



**HAL**  
open science

## Neuroimaging and Neuroarchaeology: a window on cognitive evolution

Mathilde Salagnon, Francesco D'errico, Emmanuel Mellet

► **To cite this version:**

Mathilde Salagnon, Francesco D'errico, Emmanuel Mellet. Neuroimaging and Neuroarchaeology: a window on cognitive evolution. *Intellectica - La revue de l'Association pour la Recherche sur les sciences de la Cognition (ARCo)*, In press. hal-02999774

**HAL Id: hal-02999774**

**<https://hal.science/hal-02999774>**

Submitted on 11 Nov 2020

**HAL** is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

# Neuroimaging and Neuroarchaeology: a window on cognitive evolution

Salagnon M<sup>1,2,3</sup>, d'Errico F<sup>4,5</sup>, Mellet E<sup>1,2,3\*</sup>

<sup>1</sup> Univ. Bordeaux, GIN, IMN UMR 5293, Bordeaux, France

<sup>2</sup> CNRS, GIN, IMN UMR 5293, Bordeaux, France

<sup>3</sup> CEA, GIN, IMN UMR 5293, Bordeaux, France

<sup>4</sup> Univ. Bordeaux, PACEA UMR 5199, CNRS, Pessac, France

<sup>5</sup> SFF Centre for Early Sapiens Behaviour (SapienCE), University of Bergen, Bergen, Norway.

## **\*CORRESPONDING AUTHOR**

Emmanuel Mellet

Institut des Maladies Neurodégénératives, UMR 5293

Groupe d'Imagerie Neurofonctionnelle

Université de Bordeaux F-33000 Bordeaux France

[emmanuel.mellet@u-bordeaux.fr](mailto:emmanuel.mellet@u-bordeaux.fr)

**KEYWORDS:** Neuroimaging, Neuroarchaeology, Brain evolution, Toolmaking, Symbols, Engravings.

## **Abstract**

Neuroarchaeology is an expanding research field that applies functional brain imaging techniques to participants in order to identify the cerebral regions involved in the production or perception of artefacts produced by past hominins. Neuroarchaeology allows making inferences about hominin cognitive abilities with regards to language, praxis, and cognitive control learning domains. As such, neuroarchaeology allows to postulate hypotheses about the evolution of cognition. This article reviews how neuroimaging techniques have been applied in neuroarchaeology and evaluates the novel insights gained from the merger of these fields. We further describe strategies to conduct research, propose a critical analysis of the results obtained to date, and discuss whether they could be used to propose evolutionary trends.

**Titre Français :** Neuroimagerie et neuroarchéologie : une fenêtre sur l'évolution de la cognition

**MOTS-CLES:** Neuroimagerie, Neuroarchéologie, Evolution du cerveau, Fabrication d'outils, Symboles, Gravures.

**Résumé en Français :** La neuroarchéologie est un domaine de recherche en expansion, qui utilise des techniques d'imagerie cérébrale fonctionnelle sur des participants modernes afin d'identifier les régions cérébrales impliquées dans la production ou la perception d'artefacts produits par les hominines du passé. Cela permet d'inférer leurs capacités cognitives dans les domaines du langage, des praxies, de l'apprentissage du contrôle cognitif, et de proposer des hypothèses sur l'évolution de la cognition. Cet article passe en revue les techniques d'imagerie cérébrale appliquées à ce domaine de recherche et évalue leur potentiel. Nous décrivons en outre les stratégies permettant de mener des recherches dans ce domaine, proposons une analyse critique des résultats obtenus jusqu'à présent et examinons s'ils pourraient être utilisés pour proposer des tendances évolutives.

## **Cognitive evolution and neuroarchaeology**

Over the past two decades, the growing interest in the evolution of human cognition has led to a particularly fruitful subdiscipline referred to as “neuroarchaeology” (Malafouris, 2010a; Stout & Hecht, 2015). This novel multidisciplinary field applies concepts, theories, and methods borrowed from neurosciences to answer archaeological questions.

Neuroarchaeology does not aim to reduce the evolution of human cognition to its cerebral bases. Rather, it proposes to investigate past human cognition globally by adding a novel perspective. Neuroarchaeology addresses research topics such as the origin and evolution of language and memory, the emergence of symbolic thought, theory of mind and social cognition.

Even though archaeology has developed over the last decades methods to infer cognitive abilities from past behaviour, it becomes increasingly clear that only interdisciplinary exchange will offer novel theoretical frameworks and methods to propose scenarios on the emergence and evolution of these capacities. It appears more and more clearly that only evidence from other disciplines will be able to independently test those scenarios.

The debate concerning the emergence of symbolic practices offers an excellent example of the difficulties that the sciences of the past have encountered in understanding the mechanisms that led to the emergence and complexification of this behaviour. At the end of the last century the prevailing view was that symbolically mediated behaviour abruptly developed around 40,000 years ago in Europe due to a sudden change in brain architecture (Klein, 1995, 1999; Mellars & Stringer, 1989). It was hypothesised that this led to an equally abrupt emergence of language (Chomsky, 1986). Later on, a paradigm shift led to the hypothesis that these changes took place around 200,000 years ago and first emerged in Africa (McBrearty & Brooks, 2000; Stringer, 2002). According to this model, the process of

speciation, that conducted to our species in this continent, would have provided a new cognition, associated with a substantial new brain architecture, enabling our ancestors to embody meaning in cultural artefacts. This view is now being challenged by work demonstrating that the cranial morphology that characterizes our species is the result of a gradual process that has lasted at least 300,000 years in Africa (Hublin et al., 2017; Neubauer et al., 2018; Scerri et al., 2018). It also appears that many cultural innovations, including some that play a role in symbolic practices such as the use of red pigments, appear to have emerged in Africa well before 200,000 years, at a time when cranial remains reveal archaic morphological features (Brooks et al., 2018; Watts et al., 2016). It has also been shown that other symbolic artifacts appearing between 300,000 and 60,000 years, such as personal ornaments, engravings, drawings, and burial practices emerged in Africa in different regions and not simultaneously (d'Errico & Stringer, 2011; d'Errico & Colagè, 2018). The discovery of systematic genetic exchanges between modern humans and archaic populations such as Neanderthals and Denisovians also reduces the relevance of phenotypic differences between these populations, which are now increasingly seen as members of a polymorphic species (Ackermann et al., 2016; Browning et al., 2018; Otto, 2018; Slon et al., 2018). This paradigm shift was concomitant with several archaeological discoveries - some of which are still controversial - which appear to confirm that Neanderthals had symbolic practices and that their cranial morphology was therefore not an obstacle to the development of complex cultures that were in many respects comparable to those of contemporary African populations (d'Errico, 2003; d'Errico & Colagè, 2018; Hoffmann et al., 2018; Roebroeks & Soressi, 2016). These contrasting paradigms, evoking rapid or gradual changes in brain architecture and connectivity, need to be assessed, as far as possible, by dedicated experiments. Although recent works conclude that endocasts constitute a reliable proxy for

qualifying and quantifying variations in brain shape and organization in extinct human taxa (Dumoncel et al., 2020) inferring cognitive performances from brain morphology is a notoriously tricky endeavour, particularly if conclusions are not backed with experimental evidence (see also Beaudet et Fonta, ce volume).

This review aims at synthesising the achievements of neuroarchaeology, discusses the potential of analytical tools and highlights intrinsic limitations and challenges.

One may distinguish two branches in the field of neuroarchaeology. The first utilises neuroscientific concepts to explain the emergence and spread of new behaviours documented in the archaeological record. The concept of neuroplasticity, for instance, has been used to reappraise the dynamic of cultural innovation by arguing that the brain has the potential to build on existing knowledge and embodiment to adapt to cultural innovations (Colagè & d'Errico, 2018; d'Errico & Colagè, 2018; Malafouris, 2010a). Neuroplasticity is often used to describe the brain's ability to compensate for injury and disease in the presence of pathology or to adjust its function and structure in response to new situations or changes in the environment. The effects of neuroplasticity have been observed experimentally in functional and structural MRI (Magnetic Resonance Imaging), particularly following the acquisition of new motor, perceptual, linguistic, and cognitive skills. At the functional level, this is underpinned by an increase or decrease of regional activation and/or a modification of the functional connectivity between brain regions within a network (Kelly & Garavan, 2005; Pascual-Leone et al., 2005). At the structural level, neuroplasticity can modify white matter tracts linking brain regions, change the density of gray matter areas, and cortical thickness (Zatorre et al., 2012). Within the framework of neuroarchaeology, neuroplasticity offers an explanation for the propagation and stabilisation of cultural innovations. Neuroplasticity also provides a biological scaffold to the impact of culture,

whereby reorganisation of cerebral networks reflects the transformation of an innovation into transmissible skills. Neuroplasticity, therefore, supports the concept that the evolution of cognition may have been to a large extent driven by cultural advances rather than by biological changes.

The second arm within neuroarchaeology aims to test hypotheses on the evolution of cognition by gathering empirical data. In this review, we will focus on experiments that use brain imaging. Neuroimaging-based studies aim to map, in modern humans, the cognitive functions and neural substrates that facilitated the emergence and cognitive processing of selected archaeological artefacts. The overarching goal is to infer the timepoint at which higher cognitive functions emerged in the past and how they evolved. Although this approach cannot directly reveal the networks at play in extinct hominins, it can provide critical information on the brain networks whose evolution and plasticity may have been responsible for the emergence of new cognitive skills. To date, neuroimaging studies have focused on two categories of artefacts, namely stone tools and engravings. Several studies tried to map brain areas involved in the production of stone tools as manufactured by early hominins and other extinct representatives of our genus (Putt et al., 2017, 2019; Stout et al., 2008, 2015; Stout & Chaminade, 2007). A recent study investigated the relevant brain areas involved in the visual processing of engravings from the Lower and Middle Palaeolithic (Mellet et al., 2019a). The neuroimaging arsenal available to explore neuroarchaeology has advantages and limitations (Le Bihan, 2018). In this review, we will discuss the available literature in the light of these circumstances.

