doi 10.4436/jass.94025

JASs Proceeding Paper
Journal of Anthropological Sciences
Vol. 94 (2016), pp. 81-97

Visuospatial integration and human evolution: the fossil evidence

Emiliano Bruner[1,2], **Marina Lozano**[3,4] & **Carlos Lorenzo**[3,4]

1) *Centro Nacional de Investigación sobre la Evolución Humana, Burgos, Spain*
e-mail: emiliano.bruner@cenieh.es

2) *Istituto Italiano di Antropologia, Roma, Italy*

3) *Institut Català de Paleoecologia Humana i Evolució Social, Tarragona, Spain*

4) *Universitat Rovira i Virgili (URV),Tarragona, Spain*

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 cognition, mind could be instead an emergent property of the interaction between brain, body, and environment (Clark, 2007, 2008). Following this view, the body is an active part of this process, working as an interface that filters information and activates processes (Maravita & Iriki, 2004; Iriki & Taoka, 2012). Objects, which represent the material component of culture, are essential elements too, storing external information, inducing and modulating neural mechanisms, influencing and training our sensorial and computational capacities (Malafouris 2008, 2010a, 2013, 2014). Therefore, the brain may be an essential node of this process, but the final result (described by the uncomfortable term "mind") emerges from the interaction between neural, body, and external components.

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 neontological 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

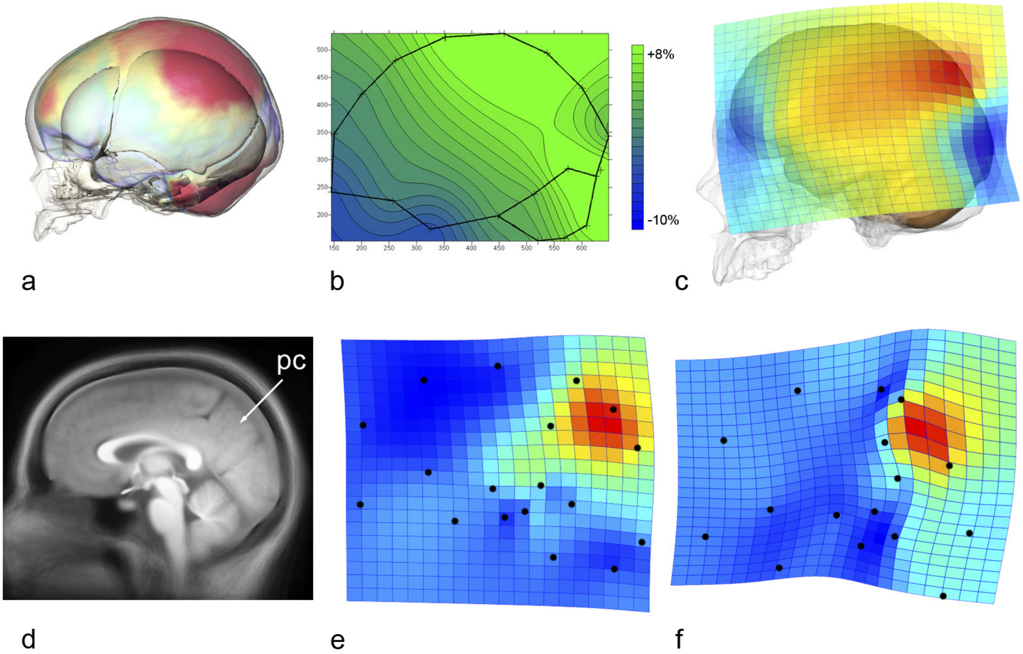

Fig. 1 - Parietal expansion in modern humans: a) areas of expansion (in red) in a newborn skull during the early post-natal stage specific of* Homo sapiens *(after Gunz et al., 2010); b) larger areas (in green) in modern human endocasts when compared with Neandertals (after Bruner, 2008); c) endocranial 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.

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 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 shows 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; Grefkes & 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 & Sherkat, 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 restrosplenial 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.

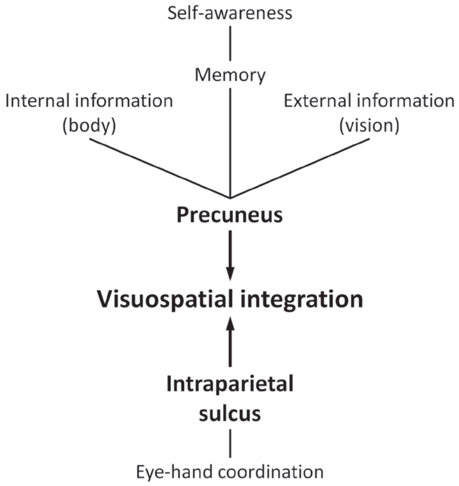

Fig. 2 - The medial and deep parietal areas (the precuneus midsagittaly and the intraparietal sulci parasagittaly) are largely involved in visuospatial integration, coordinating information from inner and outer environments. These processes are essential in the management of the body interface, and in the capacity of simulation and mental imagery.

