Visuospatial integration and human evolution: the fossil evidence

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Summary - Visuospatial integration concerns the ability to coordinate the inner and outer environments, namely the central nervous system and the outer spatial elements, through the interface of the body. This integration is essential for every basic human activity, from locomotion and grasping to speech or tooling. Visuospatial integration is even more fundamental when dealing with theories on extended mind, embodiment, and material engagement. According to the hypotheses on extended cognition, the nervous system, the body and the external objects work as a single integrated unit, and what we call “mind” is the process resulting from such interaction. Because of the relevance of culture and material culture in humans, important changes in such processes were probably crucial for the evolution of Homo sapiens. Much information in this sense can be supplied by considering issues in neuroarchaeology and cognitive sciences. Nonetheless, fossils and their anatomy can also provide evidence according to changes involving physical and body aspects. In this article, we review three sources of morphological information concerning visuospatial management and fossils: evolutionary neuroanatomy, manipulative behaviors, and hand evolution.

Keywords – Paleoneurology, Parietal lobes, Dental scratches, Hand anatomy, Embodiment, Extended mind.

Introduction

“Mind” is an elusive word which is scarcely defined in terms of scientific processes and experimental evidence. Some reductionist perspectives even condemn and reject the term as “pre-scientific”, restricting the biological realm to the hard evidence of cells and molecules. While this term is uncomfortable for some fundamentalists of science, at the same time, it represents an opportunity for philosophers and theoretical biologists to go on long metaphysical dissertations. These fields provide elegant and formal logical approaches but, unfortunately, can hardly supply objectives or conclusive contributions in experimental or applicative perspectives. Therefore, it seems that the term “mind” suffers from a bimodal distribution: those who think it is inconvenient, and those who think it is a matter of logic formalisms. Most attempts to approach the middle ground (a reasonable and practical experimental perspective) have been, to date, generally frustrating.

Whatever mind is, there is no doubt it is important, making an essential difference between humans and all the other animals and, at present, between humans and machines. Most traditional views interpreted the mind as a product of the brain, although recognizing that the brain can be influenced by the environment (e.g., Fodor, 1979; Tooby & Cosmides, 1989; Pinker, 1999; Maar, 2010). According to recent hypotheses on extended
Theories on extended mind have two main problems. First, terms are necessarily vague, and concepts are necessarily blurred (see Caramazza et al., 2014). Probably some excesses in trying to put forward formal approaches by philosophers and theoretical biologists are not helping in this sense, delaying further more practical perspectives. Second, mind extension and embodiment are based on factors and processes that are extremely difficult to test in an experimental context. All this becomes even more complicated and speculative when trying to put these concepts into consistent evolutionary hypotheses.

Visuospatial integration can be studied in experimental conditions, and its functions are probably essential for embodiment and mind extensions because they coordinate the relationships between inner and outer environments, and the interactions between body and objects (Bruner & Iriki, 2015). In evolutionary terms, visuospatial functions can be approached following the principles of cognitive archaeology, that aims to integrate archaeological evidence with psychological and neuropsychological perspectives (e.g. Wynn & Coolidge, 2003; Coolidge & Wynn, 2005). In this context, the archaeological evidence mostly deals with tools and environmental variables, as well as with some information from the fossil record. Cognitive archaeology is a field that is largely based on interpreting the available evidence through theoretical and logical assumptions, which are very difficult to investigate through quantitative approaches or even experimental settings. Although caution is required when working with such limits, cognitive archaeology can nonetheless provide relevant hypotheses in the evolutionary debate, generating new perspectives and supplying a different and integrative way to interpret phylogenetic changes. An appropriate and reasonable dose of speculation is necessary, and stimulating.