**Which neuroimaging tools can be used for neuroarchaeological studies?**

Positron emission tomography (PET): PET is a metabolic imaging technique that measures the accumulation of radioactively labelled glucose (18-fluorodeoxyglucose or  $^{18}\text{FDG}$ ) in the brain regions involved in a given task. Following the injection of  $^{18}\text{FDG}$ , the participants perform a task outside the PET scanner, where they are able to move freely. The long half-life of  $^{18}\text{FDG}$  allows obtaining brain region measurements within 40 minutes after a task has been completed. It is, therefore, possible to collect neuroimaging data without the motion artefacts often generated by a task such as stone tool knapping. However, this advantage is counterbalanced by low temporal resolution and a limited spatial resolution of 1 centimeter (Roland, 1993).

Nowadays, PET imaging is only rarely used in healthy volunteers, mainly because it requires the injection of a radioactive compound.

Functional magnetic resonance imaging (fMRI): fMRI is a hemodynamic imaging technique based on the measurement of the oxyhaemoglobin/deoxyhaemoglobin level in the blood (Hillman, 2014; Kwong et al., 1992). This ratio increases with amplified blood flow to areas of the brain activated by the execution of a task. The spatial resolution of fMRI is about five millimeters, and the temporal resolution can be up to 1 to 2 seconds with a haemodynamic delay of up to 6 sec. fMRI is highly sensitive to motion artefacts, especially when the images are acquired during a motor task.

MRI is at present, and by far, the most widely used technique for both functional and structural studies provided that no movements are required from the participants. If this is the case, fNIRS (see below) is preferred, but with the drawback that this technique does not give access to sub-cortical structures.

Functional Near-infrared spectroscopy (fNIRS): Similar to fMRI, fNIRS relies on the close coupling between haemoglobin/deoxyhaemoglobin levels and cerebral blood flow, which

increases proportional to neuronal activity. Unlike fMRI, however, these related processes are measured through spectroscopy, using pairs of infrared emitters and receptors positioned on the participant's head (Kirkpatrick, 1997). One of the advantages of this technique is that it is relatively insensitive to the movement of participants. It is, therefore, possible to record brain signals while the participant is performing a task such as stone tool making. The spatial resolution depends on the number of emitters/receivers, but it is generally in the order of two centimeters. Temporal resolution is similar to that of fMRI. Unfortunately, fNIRS only investigates the superficial parts of the cortex with the exclusion of subcortical regions and white matter networks.

Functional transcranial Doppler sonography (fTCD): fTCD non-invasively records changes in the intracranial blood flow velocity in the middle cerebral arteries during the execution of a task. It measures the dynamic component of cerebral blood perfusion by continuously measuring the velocity of cerebral blood flow in the basal cerebral arteries. fTCD is insusceptible to motion artefacts, which allows for data collection during a motor performance task. While fTCD is not sensitive enough to detect subtle differences between neighbouring brain regions, it can be instrumental in evaluating differences in blood flow between hemispheres and is therefore suitable for studies that focus on hemispheric lateralisation of cognitive activities (Knecht et al., 1998).

In sum, it should be kept in mind that functional neuroimaging studies, regardless of the technique used, are generally based on the contrast of two or more conditions (e.g. target vs control tasks). For example, in a toolmaking neuroimaging study, the contrast of interest would be between the signal collected during stone toolmaking (the task of interest) and simply hitting one stone against another (reference condition). Specific aspects of this task can be extracted by subtracting activations related to one aspect of the task (e.g., the

elementary motor processes) and isolate specific aspects (e.g., goal-directed attention and planning for toolmaking).

Structural magnetic resonance imaging (sMRI): sMRI is the most detailed in vivo method to study the structure of the brain. In neuroarchaeological applications, it is used to measure the density of gray matter in the cortex (e.g. voxel-based morphometry) or the thickness and surface area of the cortex. These measures can change with learning, which is considered as brain plasticity (Fischl & Dale, 2000; Winkler et al., 2018). While current structural acquisitions can be obtained in high resolution below 1mm, such scans provide limited information on the white matter structures connecting cortical areas.

Diffusion magnetic resonance imaging (dMRI): dMRI reveals the structure of white matter. It is sensitive to the motion of water molecules, especially within the connective tissue of the brain. The white matter consists of fibers (axons) that conduct nerve impulses originating from a cell body located in gray matter. Diffusion imaging can be used to extract parameters such as mean diffusion (MD) and fractional anisotropy (FA) which provide scalar information on the organisation of the white matter and its possible modification in the context of structural plasticity. In addition, diffusion imaging tractography is used to visualise and segment streamlines of white matter pathways that connect brain regions.

### **The neurocognitive basis of tool making**

Although tool use and simple tool making are not exclusively human behaviours, members of the genus *Homo* have developed a degree of sophistication in tool manufacturing techniques that no other species has ever achieved (Boesch et al., 2014; Haslam et al., 2009, 2017). The earliest known stone tool industry is known as the Lomekwan, after Lomekwi 3, the Kenyan site where it was recently discovered (Harmand et al., 2015). The age of the

geological layers in which the stone tools were found (3.3 million years) indicates that contrary to general belief, the first stone tool makers did not belong to our genus but rather to Australopithecines, and probably to members of species *Kenyanthropus platyops*. They are the most likely candidates as their remains were found in the same geographical region and layers. The Oldowan industry, dating back approximately 2.5 million years ago, is traditionally associated with *Homo habilis*. Oldowan toolmakers would hit a stone (the “core”) with another stone (the “hammerstone”) to remove sharp flakes or detach small flakes on one or both sides of a pebble to produce a sharp edge (Figure 1, left). The Acheulean industry emerged approximately 1.76 million years ago (Lepre et al., 2011). The “hand-axe”, a pear-shaped symmetrical tool, and the cleaver, a “U” shaped tool, are emblematic of this technology (Figure 1, right). This new technology has been traditionally associated with *Homo erectus*, but bifacial tools of Acheulean type are also found in regions inhabited by *Homo heidelbergensis*, *Homo neanderthalensis*, archaic *Homo sapiens*, and probably the first representatives of our species.



Figure 1: Experimental knapping of a quartz pebble to produce an Oldowan flake (left) and an Acheulean hand-axe made of basalt (right). Experimenter M. Brenet; Left photo A. Delagnes, right photo N. Goren-Inbar.

It has been argued that the development of the Acheulean, which is concomitant with an expansion of brain volume, probably reflects the emergence of a proto-language about 1,5 million years ago (Arbib, 2011). Increasing complexity in tool use has been linked to the emergence of language (Stout & Chaminade, 2012) and is considered as a proxy for the evolution of other cognitive functions such as fine perceptual-motor coordination, planning, and social cognition (Tomasello et al., 2005). In particular, some authors have stressed the necessity of developing working memory and executive control skills to facilitate the making of elaborate tools. Working memory is crucial for goal-oriented behaviour as information needs to be stored and manipulated to ensure proper execution of complex tasks (Chai et al., 2018). For example, Wynn and Coolidge (2011) argued that the development of problem-solving and planning skills linked to working memory (Baddeley, 2007; Baddeley & Hitch, 1974) and executive functions (Miyake et al., 2000) would underpin the ability to create new tools. As such, neuroarchaeology attempts to characterise the neural substrate of stone tool-making to infer the cognitive functions required for this activity. In turn, this allows deducing to what extent language and tool-making rely on common brain substrates, which may indicate a co-evolution of these two competencies. A secondary aim is to map to what extent the prefrontal regions involved in working memory, planning, and executive control are involved in making the most elaborate tools. If there was a functional overlap between the neural substrates of the executive functions and those of the production of stone tool making, this would support the hypothesis that classical frontal lobe functions play a pivotal role in tool making. Finally, neuroarchaeologists wish to test the hypothesis that since the manufacture of the earliest stone tools relied on visuospatial and perceptual-motor processes it must have involved motor, premotor and parietal areas.

### Tool making and language

A possible connection between tool shaping and language was investigated since the very beginning of neuroimaging studies devoted to Lower Palaeolithic stone tools production (Stout & Chaminade, 2007, Stout et al., 2008, 2011). These studies were motivated by the shared cortical and white matter structures dedicated to both language and praxis. Praxis is defined as the ability to intentionally perform actions intended to accomplish a specific goal, such as tool making and tool-use. Language and praxis share common cerebral substrates and are both strongly lateralised to the left hemisphere (Goldenberg et al., 2007; Johnson-Frey, 2004; Vingerhoets, 2014). This has led some authors to hypothesise a co-evolution of language and praxis and to propose the theory of a gestural origin of language (Arbib et al., 2008; Corballis, 2013; Hewes et al., 1973). According to this hypothesis, language articulation should be seen as a gestural system involving movements of larynx, lips and tongue (Corballis, 2015). The relationship between language and praxis is reinforced by the finding that sign language and spoken language share a common cerebral basis (Blanco-Elorrieta et al., 2018; Courtin et al., 2011; Emmorey et al., 2007; Petitto et al., 2000). It has also been suggested that the production and mimicry of tool making sounds could have given rise to vocalisations or protowords associated with the use of tools, thus linking tool making and the emergence of language (Larsson, 2015). As a consequence, the involvement of language areas during tool-making has been often investigated in neuroarchaeological studies (Hecht et al., 2015; Putt et al., 2017; Stout et al., 2008; Stout & Chaminade, 2007; Uomini & Meyer, 2013).