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 Regordou, 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.*,

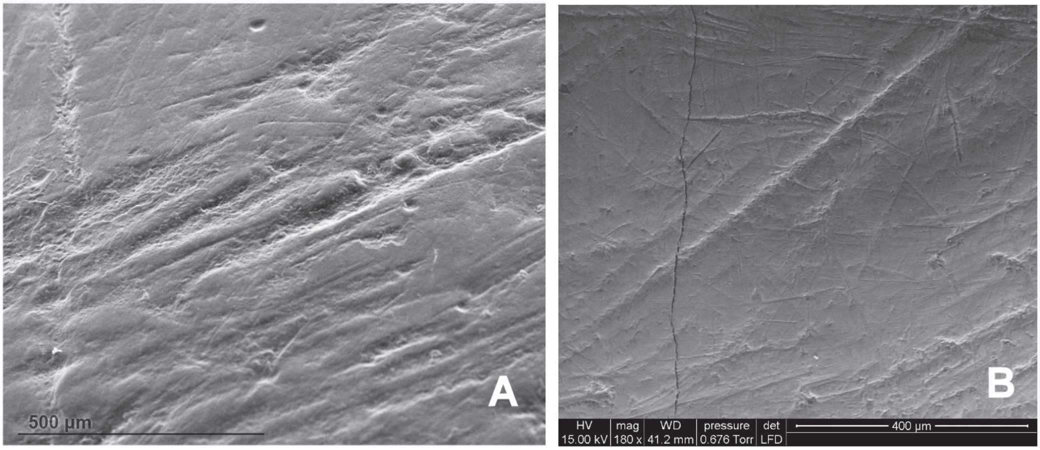

Fig. 3 - A. Labial scratches on an incisor from Sima de los Huesos site (Sierra de Atapuerca, Spain). B. Labial scratches on a Neandertal incisor from the Valdegoba site (Spain). Both are SEM images.

2012). 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; Estalrrich & 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 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 *Paranthopus* was also a toolmaker because he found many similarities between Swartkrans and modern human hands. Around 95% of the craniodental remains from Swartkrans 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