While waiting for some good ideas to promote more direct evaluations, what we can do in this field is integrate multiple evidence from different aspects, and look empirically for correlations and associations among variables and parameters able to reveal underlying schemes and relationships. In the first case data from different disciplines and topics can converge and support (or not support) hypotheses based on logic assumptions. In the second case, statistics supplies the heuristic tool to reveal correlations that, explained or not according to a formal hypothesis, can provide indirect tools for quantify variables than cannot be measured directly in extinct human groups. In ontological studies, we can count on psychometric analyses, ethnographical studies, or neuroimaging techniques, to investigate topics in neuroanthropology. When dealing with fossil species, conversely, most of these tools are not available, cognition may be something too subtle to evaluate, and we have to deal only with some background elements: residuals of anatomy and behavior.

In this article, we review three lines of evidence that can supply information on the processes of integration between brain, body, and environment, in extinct hominids: brain anatomy as inferred by paleoneurological studies, manipulative behaviors as inferred by dental marks, and manipulative capacity as inferred by hand anatomy.

Human evolution and parietal lobes

Parietal areas have received much attention in paleoanthropology because of their noticeable differences and variation among and within hominids (e.g., Dart, 1925; Weidenreich, 1941; Holloway, 1981). More than ten years ago, shape
analysis and multivariate statistics showed that the form of the modern human brain differs from the other human extinct taxa because of a specific expansion of the parietal surface, taking into account both cranial and cerebral areas (Bruner et al., 2003, 2004; Bruner, 2004). When compared with less encephalized human species, Neandertals display a lateral enlargement of the upper parietal lobules, but modern humans display a much more patent longitudinal expansion of the upper parietal surfaces (Fig.1). That is, although Neandertals and modern humans share a similar cranial capacity, the proportions of their parietal volumes are different (Bruner, 2008). The longitudinal expansion of the parietal bone represents a discrete change of the cranial proportions in modern humans, and not a gradual consequence of brain size increase (Bruner et al., 2011). Therefore, it looks like it is not a secondary morphological effect of encephalization, but an autapomorphic feature, specific of our lineage.

This morphological change is interesting, in terms of paleoneurology, because the morphogenesis of the parietal bone is pretty simple when compared with other cranial districts, this neurocranial area being directly moulded by the underlying parietal cortex (Moss & Young, 1960; Jang et al., 2002; Morriss-Kay & Wilkie 2005). Therefore, a form change of the parietal bone is probably the direct consequence of a form change

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**Fig. 1 - Parietal expansion in modern humans:**

- **a)** areas of expansion (in red) in a newborn skull during the early post-natal stage specific of Homo sapiens (after Gunz et al., 2010);
- **b)** larger areas (in green) in modern human endocasts when compared with Neandertals (after Bruner, 2008);
- **c)** endocranial shape changes in modern humans when compared with Neandertals (red: dilation; blue: contraction);
- **d)** average MRI midsagittal brain scan (90 adults) showing the position of the precuneus (pc) and e) the main pattern of midsagittal brain shape variability among adult humans (red: expansion)(after Bruner et al., 2014a); f) midsagittal brain shape difference between chimpanzees and humans. All these shape variations (ontogenetic, phylogenetic, individual) point at the same parietal area, enlarged in modern humans. In extinct species we cannot know the elements directly involved in these changes but, in living species, these morphological variations are due to the expansion of the precuneus. The colour version of this figure is available at the JASs website.
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of the parietal lobes. Beyond geometry (curvature), a recent study comparing the spatial relationships between parietal bone and parietal lobes suggests that the relative position of their respective boundaries may vary, but their dimensions show anyway a correlation even among adult individuals of the same species (Bruner et al., 2015a).

A study based on morphological correlations between cranial and cerebral areas suggested that Neandertals may have had larger occipital lobes compared with modern humans (Pearce et al., 2014). Taking into consideration that Neandertals had a comparable cranial capacity to modern humans, the inverse relationships between parietal and occipital areas (Gunz & Harvati, 2007), and a supposed evolutionary stability of the parieto-occipital cortical block (Semendeferi & Damasio, 2000), larger occipital lobes in Neandertals should consequently mean larger parietal lobes in modern humans. Also comparing living apes, modern humans have been hypothesized to show a relative reduction of the occipital lobes (De Sousa et al., 2010), which similarly should indicate a reciprocal increase of the parietal ones. Interestingly, among adult modern humans parietal volume is not inversely correlated with occipital volume, but with frontal and temporal dimensions (Allen et al., 2002). This may suggest that intra-specific and inter-specific patterns of variation may not always be based on the same rules.

