

Extended mind and visuo-spatial integration: three hands for the Neandertal lineage

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For many years, the brain was thought to be an independent and autonomous machine, with a structure that was largely determined by internal factors. Eventually, we finally recognized the importance of the environment in influencing brain organization and development. In human evolution, this perspective suggested autocatalytic models in which a complex brain produces a complex culture which, through feedback, selects for a more complex brain, generating a loop towards increasing complexity. Hence, in this case, the mind is not only an organic output, but also the result of a historical process. Recently, a further epistemological step was put forward, integrating the environment and the mind itself. Theories generally associated with the term “extended mind” strongly link brain functions and the outer environment (Clark, 2007, 2008; Malafouris, 2008a,b; Wheeler & Clark, 2008). According to this perspective, the environment is “embodied” within the cognitive processes through sensorial and neural mechanisms. Cognition is deeply rooted within the experience of the body, where the perceptual and motor systems bridge and shape the cognitive processes between brain and environment. The body works like a complex and dynamic interface, and cognition is the final result of the interaction between internal and external worlds.

Although “environment” may have a very wide meaning, material culture is the easiest and clearest case of external component, taking into

consideration that “objects” induce specific cognitive processes, amplify perceptive capacities, enhance computation power, and store extra-memory (Malafouris, 2010a, 2013). Without tools, not only couldn't our mind do what it does, but also it wouldn't even be the way it is. The induction, enhancement, and storing functions of the objects are part of the processes themselves. And such processes are rooted in the experience of the body.

Theories on extended mind are still incomplete and heterogeneous, and they lack a robust experimental context yet. Terminology is still vague in many aspects, and many concepts and definitions still lack a general agreement among authors or disciplines. Nonetheless, from the earliest proposals largely based on theoretical approaches, we are now moving toward comparative and analytical attempts (Iriki & Sakura, 2008). Experimental settings are revealing how the interaction with objects may influence the brain structure or the neural behaviour, extending the material tools into the body schemata (Maravita & Iriki, 2004). According to the theories on extended mind, the autocatalytic loop is further empowered, cognition being deeply embedded within the material world. Objects are an integrated part of the neural circuits, changing the way the brain responds and is trained to inputs. As a matter of fact, in terms of neural processes an object is interpreted differently if it is in the range of the body and if it can interact

physically with the body, occupying a peri-personal area instead of an extra-personal space in which the object cannot be reached (Maravita *et al.*, 2003; Maravita & Iriki, 2004).

Paleoneurological evidence suggests that the brain areas which have undergone the most patent morphological changes in human evolution (and most of all in our species, *Homo sapiens*) are those involved in visuospatial integration (Bruner, 2010). Neandertals display a lateral bulging of the upper parietal areas, which has not been reported in *H. erectus* or *H. heidelbergensis* (Bruner *et al.*, 2003). Most noticeably, the modern human globular brain is due to a patent spatial dilation of the whole parietal surface (Bruner, 2004), associated with a very early post-natal morphogenetic stage which is absent in apes and Neandertals (Neubauer *et al.*, 2009, 2010; Gunz *et al.*, 2010).

Two areas which are compatible with the bulging observed in modern humans are the intraparietal sulcus and the precuneus, both of which are localized in the deep parietal volumes. The intraparietal sulcus is particularly interesting because it coordinates hands and eyes, which are the main “ports” of interface between brain and environment (Bruner, 2010, 2012). Also the precuneus has an important role in visuospatial integration, bridging body coordination with vision, and integrating such a framework with memory (Cavanna & Trimble, 2006; Margulies *et al.*, 2009; Zhang & Li, 2012). This element is a major source of brain morphological variation within modern humans, and its intra-specific pattern of bulging is the same characterizing the main inter-specific differences within the human genus (Bruner *et al.*, 2014). These deep parietal areas show human-specific cellular traits (Orban *et al.*, 2006), and are the structural and functional core of the brain networks (Hagmann *et al.*, 2008). Beyond a simple mechanical function, visuospatial integration also means the possibility to generate an “inner virtual space” in which to perform simulations and mental experiments (Bruner, 2004, 2010; Hecht *et al.*, 2013). Memory is necessary to add a temporal framework within such a virtual environment (Coolidge & Wynn, 2008; Malafouris 2008a),

which makes the proximity and connection between intraparietal sulcus and precuneus an interesting issue. Because of their role in coordinating brain and environmental relationships through the body interface, it is apparent that these deep parietal areas are particularly interesting for issues associated with extended mind.