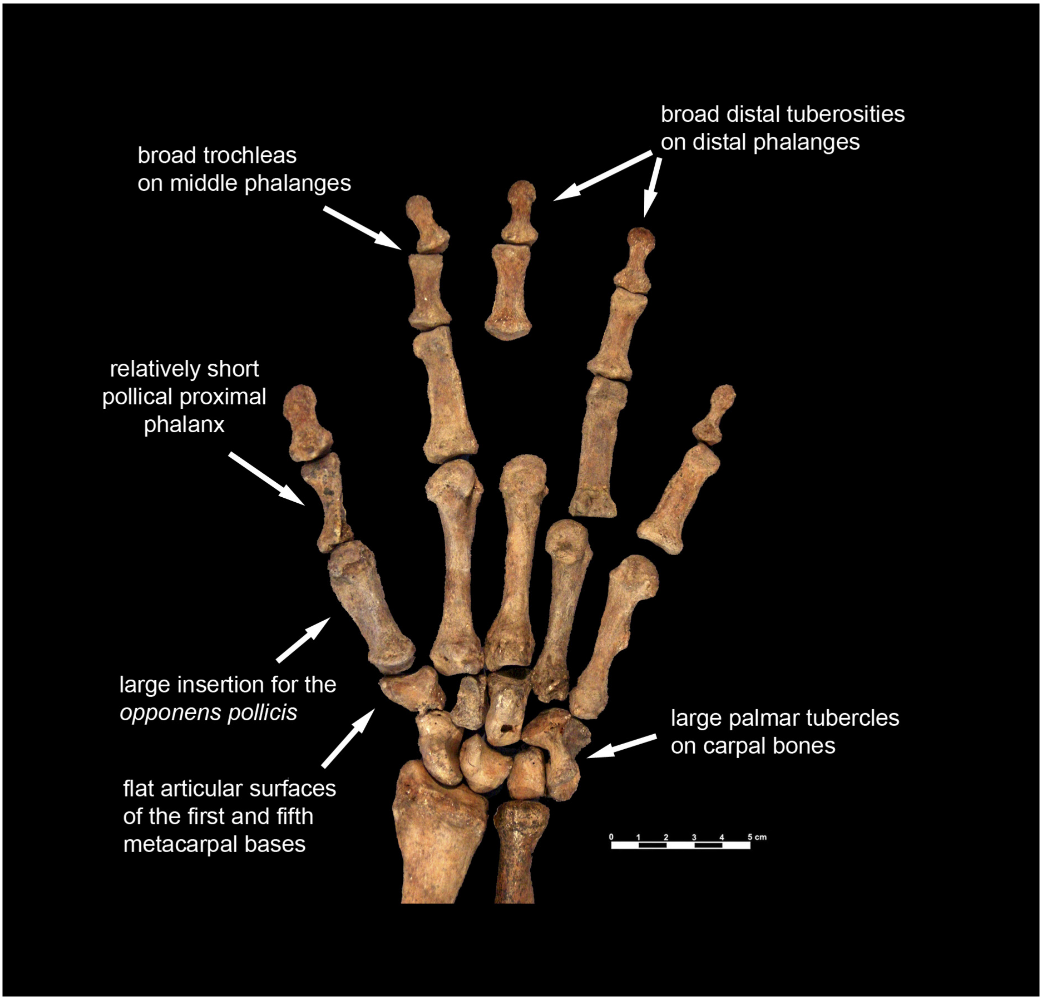

Fig. 4 - The left hand of Kebara 2, showing main Neandertal features. The colour version of this figure is available at the JASs website.

proportion, phalangeal throchlea 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 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.

Visuospatial integration and paleoanthropology

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 be also 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 (Scheperjians *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; Byrge *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

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.

References

Allen J.S., Damasio H. & Grabowski T.J. 2002. Normal neuroanatomical variation in the human brain: an MRI-Volumetric Study. *Am. J. Phys. Anthropol.* 118: 341–358.

Arsuaga J.L., Martínez I., Arnold L.J., Aranburu A., Gracia-Téllez A., Sharp W. D., Quam R., Falguères C., Pantoja-Pérez A., Bischoff J. *et al.* 2014. Neandertal roots: Cranial and chronological evidence from Sima de los Huesos. *Science*, 344: 1358-1363.

Basten U., Hilger K. & Fiebach C.J. 2015. Where smart brains are different: a quantitative meta-analysis of functional and structural brain imaging studies on intelligence. *Intelligence*, 51: 10-27.

Bello S. 2011. New results from the examination of cut-marks using three-dimensional imaging. *Develop. Quat. Sci.*, 14: 249-262.

Bermúdez de Castro J.M., Bromage T. & Fernández-Jalvo Y. 1988. Buccal striations on fossil human anterior teeth: evidence of handedness in the middle and early Upper Pleistocene. *J. Hum. Evol.*, 17: 403-412.

Binkofski F. & Buccino G. 2004. Motor functions of the Broca's region. *Brain Lang.*, 89: 362-369.

Brace C.L. 1967. Environment, tooth form, and size in the Pleistocene. *J. Dent. Res.*, 46: 809-816.

Bruner E., 2004. Geometric morphometrics and paleoneurology: brain shape evolution in the genus *Homo*. *J. Hum. Evol.*, 47: 279-303.

Bruner E. 2008. Comparing endocranial form and shape differences in modern humans and Neandertal: a geometric approach. *PaleoAnthropology,* 2008:93-106.

Bruner E. 2010. Morphological differences in the parietal lobes within the human genus. *Curr. Anthropol.*, 51: S77-S88.

Bruner E. & Iriki A. 2015. Extending mind, visuospatial integration, and the evolution of the parietal lobes in the human genus. *Quat. Int.,* doi:10.1016/j.quaint.2015.05.019.

Bruner E. & Jacobs H.I.L. 2013. Alzheimer's Disease: the downside of a highly evolved parietal lobe? *J. Alzheimers Dis.*, 35: 227-240.

Bruner E. & Lozano M. 2014. Extended mind and visuospatial integration: three hands for the Neandertal lineage. *J. Anthropol. Sci.*, 92: 273-280

Bruner E. & Lozano M. 2015. Three hands: one year later. *J. Anthropol. Sci.*, 93: 191-195.

Bruner E. & Pearson O., 2013. Neurocranial evolution in modern humans: the case of Jebel Irhoud 1. *Anthropol. Sci.*, 121: 31-41.

Bruner E. & Sherkat S. 2008. The middle meningeal artery: from clinics to fossils. *Child's Nerv. Syst.*, 24: 1289-1298.

Bruner E., Manzi G. & Arsuaga J.L. 2003. Encephalization and allometric trajectories in the genus *Homo*: evidence from the Neandertal and modern lineages. *Proc. Natl. Acad. Sci. USA*, 100: 15335-15340.

Bruner E., Mantini S., Perna A., Maffei C. & Manzi G. 2005. Fractal dimension of the middle meningeal vessels: variation and evolution in *Homo erectus*, Neanderthals, and modern humans. *Eur. J. Morphol.,* 42; 217- 224.