The first study that aimed to assess the neural correlates of Oldowan stone tool knapping used <sup>18</sup>FDG PET (Stout & Chaminade, 2007). Six subjects without prior experience in stone tool making were included in the study. The experiment was divided into four phases: a

control condition, a pre-practice tool making task, a tool making practice, and a post-practice task. In the control condition, participants had to hit two rocks for 40 minutes without attempting to produce flakes. Afterwards, participants completed a PET-scan session that lasted 45 minutes. The following day, participants were asked to produce flakes “useful for cutting” for 40 minutes and subsequently had a 45 minutes PET-scan. The third phase consisted of a training session in stone tool knapping without scanning: over the duration of 4 weeks, participants had to individually practice for 1 hour per week. They were given suitable rocks and other materials to produce stone flakes. Eventually, participants performed a post-training task which was a repetition of the second task where they had to produce flakes for 40 minutes, followed by a 45 minutes PET scanning session. For the pre-practice and post-practice tool making tasks activation was associated with the left ventral premotor cortex (PMC) and right central sulcus regions including the premotor, primary motor and somatosensory cortices. The authors point out that the ventral PMC is involved in prehension and tool use in monkeys. The activation in these regions led them to propose that the Oldowan tool making relied on an evolutionarily preserved cortical system that performs sensorimotor transformations for object manipulation. In addition, the activity in the ventral PMC was in the vicinity of Broca’s area, a critical region for language production. This prompted the authors to propose that these activations reflect a hierarchical process of information processing common to language and tool making. An effect of practice was reported in the premotor cortex, signified by a postero-medial shift of premotor activation after the training phase. This reflects a functional reorganisation (i.e. functional plasticity), which may be linked to a change in strategy as a result of learning.

It is noteworthy that no activation in the prefrontal cortex was reported by this pioneering study. The prefrontal cortex and its connections are considered to be the most recent brain

area along the phylogenetic tree and the most developed in humans compared to other non-human primates (Barrett et al., 2020; Croxson et al., 2018). This anterior part of the frontal cortex of the brain plays a crucial role in executive control (Fuster, 2001). It appears, therefore, that such control is not necessary during the production of Oldowan tools. In the posterior part of the brain, the parietal cortex and primary and associative visual areas in the occipital lobe were also activated during Oldowan tool making tasks. The dorsal parietal cortex and its connections is a region that expanded in humans compared to monkeys (Catani et al., 2017; Orban et al., 2004). The parietal cortex is involved in visuo-motor coordination. Activations in this region could thus be related to the particularly well-developed human capacity of tool making.

In a follow-up PET study using the same experimental protocol, the authors included three experts in stone tool knapping (Stout et al., 2008). A condition of Acheulean tool making was added to the Oldowan tool making and the control condition, in which participants had to hit two rocks without producing flakes. The authors report higher activations in frontal regions, including the premotor regions and the right inferior frontal gyrus, during the Acheulean tool making task compared to the Oldowan tools task. This observation led them to propose a relationship between the degree of complexity of tool making and the regions involved in the planning and hierarchy of action sequences during goal-directed motor behaviour. The authors also reported activations in the superior and inferior parietal cortex for both tasks. Regarding Oldowan tools, the activations in the parietal regions were affected by the level of expertise whereby the parietal cortex was more activated in the right hemisphere in experts than in novices (Stout & Chaminade, 2007).

Although the authors of these two studies highlight the relationship between tool making and the emergence of language, the arguments in favour of this link are only partially

supported by their results. It is true that these studies report the activation of regions involved in the implementation of a hierarchically organised activity, a typical property in tools use, stone tool making and language (Stout & Chaminade, 2012). However, the left hemisphere - usually more involved in language tasks than the right hemisphere (Vigneau et al., 2011) for right-handed people and most left-handed people - does not appear to be of relevance. No regions activated by language processes such as the left inferior frontal or left superior and middle temporal gyri were implicated in tool making tasks despite them being activated in tool use tasks (Goldenberg et al., 2007; Johnson-Frey, 2004; Vingerhoets, 2014). Furthermore, it should be considered that these studies apply a neuroimaging method in which brain activity is recorded with a delay after the tool making task had been completed. In addition, PET imaging has a relatively low temporal resolution, and the small number of participants may have further reduced the statistical power of this study to draw reliable conclusions.

The putative co-emergence of tool making and language has been investigated more recently using fTCD (Uomini & Meyer, 2013). This study compared the hemispheric lateralisation of blood flow increases in ten subjects during the shaping of Acheulean tools and a word generation task. The authors aimed to directly compare the brain response in a relatively elaborated knapping and language task. They reported that, on average, the word generation task was lateralised to the left hemisphere while the tool knapping task involved predominantly the right hemisphere. However, the laterality index measured during the two tasks was positively correlated in the first ten seconds. This result suggests that tool making involves cortical regions in the left hemisphere, dominant for language, in the initial phase of the task. Given the low spatial resolution of fTDC it is, however, difficult to localise the exact cerebral regions and hence to extrapolate a common neural substrate.

The working hypothesis stemming from the work conducted by Stout et al. (2008), Stout & Chaminade (2007), and Uomini & Meyer (2013) is that the brain circuits supporting Lower Palaeolithic tool making partially overlap with language circuits. These analyses also suggested that both language and tool making share regions involved in more general cognitive capacities, including complex and goal-oriented actions. Although there is no conclusive evidence demonstrating that the two activities use the same brain areas, the idea that language and tool making have evolved in a mutually reinforcing way is supported by these studies.

Recent work has provided some additional insights into this topic. The authors (Putt et al., 2017) used fNIRS to measure brain activity in thirty-one participants over three conditions: while they were knapping Oldowan tools, Acheulean tools and hitting two rocks without producing flakes. Notably, the seven learning sessions that preceded the fNIRS acquisition took place in two distinct ways: half of the participants learned how to make stone tools through a video with verbal instructions, while the other half were given a video without verbal instructions. The comparison of these two groups could provide insights into the role of verbal learning in the potential co-activation of language and tool-making brain regions. The main results will be presented in detail in the next section, but the point here is that the authors did not report the involvement of language areas. Instead, they found that superior and middle temporal areas were activated during Acheulean tool making (Figure 2). They propose that these activations, which reflect elaborate auditory processing, may be related to the evaluation by the participant of how the blow and the sound associated with it reflect the overall shape of the hand-axe being made (i.e. the sounds, related to the toolmaking, would be used as feedback in order to adjust the knapping behaviour). The authors thus argue that tool making may have played a role in fine-tuning sound processing (Larsson,

2015), and facilitated the perception of speech in which the superior temporal gyrus plays a crucial role (Zatorre, 2004). In contrast, the production of Oldowan tools would have activated a less extended network, involving mainly motor areas (Figure 2). This study also reported an effect of learning whereby the verbal learning group preferentially activated the right inferior frontal gyrus during Acheulean tool making and the left precentral gyrus during Oldowan tool making. By contrast, the non-verbal group preferentially activated the right temporal pole during Acheulean tool production and the left middle frontal gyrus while knapping Oldowan tools. Although this pattern is difficult to interpret, this result underlines the importance of controlling for learning effects, which might modulate neural networks.

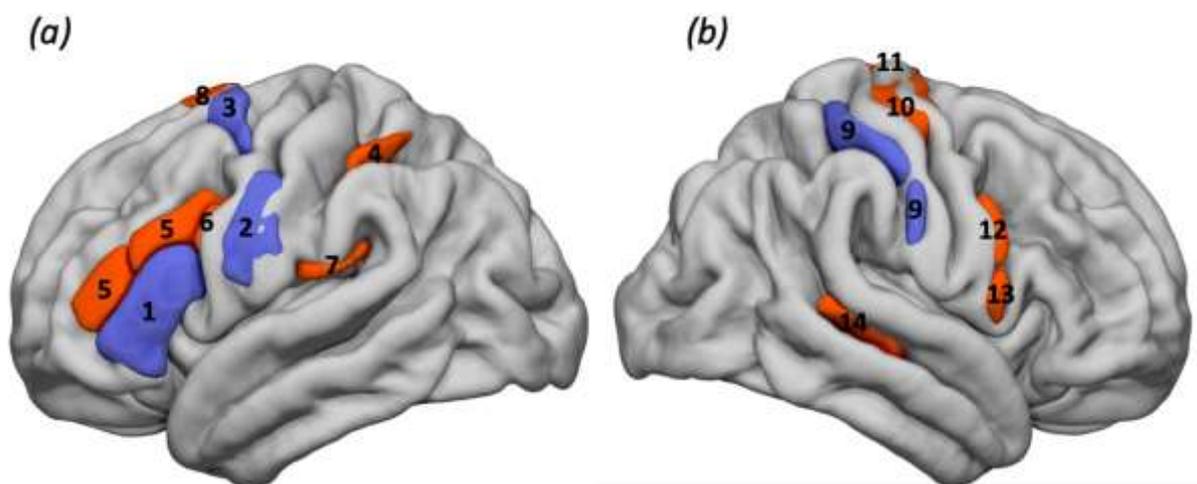


Figure 2: Brain regions (from the AICHA atlas; Joliot et al., 2015) activated by an Oldowan tools task compared to an Acheulean tools task (in purple) or vice-versa (in orange) as reported in Stout et al. (2011) and Putt et al. (2017, 2019). This figure was created with the Surf Ice software (<https://www.nitrc.org/projects/surfice/>), displaying in different colours the regions of the AICHA atlas that correspond to the MNI coordinates of significant activations, reported by Stout et al., (2011) and Putt et al., (2017, 2019). (a) Lateral view of the left hemisphere, (b) lateral view of the right hemisphere. (1) Left inferior frontal gyrus pars triangularis, (2) Left central sulcus, (3) Left superior frontal sulcus, (4) Left intraparietal sulcus, (5) Left inferior frontal sulcus, (6) Left precentral sulcus, (7) Left supramarginal gyrus (8) Left supplementary motor area, (9) Right postcentral sulcus, (10) Right central sulcus, (11) Right paracentral lobule, (12) Right precentral sulcus, (13) Right rolandic operculum (14) Right superior temporal sulcus. The figure only indicates that an activation was present in this region without quantifying it.

In conclusion, the hypothesis of a co-evolution between language and tool making is attractive and supported, for example, by the observation that both rely on common hierarchically organized cognitive processes common to both activities (Stout & Chaminade, 2012; Stout & Chaminade, 2009). However, the neuroimaging experiments conducted to

date have not provided conclusive evidence that a relationship between language and tool making exists (Roby-Brami et al., 2012). Indeed, the overlap between the language areas *per se*, for instance, the left inferior frontal gyrus and left posterior superior, and middle temporal gyri and the regions involved in tool making appears to be limited. Language and tool making might nevertheless have co-evolved with oral transmission facilitating learning and stabilising skills.