Further shape analyses have demonstrated that the parietal bulging of the modern braincase is associated with a very early post-natal ontogenetic stage (Neubauer et al., 2009), a stage which is totally absent in chimpanzees (Neubauer et al., 2010) and Neandertals (Gunz et al., 2010). Apart from the early “globularization” ontogenetic stage characteristic of our species, the rest of the endocranial morphogenetic process is quite similar in all living hominoids (Scott et al., 2014).

Preliminary inferences suggested that the geometric changes observed in the modern human braincase could be associated with morphological variations of deep parietal cortical areas, like the intraparietal sulcus (Bruner, 2010). Interestingly, the human intraparietal sulcus shows some species-specific areas which are absent in macaques (Vanduffel et al., 2002; Greffkes & Fink, 2005; Orban et al., 2006). However, a similar parietal bulging described as the principal difference between modern and non-modern braincase was lately described as a main factor determining the variability among adult modern humans, and in this case it is strictly associated with the size and proportions of the precuneus (Bruner et al., 2014a). Such variation is not only a matter of relative size or shape, but it is also due to an absolute increase/decrease of the precuneus cortical surface (Bruner et al., 2015b). The striking similarity between the geometrical variation associated with modern human cranial evolution (inter-specific) and modern human brain variation (intra-specific) suggests that the two morphological changes could be the result of similar factors, namely a relative and absolute increase of the precuneus dimensions (Bruner et al., 2014b).

Recently, midsagittal brain morphology has been compared in humans and chimpanzee, evidencing that also in this case the most apparent difference is a conspicuous enlargement of the precuneus in our species (Bruner et al., 2016). It is hence likely that the precuneus is involved in that specific post-natal parietal bulging stage characterizing the endocranial morphogenesis of Homo sapiens, and absent in chimps (Neubauer et al., 2010) as generally in all apes (Scott et al., 2014).

Interestingly, in modern humans the bulging of the parietal areas is also associated with a remarkable increase in the parietal vascular system, at least as far we can observe when analyzing the traces of the middle meningeal and diploic vessels in fossils (Bruner et al., 2005; Bruner & Sherkar, 2008; Bruner et al., 2010; Rangel de Lázaro et al., 2016). The medial parietal cortex is positioned close to the thermal core of the brain, and is characterized by high metabolic and thermal levels (Cavanna & Trimble, 2006; Sotero & Iturria-Medina 2011; Bruner et al., 2014b). Taking into account that the medial parietal cortex suffers metabolic impairment in the early stages of Alzheimer’s Disease, that this disease is a pathology particularly associated with our species, and that these same areas underwent an
increase in their cortical and vascular complexity in our species, an evolutionary background has been hypothesized to interpret vulnerability to neurodegeneration (Bruner & Jacobs, 2013).