Bruner E., De la Cuétara J.M. & Holloway R. 2011. A bivariate approach to the variation of the parietal curvature in the genus *Homo*. *Anat. Rec.*, 294: 1548-1556.

Bruner E., Rangel de Lázaro G., de la Cuétara J.M., Martín-Loeches M., Colom R. & Jacobs H.I.L. 2014a. Midsagittal brain variation and MRI shape analysis of the precuneus in adult individuals. *J. Anat.*, 224: 367-376.

Bruner E., de la Cuétara J.M., Masters M., Amano H. & Ogihara N. 2014b. Functional craniology and brain evolution: from paleontology to biomedicine. *Front. Neuroanat.*, 8: 19.

Bruner E., Amano H., de la Cuétara J.M. & Ogihara N. 2015a. The brain and the braincase:

a spatial analysis on the midsagittal profile in adult humans. *J. Anat.* 227: 268-276.

Bruner E., Román F.J., de la Cuétara J.M., Martin-Loeches M. & Colom R. 2015b. Cortical surface area and cortical thickness in the precuneus of adult humans. *Neuroscience*, 286: 345-352.

Bruner E., Preuss T., Chen X., Rilling J. 2016. Evidence for expansion of the precuneus in human evolution. *Brain Struct. Funct.,* DOI 10.1007/s00429-015-1172-y.

BuccinoG., Riggio L., Melli G., Binkofski F., Gallese V. & Rizzolatti G. 2005. Listening to action-related sentences modulates the activity of the motor system: a combined TMS and behavioral study. *Cogn. Brain Res.*, 24: 355-363.

Buckner R.L., Andrews-Hanna J.R. & Schacter D.L. 2008. The brain's default network. *Ann. NY Acad. Sci.*, 1124: 1–38.

Burke A. 2012. Spatial abilities, cognition and the pattern of Neanderthal and modern human dispersal. *Quat. Int.*, 247: 230-235.

Byrge L., Sporns O. & Smith L.B. 2014. Developmental process emerges from extended brain-body-behavior networks. *Trends Cogn. Sci.*, 18: 395-403.

Caminiti R., Innocenti G.M. & Battaglia-Mayer A. 2015. Organization and evolution of parieto-frontal processing streams in macaque monkeys and humans. *Neurosci. Biobehav. Rev.,* 56: 73-96.

Caramazza A., Anzellotti S., Strnad L. & Lingnau A. 2014. Embodied cognition and mirror neurons: a critical assessment. *Ann. Rev. Neurosci.* 37: 1-15.

Cavanna A.E. & Trimble M.R. 2006. The precuneus: a review of its functional anatomy and behavioural correlates. *Brain*, 129: 564-583.

Chen C.H., Gutierrez E.D., Thompson W., Panizzon M.S., Jernigan T.L., Eyler L.T., Fennema-Notestine C., Jak A.J., Neale M.C., Franz C.E. *et al.*, 2012. Hierarchical genetic organization of human cortical surface area. *Science*, 335: 1634-1636.

Churchill S.E. 2001. Hand morphology, manipulation, and tool use in Neandertals and early modern humans of the Near East. *Proc. Natl. Acad. Sci. USA*, 98: 2953-2955.

Clark A. 2007. Re-inventing ourselves: the plasticity of embodiment, sensing, and mind. *J. Med. Philos.*, 32: 263–282.

Clark A. 2008. *Supersizing the mind. Embodiment, action, and cognitive extension*. Oxford University Press, Oxford.

Coolidge F. & Wynn T. 2005. Working memory, its executive functions, and the emergence of modern thinking. *Cambridge Archaeol. J.*, 15: 5-26.

Dart R.A. 1925. *Australopithecus africanus*: the man-ape of South Africa. *Nature*, 2884: 195-199.

De Lumley M.A. 1973. *Anténéandertaliens et nándertaliens du bassin méditerranéen occidental européen*. Laboratoire de Paleontologie Humaine et de Prehistoire, Marsella.

De Sousa A.A., Sherwood C.C., Mohlberg H., Amunts K., Schleicher A., MacLeod C.E., Hof P.R., Frahm H. & Zilles K. 2010. Hominoid visual brain structure volumes and the position of the lunate sulcus. *J. Hum. Evol.*, 58: 281-292.

Domínguez-Rodrigo M., Pickering T.R., Almécija S., Heaton J.L., Baquedano E., Mabulla A. & Uribelarrea D. 2015. Earliest modern human-like hand bone from a new >1.84-million-year-old site at Olduvai in Tanzania. *Nature Comm.*, 6: 7987.

Dunbar R.I.M. 1998. The social brain hypothesis. *Evol. Anthropol.*, 6: 178-190.