#### Tool making, working memory, and executive functions.

Working memory is a short-term memory system that activates and temporally sustains a set of verbal or visuospatial representations (Baddeley, 2007; Baddeley & Hitch, 1974). Also, working memory includes a cognitive system called central executive that coordinates cognitive processes with increasing task load. Executive functions and cognitive control allow the processing of information to be adapted to current objectives. They are required to perform activities such as planning, organizing, and managing time and space in an adaptive and flexible way. Prefrontal areas are considered as central regions for the processing of these functions (Fuster, 2001).

Stout & Chaminade (2007) explored brain activity associated with Oldowan tool making in novice toolmakers and reported no significant activations of the prefrontal dorsolateral cortex. This suggests that Oldowan tool making might not require advanced cognitive control and executive functions. By contrast, the dorsal intraparietal sulcus (IPS) was activated during the tool making tasks. This region is involved in visual analysis during object manipulation and tool handling, suggesting that visuo-motor coordination is the primary ability required for Oldowan tool making. Stout & Chaminade (2007) appropriately assert that this type of technology is based on perceptual-motor adaptation to the constraints of

the task rather than on cognitive control. In their subsequent PET study comparing Acheulean and Oldowan, Stout et al. (2008) reported that Oldowan tool making also involves the right inferior temporal and the orbitofrontal cortex, while Acheulean toolmaking involves the prefrontal cortex. The latter would reflect a temporal organization of the gestures and the implementation of a strategy not required when producing Oldowan tools. It could be argued that the lack of prefrontal activation is related to a lack of practice, but there is little evidence supporting this hypothesis. The study by Stout et al. (2011) included participants with different levels of expertise in stone tool knapping (novice, trained, expert), and reported activation in the medial prefrontal rather than in the dorsolateral cortex in experts when performing motor imagery or tool production assessment tasks. In the study by Stout et al. (2008), the effects of expertise were located in the parietal cortex. Finally, a positive correlation between expertise and the amplitude of activation in the middle frontal gyrus is reported in the fNIRS study by Putt et al. (2019), but it only concerns the production of Acheulean tools.

More recently, Hecht et al. (2015) explored the brain structural modifications related to the learning of Oldowan and Acheulean technologies. They conducted a longitudinal sMRI study in which they assess changes in gray and white matter at different stages of stone tool making learning. The study included six participants, each trained in stone tool making for two years. The training included demonstrations, instructions, and coaching by an expert stone toolmaker as well as self-directed practice. The training, however, was not standardised and it varied considerably between participants. All participants were trained to make both Oldowan and Acheulean stone tools. Structural imaging (gray matter density in the cortex) and diffusion imaging for the white matter were acquired at the beginning (T1), during (T2) and at the end (T3) of the experiment. A voxel-based morphometric analysis

revealed gray matter expansion between the first two time points in the supramarginal gyrus (SMG), but an opposite trend between the latter two time points. For the white matter, the results revealed changes in fractional anisotropy in the vicinity of the left SMG in the inferior parietal lobe, the bilateral ventral pre-central gyrus, and the right *pars triangularis* in the frontal lobe. These changes may suggest alterations in axon density and axon caliber related to training (Sampaio-Baptista & Johansen-Berg, 2017). In this study, probabilistic tractography was employed to examine the white matter connections between brain regions. Combining tractography with voxel-based morphometry<sup>1</sup> revealed that the connections that showed fractional anisotropy changes probably connected the cortical regions that had changed between time points. In other words, structural changes, related to the white matter and its projections, were observed within a fronto-parietal network. The study also reported that these alterations were more important when subjects spent more time practicing tool making. These results thus highlight the structural gray and white matter changes of the fronto-parietal networks related to the acquisition of skills in Palaeolithic stone tool making. The changes reported in the fronto-parietal network may reflect brain plasticity associated with the use of executive functions, executive control, and working memory required for the acquisition of tool making skills. In line with these assumptions, Hecht et al. (2015) propose that fronto-parietal networks underwent modifications driven by the making of Palaeolithic tools. These modifications may have in turn favoured the emergence of other complex functions that require working memory, planning, and cognitive control.

---

<sup>1</sup> Voxel-based morphometry is a technique that measures the local density of gray matter in the brain tissue (Ashburner & Friston, 2000).

The low number of participants and the absence of a control group, however, limit the specificity of the observed changes and hence conclusions should be taken with caution. The same team conducted an additional study aimed to further assess the cognitive demands of Palaeolithic tool making (Stout et al., 2015). Six participants were trained to reproduce three Palaeolithic technologies: Oldowan, Acheulean, and Levallois. Skills were evaluated by formally comparing artefacts produced before and after training for each category. After their training, participants had to watch video snippets of 1.5-second of rotating stone artefacts from each category while in the scanner. Participants were then asked to perform two different tasks in the scanner : A “Prediction” task (answer the question “if the core were struck in the place indicated, is what you see a correct prediction of the flake that would result?”) or a “Strategy” task (answer the question “is the indicated place to hit the core a correct one given the objective of the technology?”). Functional imaging (fMRI) was acquired three times during training: at the beginning (T1), during (T2), and at the end (T3). The average total time of training was 167 hours. The authors reported that activity in a region of the left upper frontal gyrus involved in working memory and executive control was modulated by a combination of the task performed (i.e. prediction vs. strategy), the tools used (i.e. Oldowan vs. Acheulean), and the time spent on training (T1, T2, T3). Results indicate that toolmaking affected brain activity and functional connectivity (assessed by the correlation between activities in different regions) of the dorsal prefrontal cortex. The amplitude of activation was correlated with the rate of correct strategic judgements, which was predictive of success in Acheulean but not in Oldowan tool making. This observation is consistent with the cognitive control requirements of Acheulean toolmaking compared to the Oldowan, including information control and manipulation.

Putt et al. (2017; 2019) conducted two studies supporting the importance of working memory in stone tool making. They involved a larger number of subjects, thus increasing robustness and reliability of results and used fNIRS. With this technology they measured brain activity while participants were knapping Oldowan and Acheulean stone tools or performing a control task consisting of hitting a rock against another without producing flakes. The first study included 31 participants with no previous stone knapping experience (Putt et al., 2017). Each participant was trained in stone knapping for seven sessions. Each training session lasted 1 hour. All participants had to perform the same three tasks in a fixed order: a control task, an Oldowan and Acheulean tool making. Simultaneously they underwent fNIRS scanning. The authors reported that Acheulean tool making activated the left ventral premotor cortex more than Oldowan tool making. This area of the brain was already reported in Oldowan tool making previously (Stout & Chaminade, 2007) and considered to activate visual working memory processes. This suggests that more complex tools are more demanding for this function as compared to less sophisticated tools. The supplementary motor area, which is involved in cognitive control and motor coordination of complex bimanual sequences, was also more activated during Acheulean than Oldowan tool making tasks. These findings support the idea that the development of working memory and cognitive control might have played a key role in the emergence of the Acheulean and that Oldowan tool making relied on coordination of visual attention and motor control rather than on working memory. One notable point is that none of the studies discussed here identifies an involvement of the dorsolateral portion of the prefrontal cortex. This region has been greatly reorganised over the course of encephalization particularly from approximately 1.6 to 1.8 million years ago (Teffer & Semendeferi, 2012), and is, among others, a key region for working memory and executive functions. Putt et al. (2019) investigated the role of this

brain area in tool making. Their second study used fNIRS and included 33 participants who performed an Acheulean and an Oldowan tool making task. The seven training sessions were identical to those mentioned above (Putt et al., 2017). In addition, to explore how brain activity changes with learning, this activity was measured after the first, fourth and seventh learning session. Results confirmed that the left dorsolateral prefrontal cortex was more activated during Acheulean than Oldowan tool making. Moreover, the activation in this region was positively correlated with the proficiency of Acheulean tool making, approximated by the size of the produced flakes. This supports the hypothesis that working memory, reinforced by a phylogenetically recent brain region, plays an important role in Acheulean tool making. It further supports the hypothesis that encephalization resulted in an enhancement of working memory and possibly other executive functions. Notably, the activity in prefrontal regions increased with learning, reflecting their role in the control of tool making. The same pattern was found in the middle and superior temporal gyri, involved in elaborate sound processing, in particular in speech sounds, confirming that the sounds produced by hitting the stones while knapping are analysed to guide the making of tools. In sum, these studies show that it is possible to measure differential cognitive control and neural substrates involved in the earliest tool making techniques, such as the Oldowan and the Acheulean, using a neuroarcheological approach. Acheulean tool making appears to be more demanding in terms of cognitive control, as attested by the involvement of prefrontal cortex, than the making of simpler Oldowan tools, which seems to rely more on sensorimotor control regions (Putt et al., 2017; Putt et al., 2019; Stout et al., 2008, 2011, 2015; Stout & Chaminade, 2007). The results obtained so far emphasize the role of regions involved in working memory and executive control thus supporting the importance of these

functions in the development of human capabilities, particularly tool making (Putt et al., 2017, 2019; Stout et al. 2008).

### **Motor cognition and cultural transmission: Insights from brain imaging**

An important aspect of tool making concerns the implementation of efficient social cognition processes that allow for the interindividual transmission of skills.

This aspect was addressed in an fMRI study that examined the regions involved in observational understanding of the actions required for Oldowan and Acheulean tool making by naïve (n=11), trained (n=10), and expert (n=5) toolmakers (Stout et al., 2011). Participants were asked to watch video clips of 20 sec showing Oldowan and Acheulean toolmaking as well as bimanual percussion without attempting to knap the rock. After each video clip, participants had to perform either an “Imagine” task (i.e. a motor imagery task in which the participants simulated continuing the action they saw) or an “Evaluate task” (i.e. decide whether the actor was successful in achieving his/her goal). Reported activations were similar to previous studies in which participants physically performed these tasks, suggesting the existence of a motor resonance that may have played a crucial role in the interindividual transmission of toolmaking. It is noteworthy that such a resonance appears modulated by increasing complexity of the manufacture: compared to Oldowan, Acheulean knapping, which requires more complex and hierarchically organized gestures, was associated with a significantly higher activation of the left anterior intraparietal sulcus and the inferior frontal sulcus, both in the left hemisphere (Figure 2). It has been suggested that the anterior part of the intraparietal sulcus would be a core component of the putative human mirror system (Grafton & Hamilton, 2007). The inferior frontal sulcus activation might reflect a stronger integration of actions requiring more complex, and more planned, motor processes in

Acheulean than the Oldowan tool making. The results also evidenced distinct responses by naïve and expert groups. Naïve participants activated the core motor resonances structures (i.e. *pars opercularis*, another component of the putative human mirror neurons system) as well as the ventral prefrontal cortex, interpreted by the authors as reflecting a low-level strategy of understanding new actions by simulation. In contrast, expert participants activated their medial prefrontal cortex — a classical "mentalizing" region suggesting a high-level strategy based on inference of the mental states of others — and their right inferior parietal lobule, involved in visuo-spatial attention and sensorimotor matching. Such differences suggest a functional reorganisation (Kelly & Garavan, 2005), involving the adoption of different cognitive strategies for action understanding, depending on the level of expertise. More broadly, this study supports a role for motor resonance in the evolution of human social cognition and cumulative culture, at least in the context of tool making.