The upper and medial parietal lobes are largely involved in processes of visuospatial integration (see Bruner, 2010 and Bruner & Iriki 2015 for a review). Visuospatial integration aims to coordinate the internal and external environments through the body, which acts as an interface between an inner virtual space (imagined space) and the outer physical elements. Internal and external coordinates are integrated after filtering by selective attention, experience, and sensorial information in order to manage a proper interaction between self and non-self. The intraparietal sulcus is particularly relevant in the management of the eye-hand system which, in primates and especially humans, has a dominant role when compared with other mammals. Eye and hand are the main “ports” of the body interface, being responsible for the main interactions between brain and environment, in one direction (vision) and in the other (touch). The precuneus integrates information from the body (from the somatosensory cortex) with information from the external environment (through vision, from the occipital cortex) (Cavanna & Trimble, 2006; Marguelis et al., 2009; Zhang & Li, 2012). It is essential to generate internal representations and self-centered mental imagery, coordinating self, space, and time (Land, 2014; Peer et al., 2015). Simultaneously it is directly involved, through its inferior areas fading into the posterior cingulate and retrosplenial cortex, in memory, consciousness, autonoesis and self-awareness (“ibid.”). Therefore, there is a cognitive chain of functions and processes which links body management (mostly through the eye-hand system) with consciousness and deep levels of self-perception (Fig. 2). The precuneus is also the main hub of the Default Mode Network, which is the functional basal system of the brain (Buckner et al., 2008; Hagmann et al., 2008; Meunier et al., 2010). It is likely that all these functions must be interpreted within a more general network which integrates visuospatial and executive functions, as represented by the fronto-parietal system (Jung & Haier, 2007; Basten et al., 2015; Caminiti et al., 2015). For example, a human-specific network between frontal and upper parietal areas seems to be necessary to shift from emulation (reproducing results) to imitation (reproducing processes) (Hecht et al., 2013). Taking into account the importance of these areas (most of all the precuneus) in brain biology and cognition, and their possible involvement in processes associated with embodiment, its patent morphological change strictly associated with Homo sapiens merits attention.

It is worth noting that the fossil skull of Jebel Irhoud, dated to 150 ka and generally assigned to the lineage of modern humans, does not display a visible bulging of the parietal areas, suggesting that the origin of modern humans may have been chronologically separated from the origin of a modern human brain (Bruner & Pearson, 2013). These brain areas are sensitive to both genetic and environmental effects (Chen et al., 2012; Iriki & Taoka, 2012) and, therefore, the mechanisms underlying their morphological variations at inter-specific and intra-specific level are still to be investigated.
Labial scratches on Neandertals’ anterior teeth

Dental anthropology is not generally used to make inferences on cognition and brain evolution. Nonetheless, teeth are an essential component of the ecology of a species and, as such, they can reveal interesting species-specific behaviors. Hominids use their anterior teeth as a tool or as a third hand to process foodstuffs and non-diet related materials. This behavior produces different types of dental wear. Labial scratches on the labial face of incisors and canines are one of the most common forms of evidence of the use of teeth as a tool. Meat or other materials can be held between the anterior teeth, and cut with a stone tool by means of the so-called “stuff and cut” technique (Brace, 1967). Sometimes, the sharp edge of the tool can scratch the enamel, leaving a mark on the dental surface. The resulting scratches are arranged more or less obliquely, and they are visible to the naked eye. Observation under a Scanning Electron Microscope is nonetheless necessary to characterize their specific morphology (Fig. 3). The edges of these scratches are linear, well-defined, and parallel to each other along most of their extension. The bottom of the striations usually displays a “V-shape” transverse section and it is furrowed by several parallel microscratches running longitudinally along the entire length of the groove (Bermúdez de Castro et al., 1988; Lozano et al., 2004, 2008).

Labial scratches have been recorded on anterior teeth belonging to different species of the human genus. Until now, the earliest evidence comes from European Middle Pleistocene populations, like those from Boxgrove & Mauer (Bello, 2011). The Sima de los Huesos (SH) sample (Burgos, Spain) represents the largest fossil group with these scratches (Bermúdez de Castro et al., 1988; Lozano et al., 2008). Labial scratches were scored on anterior teeth from 21 SH individuals, indicating that the use of teeth as a tool was a well-established habit among these hominids as far as 430,000 years ago (Lozano et al., 2009, Arsuaga et al., 2014). Neandertals relied on this behavior more than the former species because their teeth show an even higher number of scratches when compared with SH individuals (Frayer et al., 2012). Labial scratches have been documented on Neandertal teeth of Krapina, Vindija, Le Regourdou, La Quina, Cova Negra, Shanidar, Valdegoba, Hortus and El Sidrón (De Lumley, 1973; Puech, 1979; Bermúdez de Castro et al., 1988, Lalueza Fox & Pérez Pérez, 1994; Lalueza Fox & Frayer, 1997; Frayer et al., 2010, Frayer et al., 2012, Volpato et al., 2012, Estalrrich & Rosas, 2013; Lozano et al. 2015). The “stuff and cut” technique was carried out by Neandertals throughout their evolutionary range, without any apparent differences related to chronology or geographic location.