Dunbar R.I.M. 2008. Mind the gap: or why humans aren't just great apes. *Proc. Brit. Acad.*, 154: 403-423.

Dunbar R.I.M. 2010. The social role of touch in humans and primates: behavioural function and neurobiological mechanism. *Neurosci. Behav. Rev.*, 34: 260-268.

Estalrrich A. & Rosas A. 2013. Handedness in Neandertals from the El Sidrón (Asturias, Spain): Evidence from instrumental striations with ontogenetic inferences. *PlosOne*, 8: e62797.

Estalrrich A. & Rosas A. 2015. Division of labor by sex and age in Neandertals: an approach through the study of activity-related dental wear. *J. Hum. Evol.*, 80: 51-63.

Faurie C. & Raymon M. 2004. Handedness frequency over more than 10,000 years. *Proc. R. Soc. London B*, 271: S243-S245.

Faurie C., Schiefenhövel W., Bomin S., Billiard S. & Raymond M. 2005. Variation in the Frequency of left-handedness in Traditional Societies. *Curr. Anthropol.*, 46: 142-147.

Fodor J.A. 1979. *The language of thought*. Harvard University Press, Harvard.

Frayer D.W., Fiore I., Lalueza-Fox C., Radovčić J. & Bondioli L. 2010. Right handed Neanderthals: Vindija and beyond. *J. Anthropol. Sci.*, 88: 113-127.

Frayer D.W., Lozano M., Bermúdez de Castro J.M., Carbonell E., Arsuaga J.L., Radovcic J., Fiore I. & Bondioli L. 2012. More than 500,000 years of right-handedness in Europe. *Laterality*, 17: 51-69.

Green T.J., Cochran B., Fenton T., Woods J.C., Titmus G., Tieszen L., Davis, M.A. & Miller S. 1998. The Buhl Burial: A Paleoindian Woman from Southern Idaho. *Am. Antiq.*, 63: 437-456.

Grefkes C. & Fink, G.R. 2005. The functional organization of the intraparietal sulcus in humans and monkeys. *J. Anat.*, 207: 3-17.

Gunz P. & Harvati K. 2007. The Neanderthal “chignon”: variation, integration, and homology. *J. Hum. Evol.*, 52: 262-274.

Gunz P., Neubauer S., Maureille B. & Hublin J-J. 2010. Brain development after birth differs between Neanderthals and modern humans. *Curr. Biol.*, 20: R921-R922.

Haggard P. 2005. Conscious intention and motor cognition. *Trends Cogn. Sci.*, 9: 290-295.

Haggard P. & De Boer L. 2014. Oral somatosensory awareness. *Neurosci. Biobehav. Rev.*, 47:469-484.

Hagmann P., Cammoun L., Gigandet X., Meuli R., Honey C.J., Wedeen V.J. & Sporns O. 2008. Mapping the structural core of human cerebral cortex. *PLoS Biol.*, 6: e159.

Hecht E.E., Gutman D.A., Preuss T.M., Sanchez M.M., Parr L.A. & Rilling J.K. 2013. Process versus product in social learning: comparative diffusion tensor imaging of neural systems for action execution–observation matching in macaques, chimpanzees, and humans. *Cereb. Cortex*, 23: 1014-1024.

Hills T.T., Todd P.M., Lazer D., Redish A.D., Couzin I.D & the Cognitive Search Research Group. 2015. Exploration versus exploitation in space, mind, and society. *Trends Cogn. Sci.,* 19: 46-54.

Hillson S.W., Parfitt S.A., Bello S.M., Roberts M.B. & Stringer C. 2010. Two hominin incisor teeth from the middle Pleistocene site of Boxgrove, Sussex, England. *J. Hum. Evol.*, 59: 493-503.

Holloway R.L. 1981. Exploring the dorsal surface of hominoid brain endocasts by stereoplotter and discriminant analysis. *Phil. Trans. R. Soc. London B Biol. Sci.*, 292: 155-166.

Iriki A. & Sakura O. 2008. The neuroscience of primate intellectual evolution: natural selection and passive and intentional niche construction. *Phil. Trans. R. Soc. London B Biol. Sci.*, 363: 2229-2241.

Iriki A. & Taoka M. 2012. Triadic (ecological, neural, cognitive) niche construction: a scenario of human brain evolution extrapolating tool use and language from the control of reaching actions. *Phil. Trans. R. Soc. London B Biol. Sci.*, 367: 10-23.

Jiang X., Iseki S., Maxson R.E., Sucov H.M. & Morriss-Kay G.M. 2002. Tissue origins and interactions in the mammalian skull vault. *Develop. Biol.*, 241: 106-116.