Culture and tool use are determinant hallmarks of the human genus. Humans generate and mould their niche (ecological, cultural, and social), and this niche moulds the neural system through the extension of “body schemas” and extra-neural connections (Malafouris, 2009, 2010b; Iriki & Taoka, 2012). This extreme integration between brain and culture is a key feature in cognitive archaeology, which attempts to make inferences on cognitive processes from the archaeological record (e.g., Wynn & Coolidge, 2003, 2004; Coolidge & Wynn, 2005; Malafouris & Renfrew, 2008, 2010; Langbroek, 2012). Cognitive archaeology thus needs some physical (organic or cultural) trace able to reveal some underlying cognitive structures.

A specific indirect behavioural trace in paleoanthropology is represented by those marks found on the dental surface which cannot be associated with a feeding function. In fact, dental wear is not only related to diet, since wear related to other cultural factors has been identified on anterior teeth. The use of the frontal part of the mouth for activities not directly related to chewing foodstuffs leaves characteristic features on the dental surfaces of incisors and canines. This behaviour is known as the use of teeth as a third hand or as a tool (Dahlberg, 1963; Brace, 1967). Holding materials such as meat, vegetable fibers or skin with anterior teeth and cutting them with a lithic tool could produce cuts or marks on the labial enamel. This type of feature related to the use of teeth as a tool has been described occasionally in Lower Pleistocene species. There are no data for early humans (*H. ergaster-erectus*), but in *H. antecessor* labial striations associated with non-feeding behaviour have been described in only one individual, giving with the current sample available a prevalence of 12.5% (Lozano *et al.*, unpublished data).

However, this behaviour became a common and widespread habit in *H. heidelbergensis*. The use of teeth as a third hand has been frequently reported in fossil hominids from the middle Pleistocene site of Sima de los Huesos (Sierra de Atapuerca, Spain) (Lozano *et al.*, 2008). The Sima de los Huesos (SH) deposits were dated at about 500,000 yrs (Bischoff *et al.*, 2003, 2007; Cuenca-Bescós *et al.*, 1997; Parés *et al.*, 2000). Only human and carnivore remains have been recovered at the site along with a single stone tool (Arsuaga *et al.*, 1997; Carbonell *et al.*, 2003; García *et al.*, 1997). The SH sample comprises more than 6,500 fossil remains of *H. heidelbergensis*, from at least 28 individuals (Martínez *et al.*, 2013). There are 20 out of 28 SH individuals with associated anterior teeth. This group of 20 individuals includes males and females, and different ages are represented with the exception of infants. All SH individuals (100%) have dental features which indicate the use of anterior teeth as a tool. SH hominids probably performed different activities involving the use of incisors and canines, like cutting, pulling, holding, or dragging different materials.

Despite the many uncertainties we have regarding its taxonomic level and phylogenetic role, we must recognize that *H. heidelbergensis* was a successful species, widespread in time and geography (Rightmire, 1998, 2008; Stringer, 2012). We must assume that this species had a great capacity of adaptation, inhabiting very different environments. According to the paleoneurological evidence, this species underwent an increase in absolute and relative brain size (Rightmire, 2004). Nonetheless, in terms of general morphology, its endocranium has the same anatomical organization (proportions, circumvolutions, etc.) observed in small-brained human species like *H. ergaster* or *H. erectus* (Bruner *et al.*, 2003). Hence, at least for what we know from endocrania and recognizing that the paleoneurological data for *H. heidelbergensis* are scanty, we can hypothesise that it evolved a larger brain but without a patent reorganization of the brain areas. To date, at least, there is no evidence suggesting changes in its brain complexity in terms of gross anatomical features.