Labial scratches are often used to provide information about cultural practices and the way Neandertals performed some tasks to manipulate vegetal fibers, leather and meat (Lalueza Fox & Frayer, 1997; Estalrrich & Rosas, 2013, 2015). However, apart from these cultural and ecological inferences, labial scratches can also supply information about specific behavioral aspects, like hand laterality (Bermúdez de Castro et al., 1988; Lalueza Fox & Frayer, 1997; Lozano et al., 2009; Frayer et al., 2012). The observation of detailed tooling tasks has been considered the best way to determine hand laterality (Faurie & Raymon; 2004, Faurie et al., 2005). In this sense, it was assumed that labial scratches represent direct evidence of the use of tools. In fact, labial scratches were replicated experimentally showing different orientation depending on the hand used for holding the stone tool (Bermúdez de Castro et al., 1988; Lozano et al., 2004, 2008). Right-handers produce most of the scratches with right oblique orientation, whereas left oblique orientation was the most common in the case of left-handers. The preferred orientation for both Homo heidelbergensis and Neandertals was the right oblique, indicating the use of the right hand to hold tools and carry out the “stuff and cut” technique (Lozano et al., 2009; Uomini, 2009; Frayer et al., 2012; Volpato et al., 2012; Uomini, 2015). According to this kind of data, left-handed people among Neandertals showed a prevalence which was very similar to our species, that is about 10% (Uomini, 2009; Frayer et al.,
Hand lateralization is strongly related to brain lateralization, and this, in turn, is associated with an ability in language (Lieberman, 2002; McManus, 2004; Uomini, 2009, 2015; Uomini & Meyer, 2013).

Also modern humans use their teeth for manipulation and other cultural tasks. However, the presence of labial scratches in our species declined dramatically when compared with Neandertals. The scarce evidence of labial scratches has been reported on the teeth of some Neolithic and Chalcolithic populations, American paleoindians, and modern hunter-gatherer populations such as Tasmans, Aleutians, Inuits, Australian aborigines and Fuegians (Green et al., 1998; Lalueza Fox, 1992; Lozano et al., 2008; Lucaks & Pastor, 1988; Merbs, 1968). A study on 31 Australian aborigines evidenced the presence of marks in only 43% of the individuals, showing on average just one single scratch per tooth (Lozano et al., 2008). This is pretty different from the situation described in Homo heidelbergensis and Neandertals, which show the presence of scratches in 100% of the individuals, and with an average of 44 marks per tooth (mean computed from Hillson et al., 2010; Frayer et al., 2010, 2012; Volpato et al., 2012; Estalrich & Rosas, 2013). Therefore, it is apparent that, compared with Neandertals, dental scratches in modern humans are not frequent, both in terms of number of specimens presenting the marks and in terms of number of scratches. Taking into account the evolution of Homo sapiens from its origin to its present condition, it can be easily concluded that the use of the mouth as a third hand is not necessary to develop a complex culture.

So, apart from information on ethnological and lateralization issues, what is more relevant is the high frequency of this behavior. Modern humans use the mouth for praxis only to a limited extent, regardless of their possible cultural complexity. In those modern populations that use teeth more frequently for non-alimentary purposes, such use leaves few or no scratches. Therefore, the high prevalence of scratches (percentage of individuals) and their degree of expression (number of scratches) reveal a specific behavior particularly associated with the Neandertal lineage, and not with modern humans. Taking into account the importance of the mouth from an ecological perspective (food processing), its regular involvement in manipulation represents a risky choice, which is likely the result of a non-optimal reuse of anatomical elements. Considering that Neandertals had a complex culture comparable with early Homo sapiens, but without showing a patent enlargement of those parietal areas associated with modern humans.
Visuospatial integration, it has been hypothesized that the substantial involvement of the mouth for praxis could have been the result of a mismatch between cultural processes, neuroanatomical organization, and embodiment capacity (Bruner & Lozano, 2014, 2015).