Jirak D., Menz M.M., Buccino G., Borghi A.M. & Binkofski F. 2010. Grasping language – A short story on embodiment. *Conscious. Cogn.*, 19: 711-720.

Jung R.E. & Haier R.J. 2007. The Parieto-Frontal Integration Theory (P-FIT) of intelligence: converging neuroimaging evidence. *Behav. Brain Sci.*, 30, 135-187.

Kivell T.L., Kibii J.M., Churchill S.E., Schmid P. & Berger L.R. 2011. *Australopithecus sediba* hand demonstrates mosaic evolution of locomotor and manipulative abilities. *Science*, 333: 1411-1417.

Lalueza Fox C. 1992. Information obtained from the microscopic examination of cultural striations in human dentition. *Int. J. Osteoarchaeol.*, 2: 155-169.

Lalueza Fox C. & Pérez- Pérez A. 1994. Cutmarks and post-mortem striations in fossil human teeth. *Hum. Evol.*, 9: 165-172.

Lalueza Fox C. & Frayer D. W. 1997. Non-dietary marks in the anterior dentition of the Krapina Neanderthals. *Int. J. Osteoarchaeol.*, 7: 133-149.

Land M.F. 2014. Do we have an internal model of the outside world? *Philos. Trans. R. Soc. London B*, 369: 20130045.

Leakey L.S.B., Tobias P.V. & Napier J.R. 1964. A new species of the genus *Homo* from Olduvai Gorge. *Nature*, 202: 7-9.

Lieberman P. 2002. On the Nature and Evolution of the Neural Bases of Human Language. *Yearb. Phys. Anthropol.*, 45: 36-62.

Lorenzo C., Carretero J.M. & Arsuaga J.L. 1999. Hand and foot remains from Gran Dolina Early Pleistocene site (Sierra de Atapuerca, Burgos). *J. Hum. Evol.*, 37: 501-522.

Lorenzo C., Carretero J.M., Arsuaga J.L., Martínez I., Gracia A. & Quam R. 2012. Hands, laterality and language: hand morphology in the Sima de los Huesos site (Sierra de Atapuerca). *Am. J. Phys. Anthropol.*, 147: 195-196.

Lorenzo C., Pablos A., Carretero J.M., Huguet R., Valverdú J., Martinón-Torres M., Arsuaga J.L., Carbonell E. & Bermúdez de Castro J.M. 2015. Early Pleistocene human hand phalanx from the Sima del Elefante (TE) cave site in Sierra de Atapuerca (Spain). *J. Hum. Evol.*, 78: 114-121.

Lorenzo C. 2015. The hand of the Neandertals: dexterous or handicapped? *J. Anthropol. Sci.*, 93: 181-183.

Lovejoy C.O., Simpson S.W., White T.D., Asfaw B. & Suwa G. 2009. Careful climbing in the Miocene: the forelimbs of *Ardipithecus ramidus* and humans are primitive. *Science*, 326: 70-708.

Lozano M., Bermúdez de Castro J. M., Martinón-Torres M. & Sarmiento S. 2004. Cutmarks on fossil human anterior teeth of the Sima de los Huesos site (Atapuerca, Spain). *J. Archaeol. Sci.*, 31: 1127-1135.

Lozano M., Bermúdez de Castro J. M., Carbonell E. & Arsuaga J. L. 2008. Non-masticatory uses of anterior teeth of Sima de los Huesos individuals (Sierra de Atapuerca, Spain). *J. Hum. Evol.*, 55: 713-728.

Lozano, M., Bermúdez de Castro, J.M., Arsuaga, J.L. & Carbonell, E. 2015. Diachronic analysis of cultural dental wear at the Atapuerca sites (Spain), Quat. Int. http://dx.doi.org/10.1016/j.quaint.2015.08.028.

Lozano M., Mosquera M., Bermúdez de Castro J. M., Arsuaga J. L. & Carbonell E. 2009. Right handedness of *Homo heidelbergensis* from Sima de los Huesos (Atapuerca, Spain) 500,000 years ago. *Evol. Hum. Behav.*, 30: 369-376.

Lukacs J. & Pastor R. 1988. Activity-induced patterns of dental abrasion in prehistoric Pakistan: evidence from Mehgarh and Harappa. *Am. J. Phys. Anthropol.*, 76: 377-398.

Machin A.J. & Dunbar R.I.M., 2011. The brain opiod theory of social attachment: a review of the evidence. *Behaviour*, 148: 985-1025.

Maister L., Slater M., Sanchez-Vives M.V. & Tsakiris M. 2015. Changing bodies changes minds: owning another body affects social cognition. *Trends Cogn. Sci.*, 19: 6-12.

Malafouris L. 2014. Third hand prosthesis. *J. Anthropol. Sci.*, 92: 281-283.