### **Neural basis of Palaeolithic abstract engravings perception**

So far, this review has focused on describing neural correlates of stone toolmaking. However, other elements of Palaeolithic material culture may provide information on the cognitive abilities of our ancestors. The discovery of abstract engravings dating from the Lower and Middle Palaeolithic suggests that this behaviour was not only exhibited by *Homo sapiens* but also by archaic hominins such as the *Homo erectus* (Joordens et al., 2014) and *Homo neanderthalensis* (Rodríguez-Vidal et al., 2014). Archaeologists were able to show that a number of these engravings were intentional and not due to natural or accidental causes, meaning the engraver's objective was to leave visible marks (Henshilwood et al., 2009). It has been argued that these early engravings might have had a meaning and have been the materialisation of signs or symbols used for communication (Henshilwood & d'Errico, 2011).

This hypothesis is in contradiction with the view that the ability to embed meaning in cultural artefacts was the result of a sudden cognitive revolution occurring among Modern Human populations settling in Europe some 42,000 years ago (Bar-Yosef, 1998; Klein, 2000; Mellars & Stringer, 1989) or the result of a sudden speciation event occurring in southern or eastern Africa approximately 200,000 years ago (McBrearty & Brooks, 2000). These early abstract markings represent an ideal ground for brain imaging studies because of their intriguing, controversial nature. Their emergence preceded the first figurative representations by several hundred thousand years (Aubert et al., 2019). They are a rare occurrence both in the African Middle Stone Age and in the Middle Palaeolithic of Eurasia. Their use for symbolic purposes is debated and the age of some instances unclear.

A recent neuroimaging study has focused on the cerebral regions involved in the perception of these engravings (Mellet et al., 2019a). The aim was to determine whether the engravings had a visual structure complex enough for their perception to activate visual regions engaged in patterns recognition and identification. To contrast the complexity, one condition presented engravings while the other depicted scrambled versions, in which the perceptual organization was removed (Figure 3, bottom). In addition, the study aimed to assess whether the regions involved in the perception of engravings were also involved in the perception of other visual categories such as objects, words, symbols or outdoor scenes (Figure 3, top). Inside the MRI scanner, the participants had to perform a one-back task, i.e. detect when two identical stimuli were successively repeated.

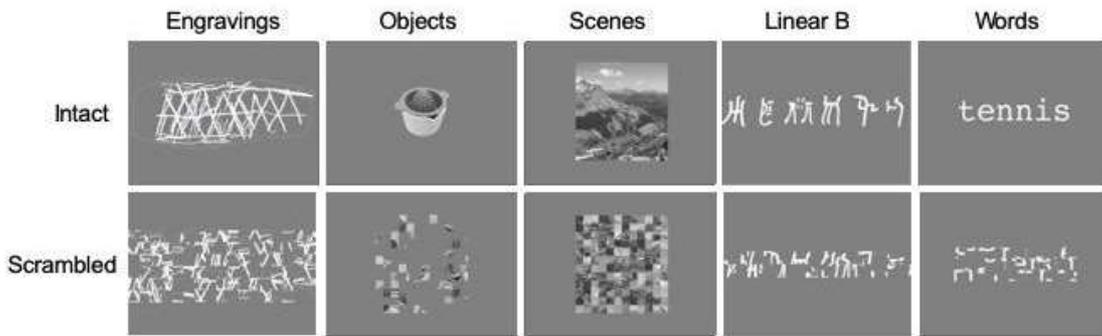


Figure 3: Examples of stimuli included in the visual categories used by Mellet et al., 2019a. The top row illustrates examples of intact stimuli, the bottom row their scrambled version, devoid of perceptual organization.

The comparison of the brain response elicited by the perception of engravings with that caused by the perception of scrambled engravings showed that although the engravings were not recognized as existing entities, their perception elicits activation in visual regions engaged in patterns recognition and identification (i.e. anterior regions of the ventral pathway sensitive to distinct visual categories; Downing et al., 2006; Grill-Spector, 2003; Grill-Spector & Weiner, 2014; Haxby, 2001). The involvement of the visual ventral pathway indicates that the perceptual processing of these early engravings requires more than the simple identification of visual primitives, such as the extraction of edges, oriented segments, or ends of lines. This implies that the level of perceptual organisation characterising the engravings is sufficiently high to recruit higher order visual areas. In fact, the activations related to the perception of engravings (Figure 4, top) were very close to those induced by the perception of objects (Figure 4, bottom).

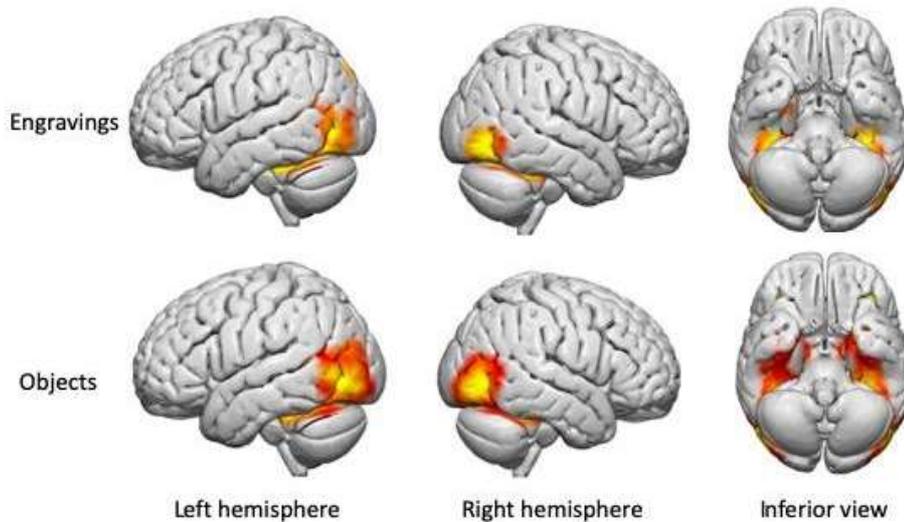


Figure 4: Lateral and inferior views of the activations elicited by the perception of the earliest known engravings (top row) and objects (bottom row). The perception of both visual categories triggered similar activations, located in the occipital lobe and the ventral part of the temporal lobe (displayed at  $p < 0.001$ , uncorrected).

This confirms that despite their simple structure, engravings recruit brain regions specialised in recognition and identification of visual input. This result is consistent with the hypothesis that abstract engravings could have been used as signs or even symbols by our ancestors (Mellet et al., 2019a; Mellet et al., 2019b). The primary visual cortex was not more activated by the perception of the engravings than by the perception of their scrambled version. This indicates that this region is not sensitive to the perceptual organization of the engravings, which contradicts the hypothesis that this region played a crucial role in the emergence of engraving production as it has been suggested (Hodgson, 2006, 2019). Rather, associative visual areas are the main regions involved in the visual processing of the earliest engravings. This observation is consistent with the hypothesis that these representations may have had fulfilled symbolic functions. It should be noted that work based on cognitive experiences has found no clear evidence that the earliest engravings were used as signs or symbols. It has been proposed that these manifestations may rather correspond to markings that could not be easily discriminated as signs, although the authors recognize a trend through time toward increasing consistency and complexity (Tylén et al., 2020). Although future research

questions and strategies need to be refined, the path is open for empirical studies of the perceptual processing of the first engravings. This will be a further step towards understanding hominin cognition and its evolution.

## **Discussion and Conclusion**

With this review, we intended to illustrate how the use of neuroimaging can shed light on the evolution of human cognition. Our purpose was also to show how challenging, theoretically and technically, such an endeavour can be. The studies presented here have identified brain regions involved in the production or perception of some categories amongst the earliest known cultural artefacts. However, they only seldomly provide definite evidence in favour of one evolutionary scenario over another and more often limit themselves to propose informed hypotheses on those trajectories. They are hampered by the fact that while their long-term goal is to identify steps in the evolution of cognition, they are limited to the study of modern humans.

Neuroarchaeology cannot use results obtained in neuroimaging experiments involving modern humans to directly infer information on structural and functional brain networks associated with hominins of the far past. It can, however, design experiments that can evaluate the cognitive and cerebral requirements of tasks performed in the past and identify changes in requirements associated with known cultural innovations by applying a number of dedicated research strategies (Stout & Hecht, 2015; Mellet et al., 2019b).

The way in which experimental protocols are conceived, justified, and implemented becomes key for increasing the robustness of inferences about ancestral cognition.

Neuroarchaeology cannot work in a void. Integration of perspectives and data from archaeology, paleogenetics, paleoanthropology, cultural anthropology, ethology and

psychology is essential. Archaeology provides chronological and contextual evidence and indispensable empirical data. Sister disciplines such as experimental archaeology and cognitive archaeology contribute to detailed accounts of the behavioural repertoires of our ancestors. Paleogenetics is supplying essential clues on biological interactions that occurred between hominin populations interpreted in the past as distinct species on the basis of morphological differences. Paleoanthropology identifies long term evolutionary trends that represent the broad framework to which all researchers interested in the biological evolution of our lineage need to refer to. Cultural anthropology illuminates us on the present-day variability of cultural practices and the way in which cultural traits evolve or coevolve at the individual and the societal level. Ethology and genetics inform us on the degree of behavioural and biological similarity between human and non-human species. Psychology has conceptual tools to identify trends in human behaviour and theoretical tools to characterize them from a variety of perspectives. Neuroimaging precisely identifies the brain areas at work in tasks performed in the present that mimic cultural practices of the past and build on recent advances in neuroscience to propose informed hypotheses on how they may have interacted in the past. It needs inputs from all other disciplines to target relevant issues, conceive informative experiments and evaluate the pertinence of their results.