Evolution of the hand in the genus *Homo*

Despite the fact there is a good fossil record of the hands of early hominids such as *Ardipithecus ramidus*, *Australopithecus afarensis* and *Australopithecus sediba* (Lovejoy et al., 2009; Kivell et al., 2011), the hand anatomy of early *Homo* is paradoxically unknown. The evolution of the hand in our genus is still a matter of debate because for many human species only a limited number of remains are clearly associated with cranial or dental evidence, which makes their taxonomic attribution difficult.

Napier (1962) and Leakey et al. (1964) included a set of hand bones found at Olduvai Gorge, together with early stone tools, in the definition of *Homo habilis*. These hand remains were basically similar to modern humans but showing some anatomical differences. The saddle shape of the articular facet between trapezium and thumb and the presence of the flexor pollicis longus insertion in the distal pollical phalanx suggest that *H. habilis* possessed modern human-like grip capabilities (Marzke & Marzke, 2000). Unfortunately, it was not possible to determine the length of the thumb relative to the rest of the fingers. However, a recent morphometric study conducted by Moyà-Solà et al. (2008) suggests that the OH7 hand most likely belongs to the genus *Paranthropus*. It is important to note that this alternative taxonomic hypothesis could have implications regarding the presence of morphological features related to human-like grasping also in robust australopithecines.

A similar taxonomic problem involves the hand remains recovered at the South African sites. The most abundant hand fossil record comes from Swartkrans Members 1 and 2, where both genus, *Homo* and *Paranthropus*, have been identified (Susman, 1988, 1994). Using this evidence, Susman (1988, 1994) advocated the hypothesis that *Paranthropus* was also a toolmaker because he found many similarities between Swartkans and modern human hands. Around 95% of the craniodental remains from Swartkans Member 1 are attributable to *P. robustus* and most of the hand remains are likely to belong to this taxon. Nonetheless, there is a substantial uncertainty in the taxonomic attribution of the isolated hand remains from this site.

Some recent studies (Ward et al., 2014; Lorenzo et al., 2015; Domínguez-Rodrigo et al., 2015) about isolated hand remains coming from two different sites, both of them older than 1 Ma., suggest that some characteristics of the modern human hand arose early in the evolution of the genus *Homo*. Ward et al. (2014) noticed the presence of a styloid process in a 1.42 Ma old third metacarpal from West Turkana, while Lorenzo et al. (2015) described remarkable similarities between modern humans and a proximal hand phalanx found at Sima del Elefante site from Sierra de Atapuerca, dated to 1.2-1.3 Ma. More recently, Domínguez-Rodrigo et al. (2015) reported the discovery of a manual proximal phalanx from Olduvai >1.84-million-year-old (Ma) showing similarities with modern human hands. Also from the Sierra de Atapuerca, the hand remains from Dolina TD6 level, dated to 800-900 ka, showed features that characterize the hands of modern humans and Neandertals (Lorenzo et al., 1999).

Hand remains from Anatomically Modern Humans (AMHs) and Neandertals are more abundant, and different studies have analyzed the similarities and differences between both populations (see Niewoehner, 2001; Lorenzo, 2015; and references therein). Also in this case, the large SH sample supplies significant evidence of the hand morphology associated with those groups that were probably ancestors of the Neandertal morphotype (Lorenzo et al., 2012). Some of the anatomical traits that characterize the Neandertal hand (Fig. 4) can be traced back to at least the Middle Pleistocene: development of the palmar tubercles related with the carpal tunnel dimension, thumb morphology and
proportion, phalangeal trochlea morphology and distal tuberosity expansion. Neandertals are characterized by having a greater general robusticity with expanded distal tuberosities, broader trochleas on the middle phalanges, large and projected palmar tubercles on the carpal bones, relatively short thumb proximal phalanges, relatively flat surfaces on the first and fifth metacarpals, and a large insertion for the *opponens pollicis* on the first metacarpal. Some authors have used this distinctive pattern of the Neandertal hand to hypothesize different manipulative capabilities between Neandertals and AMHs (Niewoehner, 2001; Churchill, 2001). However, the functional interpretation of the differences in the hand morphology between these human groups is largely speculative, and there is no agreement on possible advantages associated with their specific anatomy.