Malafouris, L., 2008. Between brains, bodies and things: tectonoetic awareness and the extended self. *Philos. Trans. R. Soc. London B*, 363: 1993–2002.

Malafouris L. 2010a. The Brain-Artefact Interface (BAI): a challenge for archaeology and cultural neuroscience. *Soc. Cogn. Affect. Neurosci.*, 5: 264-273.

Malafouris L. 2010b. Metaplasticity and the human becoming: principles of neuroarchaeology. *J. Anthropol. Sci.*, 88: 49-72.

Malafouris L. 2013. *How things shape the mind: a theory of material engagement*. MIT Press, Cambridge.

Maravita A. & Iriki A. 2004. Tools for the body (schema). *Trends Cogn. Sci.*, 8: 79-86.

Margulies D.S., Vincent J.L., Kelly C., Lohmann G., Uddin L.Q., Biswal B.B., Villringer A., Castellanos F.X., Milham M.P. & Petrides M. 2009. Precuneus shares intrinsic functional architecture in humans and monkeys. *Proc. Natl. Acad. Sci. USA*, 106: 20069-20074.

Marino B.F.M, Gallese V., Buccino G. & Riggio L. 2012. Language sensorimotor specificity modulates the motor system. *Cortex*, 48: 849-856.

Marr D. 2010. *Vision*. MIT Press.

Mars R., Jbabdi S., Sallet J., O'Reilly J.X., Croxson P.L., Olivier E., Noonan M.A.P., Bergmann C., Mitchell A.S., Baxter M.G., Behrens T.E.J., Johansen-Berg H., Tomassini V., Miller K.L. & Rushworth M.F.S. 2011. Diffusion-weighted imaging tractography-based parcellation of the human parietal cortex and comparison with human and macaque resting-state functional connectivity. *J. Neurosci.*, 31: 4087-4100.

Marzke M.W. & Marzke R.F. 2000. Evolution of the human hand: approaches to acquiring, analysing and interpreting the anatomical evidence. *J. Anat.*, 197: 121-140.

McManus C. 2004. *Right hand, left hand: the origins of asymmetry in brains, bodies, atoms and culture.* Harvard University Press, Cambridge, MA.

Merbs C. 1968. Anterior tooth loss in arctic populations. *S. J. Anthropol.*, 28: 20-32.

Meunier D., Lambiotte R. & Bullmore E.T. 2010. Modular and hierarchically modular organization of brain networks. *Front. Neurosci.*, 4: 200.

Moss M.L. & Young R.W. 1960. A functional approach to craniology. *Am. J. Phys. Anthropol.*, 18, 281-292.

Moyà-Solà S., Köhler M., Alba D.M. & Almécija S. 2008. Taxonomic attribution of the Olduvai Hominid 7 manual remains and the functional interpretation of hand morphology in robust australopithecines. *Folia Primatol.*, 79: 215-250.

Napier J.R. 1962. Fossil hand bones from Olduvai Gorge. *Nature*, 196: 409-411.

Neubauer S., Gunz P. & Hublin J-J. 2009. The pattern of endocranial ontogenetic shape changes in humans. *J. Anat.*, 215: 240-255.

Neubauer S., Gunz P. & Hublin J-J. 2010 Endocranial shape changes during growth in chimpanzees and humans: a morphometric analysis of unique and shared aspects. *J. Hum. Evol.*, 59: 555-566.

Niewoehner W.A. 2001. Behavioral inferences from the Skhul/Qafzeh early modern human hand remains. *Proc. Natl. Acad. Sci. USA*, 98: 2979-2984.

Orban G.A., Claeys K., Nelissen K., Smans R., Sunaert S., Todd J.T., Wardak C., Durand J.B. & Vanduffel W. 2006. Mapping the parietal cortex of human and non-human primates. *Neuropsychologia* 44: 2647-67.

Pearce E., Stringer C. & Dunbar, R.I. 2013. New insights into differences in brain organization between Neanderthals and anatomically modern humans. *Proc. R. Soc. London B.*, 280, 20130168.

Peer M., Salomon R., Goldberg I., Blanke O. & Arzy S. 2015. Brain system for mental orientation in space, time, and person. *Proc. Natl. Acad. Sci. USA*, 112: 11072-11077.

Pinker S. 1999. *How the mind works*. Penguin.

Puech P.F. 1979. The diet of Early Man: evidence from abrasion of teeth and tools. *Curr. Anthropol.*, 20: 590-592.

Rangel de Lázaro G., de la Cuétara J.M., Píšová H., Lorenzo C. & Bruner E. 2015. Diploic vessels and computed tomography: segmentation and comparison in modern humans and fossil hominids. *Am. J. Phys. Anthropol.,* 159: 313-324.