Although the subtle evolutionary dynamics are not known, European *H. heidelbergensis* is supposed to be the ancestor of Neandertals, even though there may be some disagreement concerning the degree and patterns of relationships (Arsuaga *et al.*, 1997; Hublin, 2009; Stringer 2012). The cultural structure of the Neandertal populations was even more complex when compared with the Middle Pleistocene hominids (Kuhn, 2013). Nonetheless, the use of the teeth to integrate manual praxis continued to be a common behaviour, with a percentage of 100% of individuals showing non-feeding marks on the dental surface (Bermúdez de Castro *et al.*, 1988; Estalrich & Rosas, 2013; Frayer *et al.*, 2010; Lalueza-Fox & Frayer, 1997; Volpato *et al.*, 2012). In this case, an increase in absolute and relative brain size was also accompanied by a change in the brain form. When compared with more archaic hominids, Neandertals display a widening of the frontal lobes, and lateral widening of the parietal areas (Bruner *et al.*, 2003; Bruner & Holloway, 2010; Bruner *et al.*, 2011). In Neandertals, these morphological changes of the fronto-parietal areas matched the introduction of the Levallois techniques. Despite the fact these techniques are not strictly specific to the Neandertals, this group is the main representative of this tool culture. Moreover, although it has been argued that a mental template may be not necessary to produce tools through these technical processes (Wynn & Coolidge, 2004), we must recognize that they entail a certain capacity of simulation necessary to compute a complex mental experiment because of the explicit differences between the starting and finished object (Boëda, 1994). Even if a fine correlation cannot be evaluated, this association between a manifest change in the tool organization and bulging of a brain area dedicated to visuospatial integration merits attention.

Although hunter-gatherer life style may influence the observed behavioural responses and promote the use of teeth as integrative support to handling, it cannot be interpreted as a decisive factor to explain such a large prevalence of non-feeding teeth use in the Neandertal lineage. In fact, modern hunter-gatherers kept on

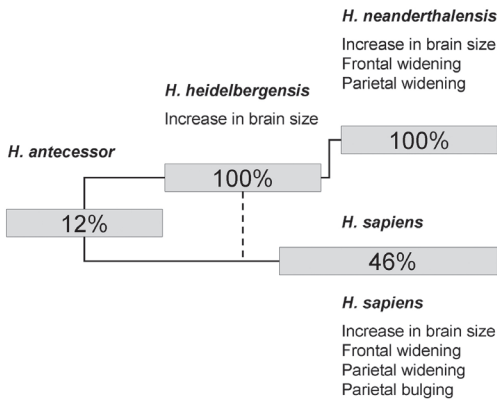


Fig. 1 - Prevalence of use of teeth as integrative elements for praxis reaches 100% in Homo heidelbergensis and Neandertals. In the first case, it is associated with a general increase of the brain size, in the second case there are also morphological changes of the brain proportions. In modern human hunter-gatherers, the percentage is definitely lower (46%), and there is a further change in the brain form associated with upper parietal bulging. Modern humans rely less on teeth as an integrative body-artefact interface, which suggests a more complete efficiency of the hands as ports between brain and environment. The fact that at the same time modern humans evolved a spatial dilation of the upper and deeper parietal areas is outstanding.

using teeth as a supplementary praxis element, but the percentage of individuals presenting such marks does not reach 50% of the samples (Lozano *et al.*, 2008) (Fig. 1). Hence, we must assume that this behaviour was more specific to *H. heidelbergensis* and Neandertals than modern humans. We may ask why they needed to use the mouth as a third interface between brain and material culture to engage integration, when for most of the other species the hands sufficed. An interpretation of this evidence within the context of extended mind can be put forward assuming a mismatch within the autocatalytic process between cultural complexity and neural substrate (Fig. 2). The dynamics of the reciprocal influence between brain and culture probably has evolutionary patterns which are not necessarily linear or gradual, generating beats and asynchronies between organic and super-organic

adaptations and changes. Thus a marked use of the mouth as an additional interface may be the sign of an inefficient visuo-spatial integration system, at least considering the corresponding level of material complexity. This is even more extreme when considering that the mouth as an additional interface was recruited from a very distinct and relevant function, which is feeding. The need of an additional body interface was so necessary to involve a structure which has a basic importance for the fundamental ecological requirement of a vertebrate, and whose efficiency and integrity can be even damaged by the new cultural function. This risky recruitment of an important functional element into praxis seems to be an extreme solution to difficulties in the brain-environment relationships, to integrate a non-sufficient brain-artefact interface.

Taking into consideration the evidence of a specific increase in the use of teeth for handling functions in the Neandertal lineage, we hypothesize that these species may have suffered a mismatch between cultural and neural complexity, in which additional anatomical elements were involved as a body interface to overcome insufficient visuospatial integration processes.