Among modern human populations, the hand displays a remarkable variation, but several features distinguish AMHs from extinct human species, such as a reduction of the distal tuberosity

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*Fig. 4 - The left hand of Kebara 2, showing main Neandertal features. The colour version of this figure is available at the JASs website.*
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in distal phalanges, relatively short distal pollical phalanx, and less broad trochleas in middle phalanges. Although we still lack any evidence of very early AMH hand anatomy associated with the African record (White et al., 2003), the Near East specimens from Qafzeh and Skhul suggest that the modern hand morphology was present at least 110,000 years ago. Those AMHs showed a hand morphology which was similar to modern populations, although generally more robust (Niewoehner, 2001). These Near East areas show an alternate presence of Neandertals and AMH between 120,000 and 50,000 years ago. Here, AMH hands are associated with Middle Paleolithic (Mousterian) stone-tool assemblages that cannot be clearly differentiated from assemblages associated with Neandertals. Therefore, despite the fact Neandertals and modern humans shared a very similar technology at that time, the anatomy of the hand displayed different traits.

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Functions associated with visuospatial integration are essential in coordinating brain, body, and environment, and hence represent a crucial aspect of processes associated with extended cognition and embodiment (Bruner & Iriki, 2015). Archaeology can supply relevant information in this sense, analyzing those cognitive capacities underlying the cultural evidence available for past populations (Malafouris, 2010b; Coolidge & Wynn, 2005). Furthermore, cognitive levels in extinct species can also be tentatively inferred reconstructing the associated behaviors and their neural parameters, from tool use and tool production (Stout & Chaminade, 2007; Stout et al., 2015) to land use and management (Burke, 2012). Nonetheless, fossils can also add further evidence on visuospatial capacities, taking into account variations associated with anatomical elements which are involved in visuospatial processes.

Modern humans show a specific enlargement of the upper and medial parietal areas, which are critical nodes for visuospatial integration. Modern humans also largely rely on hands for manipulation, whereas Neandertals and Middle Pleistocene humans needed further anatomical elements (the mouth) as a body interface between brain and culture. Furthermore, although they shared a similar technology with Neandertals, the morphology of their hands displayed some specific characters, suggesting a different manipulative dynamic.

Concerning praxis and the use of the mouth for handling procedures, it is worth noting that according to the somatosensory representation in our cortex (the so called “homunculus”), the mouth is the second largest element after the hands. It is therefore the natural and automatic alternative as a body interface when hands are not sufficient. Actually, the mouth is a central somatosensory element, because of its complex innervations and multiple histological components, integrating external and internal information (Haggard & De Boer, 2014). In human infants mouth is a main interface to interact with the environment, but the hand-mouth coordination loses importance the more the hand-eye system reaches a sufficient degree of maturation (Rochat, 1989, 1993). In this sense, developmental neuropsychology can provide useful information on the reciprocal (and antagonistic) somatosensory and cognitive relationships between mouth and hand, mostly when considering that the former has a peculiar limitation: its exploratory behavior can be hardly integrated with vision.

Concerning hand morphology, apart from strict biomechanical issues (like strength or precision) it must be taken into account that hand is the terminal component of the corticospinal axis, and the direct interface between neural networks and the extra-neural outer components of the material culture (Iriki & Sakura, 2008; Iriki & Taoka, 2012). It is integrated as an “extension” in neural terms, and such integration is further extended when the hand contacts an object (Maravita & Iriki, 2004). Structurally, it is an active interface operating and sensing through dynamic touching, and biomechanically organized on tensional forces that generate large-scale functional responses (Turvey & Carello, 2011).
The fact that evolutionary changes in these elements are associated with changes of those brain areas involved in visuospatial integration may not be due to chance.