### **Acknowledgments**

This work was supported by a CNRS project 80 Prime, a grant from the IdEx Bordeaux/CNRS (PEPS 2015), the Research Council of Norway through its Centres of Excellence funding scheme (Centre for Early Sapience Behaviour, project number 262618), the Labex LaScArBx-ANR no ANR-10-LABX-52, and the Talents program of the University of Bordeaux 'Initiative

d'Excellence'. We would like to warmly thank Stephanie Forkel for her editing and useful critical reading of the manuscript. We also thank Michel Brenet, Anne Delagnes, Marianne Deschamp and Nama Goren-Inbar for providing photos of experimental knapping conducted in the framework of their ongoing research projects "Old" and "Partenariat Hubert Curien – Maimonide".

## References

- Ackermann, R. R., Mackay, A., & Arnold, M. L. (2016). The Hybrid Origin of “Modern” Humans. *Evolutionary Biology*, 43(1), 1-11. <https://doi.org/10.1007/s11692-015-9348-1>
- Arbib, M. A. (2011). From Mirror Neurons to Complex Imitation in the Evolution of Language and Tool Use. *Annual Review of Anthropology*, 40(1), 257-273. <https://doi.org/10.1146/annurev-anthro-081309-145722>
- Arbib, M. A., Liebal, K., & Pika, S. (2008). Primate Vocalization, Gesture, and the Evolution of Human Language. *Current Anthropology*, 49(6), 1053-1076. <https://doi.org/10.1086/593015>
- Ashburner, J., & Friston, K. J. (2000). Voxel-Based Morphometry—The Methods. *NeuroImage*, 11(6), 805-821. <https://doi.org/10.1006/nimg.2000.0582>
- Aubert, M., Lebe, R., Oktaviana, A.A. *et al.* Earliest hunting scene in prehistoric art. *Nature* 576, 442–445 (2019). <https://doi.org/10.1038/s41586-019-1806-y>
- Baddeley, A. (2007). *Working Memory, Thought, and Action*. Oxford University Press. <https://doi.org/10.1093/acprof:oso/9780198528012.001.0001>
- Baddeley, A. D., & Hitch, G. (1974). Working Memory. In *Psychology of Learning and Motivation* (Vol. 8, p. 47-89). Elsevier. [https://doi.org/10.1016/S0079-7421\(08\)60452-1](https://doi.org/10.1016/S0079-7421(08)60452-1)
- Barrett, R. L. C., Dawson, M., Dyrby, T. B., Krug, K., Ptito, M., D’Arceuil, H., Croxson, P. L., Johnson, P. J., Howells, H., Forkel, S. J., Dell’Acqua, F., & Catani, M. (2020). Differences in Frontal Network Anatomy Across Primate Species. *The Journal of Neuroscience*, 40(10), 2094-2107. <https://doi.org/10.1523/JNEUROSCI.1650-18.2019>
- Bar-Yosef, O. (1998). On the Nature of Transitions: The Middle to Upper Palaeolithic and the Neolithic Revolution. *Cambridge Archaeological Journal*, 8(2), 141-163. <https://doi.org/10.1017/S0959774300001815>
- Blanco-Elorrieta, E., Kastner, I., Emmorey, K., & Pyllkänen, L. (2018). Shared neural correlates for building phrases in signed and spoken language. *Scientific Reports*, 8(1), 5492. <https://doi.org/10.1038/s41598-018-23915-0>
- Boesch, C., Call, J., & Sanz, C. (2014). *Tool Use in Animals Cognition and Ecology*. Cambridge University Press. <https://doi.org/10.1017/CBO9780511894800>
- Brooks, A. S., Yellen, J. E., Potts, R., Behrensmeier, A. K., Deino, A. L., Leslie, D. E., Ambrose, S. H., Ferguson, J. R., d’Errico, F., Zipkin, A. M., Whittaker, S., Post, J., Veatch, E. G., Foecke, K., & Clark, J. B. (2018). Long-distance stone transport and pigment use in the earliest Middle Stone Age. *Science*, 360(6384), 90-94. <https://doi.org/10.1126/science.aao2646>
- Browning, S. R., Browning, B. L., Zhou, Y., Tucci, S., & Akey, J. M. (2018). Analysis of Human Sequence Data Reveals Two Pulses of Archaic Denisovan Admixture. *Cell*, 173(1), 53-61.e9.

<https://doi.org/10.1016/j.cell.2018.02.031>

Catani, M., Robertsson, N., Beyh, A., Huynh, V., de Santiago Requejo, F., Howells, H., Barrett, R. L. C., Aiello, M., Cavaliere, C., Dyrby, T. B., Krug, K., Ptito, M., D'Arceuil, H., Forkel, S. J., & Dell'Acqua, F. (2017). Short parietal lobe connections of the human and monkey brain. *Cortex; a Journal Devoted to the Study of the Nervous System and Behavior*, 97, 339-357. <https://doi.org/10.1016/j.cortex.2017.10.022>

Chai, W. J., Abd Hamid, A. I., & Abdullah, J. M. (2018). Working Memory From the Psychological and Neurosciences Perspectives: A Review. *Frontiers in Psychology*, 9, 401. <https://doi.org/10.3389/fpsyg.2018.00401>

Chomsky, N. (1986). *Knowledge of language : Its nature, origin, and use*. Praeger.

Colagè, I., & d'Errico, F. (2018). Culture: The Driving Force of Human Cognition. *Topics in Cognitive Science*. <https://doi.org/10.1111/tops.12372>

Corballis, M. C. (2013). Gestural theory of the origins of language. In C. Lefebvre, B. Comrie, & H. Cohen (Éds.), *Studies in Language Companion Series* (Vol. 144, p. 171-184). John Benjamins Publishing Company. <https://doi.org/10.1075/slcs.144.07cor>

Corballis, M. C. (2015). What's left in language? Beyond the classical model: What's left in language? *Annals of the New York Academy of Sciences*, 1359(1), 14-29. <https://doi.org/10.1111/nyas.12761>

Courtin, C., Jobard, G., Vigneau, M., Beaucousin, V., Razafimandimby, A., Hervé, P.-Y., Mellet, E., Zago, L., Petit, L., Mazoyer, B., & Tzourio-Mazoyer, N. (2011). A common neural system is activated in hearing non-signers to process French Sign language and spoken French. *Brain Research Bulletin*, 84(1), 75-87. <https://doi.org/10.1016/j.brainresbull.2010.09.013>

Croxson, P. L., Forkel, S. J., Cerliani, L., & Thiebaut de Schotten, M. (2018). Structural Variability Across the Primate Brain: A Cross-Species Comparison. *Cerebral Cortex* (New York, N.Y.: 1991), 28(11), 3829-3841. <https://doi.org/10.1093/cercor/bhx244>

d'Errico, F. (2003). The invisible frontier. A multiple species model for the origin of behavioral modernity. *Evolutionary Anthropology: Issues, News, and Reviews*, 12(4), 188-202. <https://doi.org/10.1002/evan.10113>

d'Errico, F., & Colagè, I. (2018). Cultural Exaptation and Cultural Neural Reuse: A Mechanism for the Emergence of Modern Culture and Behavior. *Biological Theory*, 13(4), 213-227. <https://doi.org/10.1007/s13752-018-0306-x>

Downing, P. E., Chan, A. W.-Y., Peelen, M. V., Dodds, C. M., & Kanwisher, N. (2006). Domain Specificity in Visual Cortex. *Cerebral Cortex*, 16(10), 1453-1461. <https://doi.org/10.1093/cercor/bhj086>

Dumoncel, J., Subsol, G., Durrleman, S., Bertrand, A., Jager, E., Oettlé, A. C., Lockhat, Z.,

Suleman, F. E., & Beaudet, A. (2020). Are endocasts reliable proxies for brains? A 3D quantitative comparison of the extant human brain and endocast. *Journal of Anatomy*, joa.13318. <https://doi.org/10.1111/joa.13318>

Emmorey, K., Mehta, S., & Grabowski, T. J. (2007). The neural correlates of sign versus word production. *NeuroImage*, 36(1), 202-208. <https://doi.org/10.1016/j.neuroimage.2007.02.040>

Fischl, B., & Dale, A. M. (2000). Measuring the thickness of the human cerebral cortex from magnetic resonance images. *Proceedings of the National Academy of Sciences*, 97(20), 11050-11055. <https://doi.org/10.1073/pnas.200033797>

Fuster, J. M. (2001). The prefrontal cortex--an update: Time is of the essence. *Neuron*, 30(2), 319-333. [https://doi.org/10.1016/s0896-6273\(01\)00285-9](https://doi.org/10.1016/s0896-6273(01)00285-9)

Goldenberg, G., Hermsdorfer, J., Glindemann, R., Rorden, C., & Karnath, H.-O. (2007). Pantomime of Tool Use Depends on Integrity of Left Inferior Frontal Cortex. *Cerebral Cortex*, 17(12), 2769-2776. <https://doi.org/10.1093/cercor/bhm004>

Grafton, S. T., & de C. Hamilton, A. F. (2007). Evidence for a distributed hierarchy of action representation in the brain. *Human Movement Science*, 26(4), 590-616. <https://doi.org/10.1016/j.humov.2007.05.009>

Grill-Spector, K. (2003). The neural basis of object perception. *Current Opinion in Neurobiology*, 13(2), 159-166. [https://doi.org/10.1016/S0959-4388\(03\)00040-0](https://doi.org/10.1016/S0959-4388(03)00040-0)