We are aware that the relationships between brain and environment through the body interface may be extremely relevant for generating a mind. We are also persuaded that visuospatial integration has a major role in human-specific cognitive processes like simulation and self representation. And we know that the parietal areas of the brain, largely involved in those processes, experienced remarkable morphological changes during hominid evolution, most notably in modern humans. Hence, recognizing the new emerging behavioural complexity of *H. heidelbergensis* and Neandertals, the minor evolutionary changes in its brain morphology, and the common use of the mouth as an additional body interface, we are taking into consideration the hypothesis of a sub-optimal degree of coordination between the cultural and neural systems. The European Middle Pleistocene lineage may be a case of mismatch between neural and cultural networks, in which a boost of cultural evolution

may have found an untrained brain-body structure which needed additional elements to work as an interface. The percentage of teeth use for praxis decreases considerably in modern humans, a species which is characterized by a further and more patent enlargement of those areas involved in visuospatial integration.

It must be stated that a decrease in the necessity of additional body interfaces may be directly associated with enhancement of the visuospatial integration system at neural level, but also with improvement of the brain-hand integration or with improvement of the anatomy involved in the interface. In fact, it has been also hypothesized that modern humans enhance their precision grip capability when compared with extinct human taxa (Marzke, 1997, 2013; Lorenzo, 2007). Finally, less dependence from additional body components can be also achieved through cultural adaptations, thus evolving material tools which can substitute the additional body interfaces. In *H. sapiens*, we have evidence of changes in all these three factors which cooperate to enhance relationships between brain and body: visuospatial integration areas (parietal lobes), body interface (hand) and material culture (tools).

Previously, Wynn & Coolidge proposed that the main differences between modern humans and Neandertals can be based on the working memory capacity (2004). In their view, Neandertals were comparable to modern humans regarding their long-term memory and “expert” ability based on generational apprenticeship, but less capable of individual and innovative responses because of minor working memory capacity. This would explain, among other differences, the relative stability of their cultural outputs. Interestingly, among the recognized components of the working memory system (Baddeley & Hitch, 1974), they point towards the phonological loop (lower parietal areas) or towards the executive functions (frontal areas) as a possible neural substrate for such differences, because of their association with language capacity and attention and decision-making, respectively. Instead, although insisting on the same fronto-parietal network, we are here putting attention and

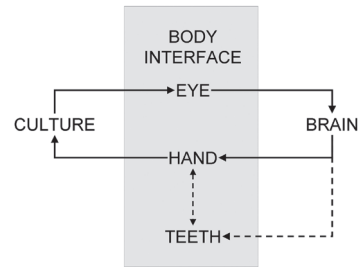


Fig. 2 - According to the Extended Mind Hypothesis, cognition is based into the body experience. Neural processes are influenced by the feedback and integration between brain, body, and tools. Visuospatial functions and deep parietal areas are particularly dedicated to such integration between outer and inner environments. The eye and hand are the principal body interfaces between inner and outer world. Evolutionary mismatches between the rates of cultural and biological evolution may generate temporary and transitional solutions. The frequent use of mouth and teeth to integrate praxis in Middle Pleistocene hominids may have been the result of a brain organization which had not completely adjusted to the actual degree of cultural complexity, requiring additional body interface elements recruited from other functional districts.

importance on the third component of the working memory, namely the visuospatial sketchpad (upper and deeper parietal areas), and its role in generating inner virtual spaces, coordinating the body interface between brain and environment.

The current ideas on extended mind can promote a real revolution in neuroscience. Nonetheless, studies in paleoanthropology, brain evolution, and cognition, necessarily suffer due to the impossibility of testing many hypotheses. Hence, inevitably cognitive archaeology has a relevant speculative and theoretical component. While we must not stress this limit, avoiding excessive speculations, at the same time we should not reject the possibility to orientate research according to sensate scientific perspectives. The theoretical structure should be constrained within the safe framework of logic and actual scientific knowledge. Compatibility of theories is not always sufficient, and convergence of different fields and methods is the only suitable way to achieve robust evolutionary hypotheses.

Our hypothesis on the use of the mouth as an additional interface in the Neandertal lineage because of an incomplete brain-environment body interface and limits in visuospatial integration ability is difficult to test in an experimental way. Nonetheless it provides a different interpretation of the paleontological and archaeological evidence, which integrates biological and cultural information. Further studies on the parietal lobe organization and on the role of the embodied cognition will supply essential information to assess the existence of periods of mismatch between biological and cultural evolution along the human lineages.