Recently it has been further hypothesized that embodiment can also be a main factor in language processing (see Jirak et al., 2010). There is a general agreement on the possibility that hand and speech may have co-evolved sharing neural structures and functions (e.g., Binkofski & Buccino, 2004). Now the evidence is going even further, suggesting that sensorimotor simulation involving mirror neuron mechanisms is associated with words processing, providing a direct link between body and language (e.g., Buccino et al., 2005; Marino et al., 2012).

It is evident that cognitive archaeology must necessarily rely on speculations and logic assumptions. Integrating multiple sources of evidence, we can nonetheless orientate research toward robust and reasonable hypotheses. We cannot forget that the anatomical changes described in this article and associated with Upper Pleistocene modern humans are also associated with cultural changes which are patently related to visuospatial abilities, like for example the successive development of a very different technology, explicit indications of projectile techniques, and development of a remarkable graphic capacity. The role of the parietal cortex (and specifically of the precuneus) in the management of internal representations and egocentric memory (Land, 2014) is in fact patently relevant when considering that parietal changes in modern humans were associated with noticeable changes in drawing capacities, as far as we can evince from the current archaeological record. Interestingly, visuospatial differences between modern humans and Neandertals have also been hypothesized to explain differences in the use and perception of environmental space (Burke, 2012). It remains to be evaluated whether such differences could have been the result of specific genetic changes undergoing selection, or else of epigenetic and physiological feedbacks induced by environmental and cultural factors (Bruner & Iriki, 2015). It must be also taken into account that humans and non-human primates share a very similar organization of the upper parietal areas (Mars et al., 2011; Caminiti et al., 2015), suggesting that human specific traits or processes can be a matter of degree or “neural reuse”, more than brand-new features. These areas display nonetheless complex parcellation schemes (Scheperjans et al., 2008a,b), and subtle but relevant changes can be difficult to recognize and quantify.

We are now realizing that probably the body and the environment have a more active and dynamic role within the mechanisms of cognition (Haggard, 2005; Byrne et al., 2014). The situation is even more complex when brains and bodies interact with other brains and bodies, and we are just discovering how much space and body can influence our social structure (e.g., Hills et al., 2015; Maister et al., 2015). In fact, a self-based coordination is essential to integrate spatial, chronological, and social perception (Peer et al., 2015). Primate evolution is characterized by a peculiar rule: brain size is proportional to the size of the social group (Dunbar, 1998, 2008). Interestingly, the size and degree of social relationships in primates are strongly correlated with endorphin release which, in terms of behavior, shows a remarkable correlation with grooming activity (Dunbar, 2010; Machin & Dunbar, 2011). This means that, even in a social context, psychological and neurophysiological processes largely rely on one forgotten but evolving sense: touch.

Acknowledgments

We are grateful to Stefano Parmigiani, Telmo Pievani and Ian Tattersall, for the invitation to write this article, and for the organization of the meeting “What made us human?” (Erice, 2014). EB, CL, and ML are funded by the Spanish Government (CGL2012-38434-C03-01/02/03). EB is also funded by the Italian Institute of Anthropology (ISItA). CL is supported by AGAUR 2014 SGR 899. ML is funded by 2014 SGR 900 Group of Analyses on Socio-ecological Processes, Cultural Changes and Population dynamics during Prehistory (GAPS) of the
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Generalitat de Catalunya. We are grateful to Enza Spinapolice, Karenleigh Overmann, Ariane Burke, Annapaola Fedato, Joseba Ríos Garaizar, Lambros Malafouris and Duilio Garofoli for their help and comments on visuospatial integration and cognitive archaeology. Stefano Parmigiani, Pier Francesco Ferrari, and Antonella Tremacere, supplied further comments on the early draft of this article.

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