Grill-Spector, K., & Weiner, K. S. (2014). The functional architecture of the ventral temporal cortex and its role in categorization. *Nature Reviews Neuroscience*, 15(8), 536-548. <https://doi.org/10.1038/nrn3747>

Harmand, S., Lewis, J. E., Feibel, C. S., Lepre, C. J., Prat, S., Lenoble, A., Boès, X., Quinn, R. L., Brenet, M., Arroyo, A., Taylor, N., Clément, S., Daver, G., Brugal, J.-P., Leakey, L., Mortlock, R. A., Wright, J. D., Lokorodi, S., Kirwa, C., ... Roche, H. (2015). 3.3-million-year-old stone tools from Lomekwi 3, West Turkana, Kenya. *Nature*, 521(7552), 310-315. <https://doi.org/10.1038/nature14464>

Haslam, M., Hernandez-Aguilar, A., Ling, V., Carvalho, S., de la Torre, I., DeStefano, A., Du, A., Hardy, B., Harris, J., Marchant, L., Matsuzawa, T., McGrew, W., Mercader, J., Mora, R., Petraglia, M., Roche, H., Visalberghi, E., & Warren, R. (2009). Primate archaeology. *Nature*, 460(7253), 339-344. <https://doi.org/10.1038/nature08188>

Haslam, M., Hernandez-Aguilar, R. A., Proffitt, T., Arroyo, A., Falótico, T., Fragaszy, D., Gumert, M., Harris, J. W. K., Huffman, M. A., Kalan, A. K., Malaivijitnond, S., Matsuzawa, T., McGrew, W., Ottoni, E. B., Pascual-Garrido, A., Piel, A., Pruett, J., Schuppli, C., Stewart, F., ... Luncz, L. V. (2017). Primate archaeology evolves. *Nature Ecology & Evolution*, 1(10), 1431-1437. <https://doi.org/10.1038/s41559-017-0286-4>

Haxby, J. V. (2001). Distributed and Overlapping Representations of Faces and Objects in

Ventral Temporal Cortex. *Science*, 293(5539), 2425-2430.  
<https://doi.org/10.1126/science.1063736>

Hecht, E. E., Gutman, D. A., Khreisheh, N., Taylor, S. V., Kilner, J., Faisal, A. A., Bradley, B. A., Chaminade, T., & Stout, D. (2015). Acquisition of Paleolithic toolmaking abilities involves structural remodeling to inferior frontoparietal regions. *Brain Structure and Function*, 220(4), 2315-2331. <https://doi.org/10.1007/s00429-014-0789-6>

Henshilwood, Christopher S., d'Errico, F., & Watts, I. (2009). Engraved ochres from the Middle Stone Age levels at Blombos Cave, South Africa. *Journal of Human Evolution*, 57(1), 27-47. <https://doi.org/10.1016/j.jhevol.2009.01.005>

Henshilwood, Christopher Stuart, & D'Errico, F. (2011). *Homo symbolicus the dawn of language, imagination and spirituality*. John Benjamins Pub. Co.  
<http://site.ebrary.com/id/10509457>

Hewes, G. W., Andrew, R. J., Carini, L., Choe, H., Gardner, R. A., Kortlandt, A., Krantz, G. S., McBride, G., Nottebohm, F., Pfeiffer, J., Rumbaugh, D. G., Steklis, H. D., Ralieggh, M. J., Stopa, R., Suzuki, A., Washburn, S. L., & Wescott, R. W. (1973). Primate Communication and the Gestural Origin of Language [and Comments and Reply]. *Current Anthropology*, 14(1/2), 5-24. <https://doi.org/10.1086/201401>

Hillman, E. M. C. (2014). Coupling Mechanism and Significance of the BOLD Signal: A Status Report. *Annual Review of Neuroscience*, 37(1), 161-181. <https://doi.org/10.1146/annurev-neuro-071013-014111>

Hodgson, D. (2006). Understanding the origins of paleoart: The neurovisual resonance theory and brain functioning. *Paleoanthropology*, 2006, 54-67.

Hodgson, D. (2019). Response to the critique by Mellet et al. Of Hodgson's Neurovisual resonance theory. *Journal of Archaeological Science: Reports*, 28, 102041.  
<https://doi.org/10.1016/j.jasrep.2019.102041>

Hoffmann, D. L., Standish, C. D., García-Diez, M., Pettitt, P. B., Milton, J. A., Zilhão, J., Alcolea-González, J. J., Cantalejo-Duarte, P., Collado, H., de Balbín, R., Lorblanchet, M., Ramos-Muñoz, J., Weniger, G.-Ch., & Pike, A. W. G. (2018). U-Th dating of carbonate crusts reveals Neandertal origin of Iberian cave art. *Science*, 359(6378), 912-915.  
<https://doi.org/10.1126/science.aap7778>

Hublin, J.-J., Ben-Ncer, A., Bailey, S. E., Freidline, S. E., Neubauer, S., Skinner, M. M., Bergmann, I., Le Cabec, A., Benazzi, S., Harvati, K., & Gunz, P. (2017). New fossils from Jebel Irhoud, Morocco and the pan-African origin of *Homo sapiens*. *Nature*, 546(7657), 289-292.  
<https://doi.org/10.1038/nature22336>

Johnson-Frey, S. H. (2004). The neural bases of complex tool use in humans. *Trends in Cognitive Sciences*, 8(2), 71-78. <https://doi.org/10.1016/j.tics.2003.12.002>

Joliot, M., Jobard, G., Naveau, M., Delcroix, N., Petit, L., Zago, L., Crivello, F., Mellet, E., Mazoyer, B., & Tzourio-Mazoyer, N. (2015). AICHA: An atlas of intrinsic connectivity of homotopic areas. *Journal of Neuroscience Methods*, 254, 46-59. <https://doi.org/10.1016/j.jneumeth.2015.07.013>

Joordens, J. C. A., d'Errico, F., Wesselingh, F. P., Munro, S., de Vos, J., Wallinga, J., Ankjærgaard, C., Reimann, T., Wijbrans, J. R., Kuiper, K. F., Mûcher, H. J., Coqueugniot, H., Prié, V., Joosten, I., van Os, B., Schulp, A. S., Panuel, M., van der Haas, V., Lustenhouwer, W., ... Roebroeks, W. (2014). Homo erectus at Trinil on Java used shells for tool production and engraving. *Nature*, 518(7538), 228-231. <https://doi.org/10.1038/nature13962>

Kelly, A. M. C., & Garavan, H. (2005). Human Functional Neuroimaging of Brain Changes Associated with Practice. *Cerebral Cortex*, 15(8), 1089-1102. <https://doi.org/10.1093/cercor/bhi005>

Kirkpatrick, P. J. (1997). Use of near-infrared spectroscopy in the adult. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences*, 352(1354), 701-705. <https://doi.org/10.1098/rstb.1997.0052>

Klein, R. G. (1995). Anatomy, behavior, and modern human origins. *Journal of World Prehistory*, 9(2), 167-198. <https://doi.org/10.1007/BF02221838>

Klein, R. G. (1999). *The human career: Human biological and cultural origins*. The University of Chicago Press.

Klein, R. G. (2000). Archeology and the evolution of human behavior. *Evolutionary Anthropology Issues News and Reviews*, 9(1), 17-36.

Knecht, S., Deppe, M., Ringelstein, E.-B., Wirtz, M., Lohmann, H., Dräger, B., Huber, T., & Henningsen, H. (1998). Reproducibility of Functional Transcranial Doppler Sonography in Determining Hemispheric Language Lateralization. *Stroke*, 29(6), 1155-1159. <https://doi.org/10.1161/01.STR.29.6.1155>

Kwong, K. K., Belliveau, J. W., Chesler, D. A., Goldberg, I. E., Weisskoff, R. M., Poncelet, B. P., Kennedy, D. N., Hoppel, B. E., Cohen, M. S., & Turner, R. (1992). Dynamic magnetic resonance imaging of human brain activity during primary sensory stimulation. *Proceedings of the National Academy of Sciences*, 89(12), 5675-5679. <https://doi.org/10.1073/pnas.89.12.5675>

Larsson, M. (2015). Tool-use-associated sound in the evolution of language. *Animal Cognition*, 18(5), 993-1005. <https://doi.org/10.1007/s10071-015-0885-x>

Le Bihan, D. (2018). Que voit-on (ou pas) en IRM ? In Monier Cyril & Sarti Alessandro (Eds), *Les Neurosciences au sein des sciences de la cognition entre neuroenthousiasme et neuroscepticisme*, *Intellectica*, 69, 187-200.

Lepre, C. J., Roche, H., Kent, D. V., Harmand, S., Quinn, R. L., Brugal, J.-P., Texier, P.-J.,