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References

- Arsuaga J.L., Martínez I., Gracia A. & Lorenzo C. 1997. The Sima de los Huesos Crania (Sierra de Atapuerca, Spain). A comparative study. *J. Hum. Evol.*, 33: 219-281.
- Baddeley A.D. & Hitch G.J. 1974. Working Memory. In G.A. Bower (ed): *Recent advances in learning and motivation*, pp. 47-90. Academic Press, New York.
- 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.
- Bischoff J.L., Shamp D.D., Aramburu A., Arsuaga J.L., Carbonell E. & Bermúdez de Castro J.M. 2003. The Sima de los Huesos hominids date to beyond U/Th equilibrium (>350 kyr) and perhaps to 400-500 kyr: new radiometric dates. *J. Archaeol. Sci.*, 30: 275-280.
- Bischoff J.L., Williams R.W., Rosenbauer R.J., Aramburu A., Arsuaga J.L., García N. & Cuenca-Bescós G. 2007. High-resolution U-series dates from the Sima de los Huesos hominids yields 600 -66 + ∞ kyrs : implications for the evolution of the early Neandertal lineage. *J. Archaeol. Sci.*, 34: 763-770.
- Boëda E. 1994. *Le concept Levallois: variabilité des méthodes*. Monographie du CRA, 9. CNRS Editions, Paris.
- 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. 2010. Morphological differences in the parietal lobes within the human genus. *Curr. Anthropol.*, 51: S77-S88.
- Bruner E. 2012. Comment to Coolidge and Overmann. *Curr. Anthropol.*, 5:214-215.
- Bruner E. & Holloway R. 2010. bivariate approach to the widening of the frontal lobes in the genus *Homo*. *J. Hum. Evol.*, 58: 138-146.
- 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. U.S.A.*, 100: 15335-15340.
- 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. 2014. Midsagittal brain variation and MRI shape analysis of the precuneus in adult individuals. *J. Anat.* doi: 10.1111/joa.12155.
- Carbonell E., Mosquera M., Ollé A., Rodríguez X.P., Sala R., Vergès J.M., Arsuaga J.L. & Bermúdez de Castro J.M. 2003. Les premiers comportements

- funeraires auraient-ils pris place à Atapuerca, il y a 350,000 ans? *L'Anthropologie*, 107: 1-14.
- Cavanna A.E. & Trimble M.R. 2006. The precuneus: a review of its functional anatomy and behavioural correlates. *Brain*, 129: 564-583.
- 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 Archaeological Journal*, 15: 5-26.
- Coolidge F. & Wynn T. 2008. The role of episodic memory and autozoetic thought in Upper Paleolithic life. *PaleoAnthropology*, 2008: 212-217.
- Cuenca-Bescós G., Laplana C., Canudo J.I. & Arsuaga J.L. 1997. Small mammal from Sima de los Huesos. *J. Hum. Evol.*, 33: 175-190.
- Dahlberg, A.A. 1963. Dental evolution and culture. *Hum. Biol.*, 35: 237-249.
- Estalrich A., & Rosas A. 2013. Handedness in Neandertals from the El Sidrón (Asturias, Spain): evidence from instrumental striations with ontogenetic inferences. *PLoS One*, 8: e62797.
- Fruyer D.W., Fiore I., Lalueza Fox C., Radović J. & Bondioli L. 2010. Right handed Neandertals: Vindija and beyond. *J. Anthropol. Sci.*, 88: 113-127.
- García N., Arsuaga J.L. & Torres T. 1997. The carnivore remains from the Sima de los Huesos Middle Pleistocene site (Sierra de Atapuerca, Spain). *J. Hum. Evol.*, 33: 155-174.
- 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.
- 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.
- Hublin J.J. 2009. The origin of Neandertals. *Proc. Natl. Acad. Sci. U.S.A.*, 106: 16022-16027.
- Iriki A. & Sakura O. 2008. The neuroscience of primate intellectual evolution: natural selection and passive and intentional niche construction. *Philos. Trans. R. Soc. B*, 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. *Philos. Trans. R. Soc. B*, 367: 10-23.
- Kuhn S.L. 2013. Roots of the Middle Paleolithic in Eurasia. *Curr. Anthropol.*, 54: 255-268.
- Lalueza-Fox C. & Fruyer D.W. 1997. Non-dietary marks in the anterior dentition of the Krapina Neanderthals. *Int. J. Osteoarchaeol.*, 7: 133-149.
- Langbroek M., 2012. Trees and ladders: A critique of the theory of human cognitive and behavioural evolution in Palaeolithic archaeology. *Quat. Int.*, 270: 4-14.
- Lorenzo C. 2007. *Evolución de la mano en los homínidos. Análisis morfológico de los fósiles de la Sierra de Atapuerca. Geografía e Historia*. PhD Thesis. Universidad Complutense, Madrid.
- Lozano M., Bermúdez de Castro J.M., Carbonell E. & Arsuaga J.L. 2008. Nonmasticatory uses of anterior teeth of Sima de los Huesos individuals (Sierra de Atapuerca, Spain). *J. Hum. Evol.*, 55: 713-728.
- Lozano M., Estalrich A., Bondioli L., Fiore I., Bermúdez de Castro J.M., Arsuaga J.L., Carbonell E., Rosas A. & Fruyer D.W. 2014. *Predominantly right-handed fossil Europeans and the implications for an ancient origin of language*. Manuscript.
- Malafouris L. 2008a. Between brains, bodies and things: tectonoetic awareness and the extended self. *Phil. Trans. R. Soc. B*, 363: 1993-2002.
- Malafouris L. 2008b. Beads for a plastic mind: the 'Blind man's stick' (BMS) hypothesis and the active nature of material culture. *Cambridge Archaeological Journal*, 18: 401-414.
- Malafouris L. 2009. 'Neuroarchaeology': Exploring the links between neural and cultural plasticity. *Prog. Brain Res.*, 178: 251-259.