Rochat P. 1989. Object manipulation and exploration in 2- to 5-month-old infants. *Develop. Psychol.,* 25: 871-884.

Rochat P. 1993. Hand-mouth coordination in the newborn: morphology, determinants, and early development of a basic act. In Savelsbergh G.J.P. (ed): *The development of coordination in infancy,* pp. 265-288. Elsevier, The Netherlands.

Scheperjans F., Hermann K., Eickhoff S.B., Amunts K., Schleicher A. & Zilles K. 2008a. Observer-independent cytoarchitectonic mapping of the human superior parietal cortex. *Cereb. Cortex*, 18: 846-867.

Scheperjans F., Eickhoff S.B., Hömke L., Mohlberg H., Hermann K., Amunts K. & Zilles K. 2008b. Probabilistic maps, morphometry, and variability of cytoarchitectonic areas in the human superior parietal cortex. *Cereb. Cortex*, 18: 2141-2157.

Scott N., Neubauer S., Hublin J-J. & Gunz P. 2014. A shared pattern of postnatal endocranial development in extant hominoids. *Evol. Biol.*, 41: 572-592.

Semendeferi K. & Damasio H. 2000. The brain and its main anatomical subdivisions in living hominoids using magnetic resonance imaging. *J. Hum. Evol.*, 38: 317-332.

Sotero R.C.. & Iturria-Medina Y. 2011. From blood oxygenation level dependent (BOLD) signals to brain temperature maps. *Bull. Math. Biol.*, 73: 2731-2747.

Stout D. & Chaminade T. 2007. The evolutionary neuroscience of tool making. *Neuropsychologia*, 45: 1091-100.

Stout D., Hecht E., Khreisheh N, Bradley B. & Chaminade T. 2015. Cognitive demands of lower Paleolithic toolmaking. *PlosOne*, 10: e0121804.

Susman R.L. 1988. Hand of *Paranthropus robustus* from Member I, Swartkrans: fossil evidence for tool behavior. *Science*, 240: 781-782.

Susman R.L. 1994. Fossil evidence for early hominid tool use. *Science*, 265: 1570-1573.

Tooby J. & Cosmides L. 1989. Evolutionary psychology and generation of culture, Part I. *Ethol. Sociobiol.*, 10: 29-49.

Tocheri M.W., Orr C.M., Larson S.G., Sutikna T., Jatmiko, Saptomo E.W., Awe Due R., Djubiantono T., Morwood M.J. & Jungers W.L. 2007. The primitive wrist of *Homo floresiensis* and its implications for hominin evolution. *Science*, 317: 1743-1745.

Turvey M.T. & Carello C. 2011. Obtaining information by dynamic (effortful) touching. *Phil. Trans. R. Soc. London B.*, 366, 3123-3132.

Uomini N. T. 2009. The prehistory of handedness: archaeological data and comparative ethology. *J. Hum. Evol.*, 57: 411-419.

Uomini N. T. 2015. Paleoneurology and behavior. In Bruner E. (ed): *Human Paleoneurology*, pp. 121-143. Springer, Zurich.

Uomini N.T. & Meyer G.F. 2013. Shared brain lateralization patterns in language and Acheulean stone tool production: a functional transcranial doppler ultrasound study. *PlosOne,* 8: e72693.

Vanduffel W., Fize D., Peuskens H., Denys K., Sunaert A., Todd J.T. & Orban G.A. 2002. Extracting 3D from motion: differences in human and monkey intraparietal cortex. *Science*, 298: 413-5.

Volpato V., Macchiarelli R., Guatelli-Steinberg D., Fiore I., Bondioli L. & Frayer D. W. 2012. Hand to mouth in a Neandertal: right-handedness in Regordou 1. *PlosOne,* 7: e43949.

Ward C.V., Tocheri M.W., Plavcan J.M., Brown F.H. & Manthi F.K. 2014. Early Pleistocene third metacarpal from Kenya and the evolution of modern human-like hand morphology. *Proc. Natl. Acad. Sci. USA.*, 111: 121-124.

Weidenreich F. 1941. The brain and its role in the phylogenetic transformation of the human skull. *Trans. Am. Phil. Soc.*, XXXI: 321-442.

White T.D., Asfaw B., DeGusta D., Gilbert H., Richards G.D., Suwa G. & Howell F.C. 2003. Pleistocene *Homo sapiens* from Middle Awash, Ethiopia. *Nature*, 423: 742-747.

Wynn T. & Coolidge F., 2003. The role of working memory in the evolution of managed foraging. *Before Farming,* 2: 1-16.

Zhang S. & Li C.S.R. 2012. Functional connectivity mapping of the human precuneus by resting state fMRI. *Neuroimage*, 59: 3548-3562.