- Lenoble, A., & Feibel, C. S. (2011). An earlier origin for the Acheulian. *Nature*, 477(7362), 82-85. <https://doi.org/10.1038/nature10372>
- Malafouris, L. (2010a). Metaplasticity and the human becoming: Principles of neuroarchaeology. *Journal of Anthropological Sciences*, 88(4), 49–72.
- Malafouris, L. (2010b). The brain–artefact interface (BAI): A challenge for archaeology and cultural neuroscience. *Social Cognitive and Affective Neuroscience*, 5(2-3), 264-273. <https://doi.org/10.1093/scan/nsp057>
- Mcbrearty, S., & Brooks, A. S. (2000). The revolution that wasn't: A new interpretation of the origin of modern human behavior. *Journal of Human Evolution*, 39(5), 453-563. <https://doi.org/10.1006/jhev.2000.0435>
- Mellars, P., & Stringer, Chris (Éds.). (1989). *The human revolution: Behavioural and biological perspectives on the origins of modern humans*. Edinburgh Univ. Press.
- Mellet, E., Salagnon, M., Majkić, A., Cremona, S., Joliot, M., Jobard, G., Mazoyer, B., Tzourio Mazoyer, N., & d'Errico, F. (2019a). Neuroimaging supports the representational nature of the earliest human engravings. *Royal Society Open Science*, 6(7), 190086. <https://doi.org/10.1098/rsos.190086>
- Mellet, E., Colagè, I., Bender, A., Henshilwood, C. S., Hugdahl, K., Lindstrøm, T. C., & d'Errico, F. (2019b). What processes sparked off symbolic representations? A reply to Hodgson and an alternative perspective. *Journal of Archaeological Science: Reports*, 102043. <https://doi.org/10.1016/j.jasrep.2019.102043>
- Miyake, A., Friedman, N. P., Emerson, M. J., Witzki, A. H., Howerter, A., & Wager, T. D. (2000). The Unity and Diversity of Executive Functions and Their Contributions to Complex “Frontal Lobe” Tasks: A Latent Variable Analysis. *Cognitive Psychology*, 41(1), 49-100. <https://doi.org/10.1006/cogp.1999.0734>
- Neubauer, S., Hublin, J.-J., & Gunz, P. (2018). The evolution of modern human brain shape. *Science Advances*, 4(1), eaao5961. <https://doi.org/10.1126/sciadv.aao5961>
- Orban, G. A., Van Essen, D., & Vanduffel, W. (2004). Comparative mapping of higher visual areas in monkeys and humans. *Trends in Cognitive Sciences*, 8(7), 315-324. <https://doi.org/10.1016/j.tics.2004.05.009>
- Otto, G. (2018). Archaic admixture with Denisovans. *Nature Reviews Genetics*, 19(5), 251-251. <https://doi.org/10.1038/nrg.2018.18>
- Pascual-Leone, A., Amedi, A., Fregni, F., & Merabet, L. B. (2005). THE PLASTIC HUMAN BRAIN CORTEX. *Annual Review of Neuroscience*, 28(1), 377-401. <https://doi.org/10.1146/annurev.neuro.27.070203.144216>
- Petitto, L. A., Zatorre, R. J., Gauna, K., Nikelski, E. J., Dostie, D., & Evans, A. C. (2000). Speech-

like cerebral activity in profoundly deaf people processing signed languages: Implications for the neural basis of human language. *Proceedings of the National Academy of Sciences*, 97(25), 13961-13966. <https://doi.org/10.1073/pnas.97.25.13961>

Putt, S. S., Wijekumar, S., & Spencer, J. P. (2019). Prefrontal cortex activation supports the emergence of early stone age toolmaking skill. *NeuroImage*, 199, 57-69. <https://doi.org/10.1016/j.neuroimage.2019.05.056>

Putt, S. S., Wijekumar, S., Franciscus, R. G., & Spencer, J. P. (2017). The functional brain networks that underlie Early Stone Age tool manufacture. *Nature Human Behaviour*, 1(6), 0102. <https://doi.org/10.1038/s41562-017-0102>

Roby-Brami, A., Hermsdörfer, J., Roy, A. C., & Jacobs, S. (2012). A neuropsychological perspective on the link between language and praxis in modern humans. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 367(1585), 144-160. <https://doi.org/10.1098/rstb.2011.0122>

Rodríguez-Vidal, J., d'Errico, F., Pacheco, F. G., Blasco, R., Rosell, J., Jennings, R. P., Queffelec, A., Finlayson, G., Fa, D. A., Gutiérrez López, J. M., Carrión, J. S., Negro, J. J., Finlayson, S., Cáceres, L. M., Bernal, M. A., Fernández Jiménez, S., & Finlayson, C. (2014). A rock engraving made by Neanderthals in Gibraltar. *Proceedings of the National Academy of Sciences*, 111(37), 13301-13306. <https://doi.org/10.1073/pnas.1411529111>

Roland, P. E. (1993). *Brain activation*. Wiley-Liss.

Sampaio-Baptista, C., & Johansen-Berg, H. (2017). White Matter Plasticity in the Adult Brain. *Neuron*, 96(6), 1239-1251. <https://doi.org/10.1016/j.neuron.2017.11.026>

Scerri, E. M. L., Thomas, M. G., Manica, A., Gunz, P., Stock, J. T., Stringer, C., Grove, M., Groucutt, H. S., Timmermann, A., Rightmire, G. P., d'Errico, F., Tryon, C. A., Drake, N. A., Brooks, A. S., Dennell, R. W., Durbin, R., Henn, B. M., Lee-Thorp, J., deMenocal, P., ... Chikhi, L. (2018). Did Our Species Evolve in Subdivided Populations across Africa, and Why Does It Matter? *Trends in Ecology & Evolution*, 33(8), 582-594. <https://doi.org/10.1016/j.tree.2018.05.005>

Slon, V., Mafessoni, F., Vernot, B., de Filippo, C., Grote, S., Viola, B., Hajdinjak, M., Peyrégne, S., Nagel, S., Brown, S., Douka, K., Higham, T., Kozlikin, M. B., Shunkov, M. V., Derevianko, A. P., Kelso, J., Meyer, M., Prüfer, K., & Pääbo, S. (2018). The genome of the offspring of a Neanderthal mother and a Denisovan father. *Nature*, 561(7721), 113-116. <https://doi.org/10.1038/s41586-018-0455-x>

Stout, D., & Chaminade, T. (2012). Stone tools, language and the brain in human evolution. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 367(1585), 75-87. <https://doi.org/10.1098/rstb.2011.0099>

Stout, D., Toth, N., Schick, K., & Chaminade, T. (2008). Neural correlates of Early Stone Age toolmaking: Technology, language and cognition in human evolution. *Philosophical*

Transactions of the Royal Society B: Biological Sciences, 363(1499), 1939-1949.  
<https://doi.org/10.1098/rstb.2008.0001>

Stout, D., & Chaminade, T. (2007). The evolutionary neuroscience of tool making. *Neuropsychologia*, 45(5), 1091-1100.  
<https://doi.org/10.1016/j.neuropsychologia.2006.09.014>

Stout, D., & Chaminade, T. (2009). Making Tools and Making Sense: Complex, Intentional Behaviour in Human Evolution. *Cambridge Archaeological Journal*, 19(1), 85-96.  
<https://doi.org/10.1017/S0959774309000055>

Stout, D., & Hecht, E. (2015). Neuroarchaeology. In E. Bruner (Éd.), *Human Paleoneurology* (Vol. 3, p. 145-175). Springer International Publishing. [https://doi.org/10.1007/978-3-319-08500-5\\_7](https://doi.org/10.1007/978-3-319-08500-5_7)

Stout, D., Hecht, E., Khreisheh, N., Bradley, B., & Chaminade, T. (2015). Cognitive Demands of Lower Paleolithic Toolmaking. *PLOS ONE*, 10(4), e0121804.  
<https://doi.org/10.1371/journal.pone.0121804>

Stout, D., Passingham, R., Frith, C., Apel, J., & Chaminade, T. (2011). Technology, expertise and social cognition in human evolution: Technology and cognition in human evolution. *European Journal of Neuroscience*, 33(7), 1328-1338. <https://doi.org/10.1111/j.1460-9568.2011.07619.x>

Stringer, C. (2002). Modern human origins : Progress and prospects. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences*, 357(1420), 563-579. <https://doi.org/10.1098/rstb.2001.1057>

Teffer, K., & Semendeferi, K. (2012). Human prefrontal cortex: Evolution, development, and pathology. *Progress in Brain Research*, 195, 191-218. <https://doi.org/10.1016/B978-0-444-53860-4.00009-X>

Tomasello, M., Carpenter, M., Call, J., Behne, T., & Moll, H. (2005). Understanding and sharing intentions: The origins of cultural cognition. *Behavioral and Brain Sciences*, 28(5), 675-691. <https://doi.org/10.1017/S0140525X05000129>

Tylén, K., Fusaroli, R., Rojo, S., Heimann, K., Fay, N., Johannsen, N. N., Riede, F., & Lombard, M. (2020). The evolution of early symbolic behavior in *Homo sapiens*. *Proceedings of the National Academy of Sciences*, 117(9), 4578-4584.  
<https://doi.org/10.1073/pnas.1910880117>

Uomini, N. T., & Meyer, G. F. (2013). Shared Brain Lateralization Patterns in Language and Acheulean Stone Tool Production: A Functional Transcranial Doppler Ultrasound Study. *PLoS ONE*, 8(8), e72693. <https://doi.org/10.1371/journal.pone.0072693>

Vigneau, M., Beaucousin, V., Hervé, P.-Y., Jobard, G., Petit, L., Crivello, F., Mellet, E., Zago, L., Mazoyer, B., & Tzourio-Mazoyer, N. (2011). What is right-hemisphere contribution to

phonological, lexico-semantic, and sentence processing? *NeuroImage*, 54(1), 577-593.  
<https://doi.org/10.1016/j.neuroimage.2010.07.036>

Vingerhoets, G. (2014). Praxis, language, and handedness: A tricky triad. *Cortex*, 57, 294-296.  
<https://doi.org/10.1016/j.cortex.2014.01.019>

Watts, I., Chazan, M., & Wilkins, J. (2016). Early Evidence for Brilliant Ritualized Display: Specularite Use in the Northern Cape (South Africa) between ~500 and ~300 Ka. *Current Anthropology*, 57(3), 287-310. <https://doi.org/10.1086/686484>

Winkler, A. M., Greve, D. N., Bjuland, K. J., Nichols, T. E., Sabuncu, M. R., Håberg, A. K., Skranes, J., & Rimol, L. M. (2018). Joint Analysis of Cortical Area and Thickness as a Replacement for the Analysis of the Volume of the Cerebral Cortex. *Cerebral Cortex*, 28(2), 738-749. <https://doi.org/10.1093/cercor/bhx308>

Wynn, T., & Coolidge, F. L. (2011). The Implications of the Working Memory Model for the Evolution of Modern Cognition. *International Journal of Evolutionary Biology*, 2011, 1-12.  
<https://doi.org/10.4061/2011/741357>

Zatorre, R. J. (2004). Sensitivity to Auditory Object Features in Human Temporal Neocortex. *Journal of Neuroscience*, 24(14), 3637-3642. <https://doi.org/10.1523/JNEUROSCI.5458-03.2004>

Zatorre, R. J., Fields, R. D., & Johansen-Berg, H. (2012). Plasticity in gray and white: Neuroimaging changes in brain structure during learning. *Nature Neuroscience*, 15(4), 528-536. <https://doi.org/10.1038/nn.3045>