- 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.
- Malafouris L. & Renfrew C. 2008. Steps to a 'Neuroarchaeology' of mind. *Cambridge Archaeological Journal*, 18: 3, 381-5.
- Malafouris L. & Renfrew C. 2010. The cognitive life of things: archaeology, material engagement and the extended mind. In L. Malafouris & C. Renfrew (eds): *The cognitive life of things: recasting the boundaries of the mind*, pp. 1-12. McDonald Institute Monographs, Cambridge.
- Maravita A. & Iriki A. 2004. Tools for the body (schema). *Trends Cogn. Sci.*, 8: 79-86.
- Maravita A., Spence C. & Driver J. 2003. Multisensory integration and the body schema: close to hand and within reach. *Curr. Biol.*, 13: R531-R539.
- 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. U.S.A.*, 106: 20069-20074.
- Martínez I., Rosa M., Quam R., Jarabo P., Lorenzo C., Bonmatí A., Olivencia A.G., Gracia A. & Arsuaga J.L. 2013. Communicative capacities in middle pleistocene humans from the Sierra de Atapuerca in Spain. *Quat. Int.*, 295: 94-101.
- Marzke M.W. 1997. Precision grips, hand morphology, and tools. *Am. J. Phys. Anthropol.*, 102: 91-110.
- Marzke M.W. 2013. Tool making, hand morphology and fossil hominins. *Phil. Trans. R. Soc. B*, 368: 20120414.
- 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.
- 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. *Neuropsychology*, 44: 2647-67.
- Parés J.M., Pérez-González A., Weil A.B. & Arsuaga J.L. 2000. On the age of the hominid fossils at the Sima de los Huesos, Sierra de Atapuerca, Spain: paleomagnetic evidence. *Am. J. Phys. Anthropol.*, 111: 451-461.
- Rightmire G.P. 1998. Human evolution in the Middle Pleistocene: the role of *Homo heidelbergensis*. *Evol. Anthropol.*, 6: 218-227.
- Rightmire G.P. 2004. Brain size and encephalization in early to mid-Pleistocene *Homo*. *Am. J. Phys. Anthropol.*, 124: 109-123.
- Rightmire G.P. 2008. *Homo* in the Middle Pleistocene: hypodigms, variation, and species recognition. *Evol. Anthropol.*, 17: 8-21.
- Stringer C. 2012 The status of *Homo heidelbergensis* (Schoetensack 1908). *Evol. Anthropol.*, 21: 101-107
- Volpato V., Macchiarelli R., Guatelli-Steinberg D., Fiore I., Bondioli L. & Frayer D.W. 2012. Hand to mouth in a Neandertal: right-handedness in Regourdou 1. *PLoS One*, 7: e43949.
- Wheeler M. & Clark A. 2008. Culture, embodiment and genes: unravelling the triple helix. *Phil. Trans. R. Soc. B*, 363: 3563-3575
- Wynn T. & Coolidge F. 2003. The role of working memory in the evolution of managed foraging. *Before Farming*, 2: 1-16.
- Wynn T. & Coolidge F. 2004. The expert Neandertal mind. *J. Hum. Evol.*, 46: 467-87.
- Zhang S. & Li C.S.R. 2012. Functional connectivity mapping of the human precuneus by resting state fMRI. *Neuroimage*, 59: 3548-3562.