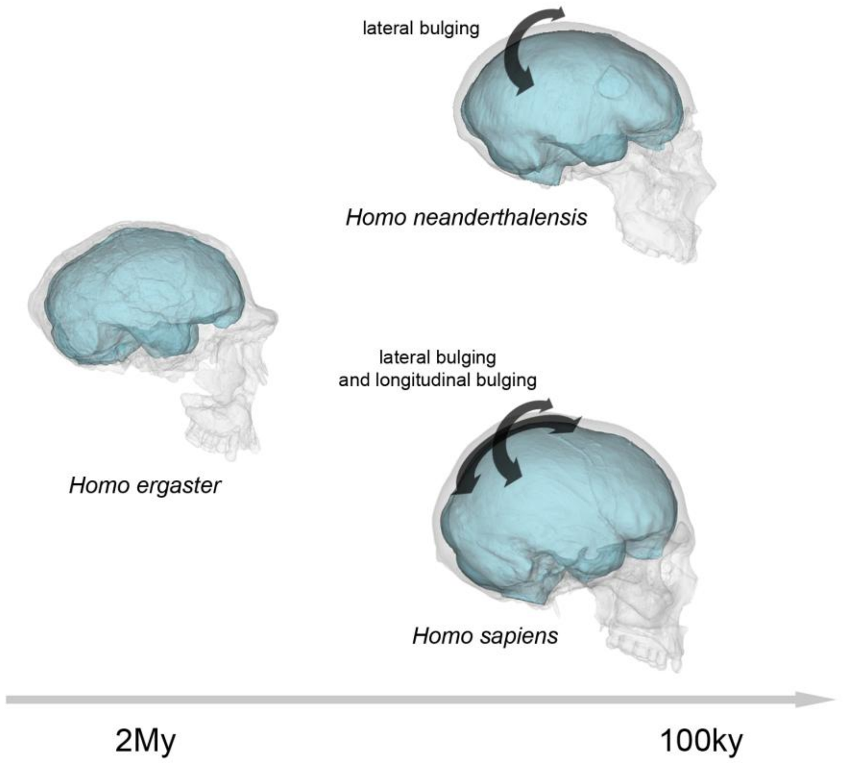

Figure 6. Compared to early humans (*Homo ergaster*), both Neandertals and modern humans have undergone changes in their parietal morphology. The former displayed a lateral bulging of the upper parietal surface, leading to a general “en bombe” profile of the vault in rear view. The latter displayed a similar change, plus a marked longitudinal bulging of the whole upper parietal profile. Both changes were already apparent around 100,000 years ago. However, Neandertals reached their ultimate morphology 50,000 years later, further increasing their cranial capacity.