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1 From stone tools to fMRI, studying human cognitive evolution
2 when the mind doesn't fossilize

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10 [chloe](https://emc.univ-lyon2.fr/equipes/memoire-emotion-et-attention-mea/bryche-chloe)

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15

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18

19 **Abstract**

20 Successive cognitive upswings could have been decisive in our ancestors' ability to
21 develop increasingly complex tool systems and functional forms of communication. The
22 recent incursion of neuroarchaeology experiments focusing on lithic tool-based stimuli
23 has intensified discussions on the brain regions of interest that could have played a role
24 in the development of the modern brain. Executive functions, language, and technical
25 reasoning are now being investigated. The question here is not so much which cognitive
26 function deserves the most attention by its more significant likelihood of explaining the
27 cognitive enhancement that took place in our species during the Paleolithic. Instead, it is
28 a question of why certain brain areas, such as the frontal or parietal lobes, are considered
29 regions of interest, and how neuroarchaeology studies them, presented here in a non-
30 expert-friendly manner. Between methodological challenges and new hypotheses, the
31 incursion of modern technologies such as neuroimaging and eye-tracking into
32 paleoanthropological debates seems to open up new scientific opportunities.

33

34 **Keywords:** cognitive evolution, stone tools, neuroarchaeology, cognitive archaeology.

35

36 **Statements and Declarations**

37 The authors declare that there are no financial or non-financial competing interests.

38 The data that support the findings of this study are available in the supplementary
39 material of this article.

40

41 **1. Introduction**

42 The earliest lithic technologies associated with Hominina date back at least several
43 million years ago (Mya). Whether the Lomekwian, dating from over 3 Mya (Harmand et
44 al., 2015; Lewis & Harmand, 2016), is considered the oldest lithic industry, or the
45 Oldowan, dating from around 2.5 Mya (Semaw et al., 1997; Semaw et al., 2003) or even
46 earlier around 2.9 from Mya (Plummer et al., 2023), those industries mark the emergence
47 of ancient tool use among our ancestors. Since then, stone tools have undergone
48 successive technological modifications (Muller et al., 2017), associated with improvement
49 and complexity over time and especially over the representatives of the genus *Homo*
50 (Foley, 1987). The origins of this complexification are the source of many debates and
51 theories in paleoanthropology, in which the role of cognition is often questioned (Wynn,
52 1991; A. De Beaune, 2004; Nowell et al., 2011; Stout, 2011; Heyes, 2012). Cognition refers
53 to a set of concepts and theories encompassing the mental capacities of a living being like
54 thinking, imagining, creating, understanding or memorizing (Bayne et al., 2019). Its study
55 can answer significant questions concerning the evolution of stone tools associated with
56 hominins.

57 Cognitive science and neuroscience emerged in the second half of the 20th century
58 (Hatfield, 2002; Miller, 2003). The same century was also marked by discovery of several
59 fossils that contributed to studying the evolution of the genus *Homo* (Villmoare, 2018),
60 which have led to questioning cognition not only in its modernity but also its role in the
61 evolution of the genus *Homo*. Stone tools and, more recently, fossilized wood artefacts
62 (Barham et al., 2023) represent a privileged case study due to their non-perishable
63 nature. Unlike the mind, stone tools preserve over time, thereby offering tangible material
64 support for investigating immaterial past cognition (Overmann & Wynn, 2019a;

65 Overmann & Wynn, 2019b). In this context, the transition between lithic industries,
 66 notably between the Oldowan and Acheulean (de la Torre, 2016) offers a privileged
 67 comparative case study. This technological transition may reflect an increase in the
 68 cognitive capacities of the associated hominins due to the growing complexity of the
 69 Acheulean production mode compared to the Oldowan. The question is to understand the
 70 neurocognitive prerequisites that may have been necessary for such a transition to take
 71 place, allowing hominins to become remarkable tool makers and tool users (see Table 1
 72 for definitions), making us a tooling species (Fragaszy & Mangalam, 2018).

Table 1. Definitions of tool use and tool making

Term	Definition	Reference
Tool use	“The external use of a manipulable object from the environment to alter the form, position or condition of another object, an organism, or the user more effectively himself. Usage implies that the user holds the tool directly before or during manipulation while being responsible for the tool’s correct and efficient orientation”	Shumaker et al. (2011), p. 5
Tool making	“The fact that a user structurally modifies an already existing object or tool, thus making the object or tool either useful or even more useful, as a tool”	Shumaker et al. (2011), p. 11

73

74 The objective is to understand how new technologies, such as brain imaging, can
 75 help study past cognition. To better exemplify it, we will focus on cognitive skills that
 76 could have played a decisive role in the evolution of Paleolithic technologies, focusing on
 77 the transition from Oldowan to Acheulean. Since they have been at least addressed, if not
 78 well documented, by disciplines such as neuroarchaeology, those precise study cases
 79 might be good examples to underline how advanced neurosciences can contribute to
 80 paleoanthropological questions. Thus, we will discuss how archaeology,
 81 paleoanthropology, neuroscience, psychology, and cognitive science can come together to

82 address the question of the evolution of human cognition, which will also lead us to stress
83 the associated methodological limitations.

84 **2. When archeology meets cognitive science... and neuroscience**

85 In 1969, the anthropologist Ralph Holloway (Holloway, 1969) wrote about how
86 stone tools and fossil records, taken as a whole, might be studied to bring new information
87 and hypotheses about human past cognition, especially the evolution of language. This
88 work led to a new approach combining psychology and archaeological knowledge. The
89 second half of the 20th century thus saw the beginnings of cognitive archaeology, with
90 subsequent publications inspired by the work of Jean Piaget (Fairservis, 1975; Wynn,
91 1979) or by the study of great apes with primatology (Parker & Gibson, 1979; Wynn &
92 McGrew, 1989). Then, the British archaeologist Colin Renfrew truly promoted this
93 interdisciplinarity, bringing with him the idea that an archaeology of thought was possible
94 (Renfrew & Zubrow, 1994). This new interdisciplinary approach to archaeological
95 questions aimed to apply theories from psychology and cognitive science to artifacts and
96 various remains left by past civilizations to understand the cognitive evolution of
97 humankind (Coolidge & Wynn, 2016; Lombard & Gärdenfors, 2023). Studying a stone tool
98 could lead to conjecture on how tasks were prioritized to produce it, the psychomotricity
99 required to execute each production gesture, or even the ability to hold information in
100 memory (Vaesen, 2012).

101 Although paleoanthropologists did not wait for the advent of in-depth brain study
102 to set out the various possible scenarios concerning our cognitive evolution, the
103 institutionalization of these questions marked the emergence of new fields of study. The
104 modern brain, the result of thousands of years of evolution, became an object of study for
105 evolution, thanks to neuroimaging in the early 2000s. Archaeologists and

106 paleoanthropologists began to set up paradigms combining archaeology, brain imaging,
107 and evolutionary neuroscience (Stout et al., 2000; Stout & Chaminade, 2007; Stout et al.,
108 2008). The first aim of this new research field, first developed at the Indiana University,
109 was to observe peaks in brain activity related to modern humans' use of lithic tools, using
110 positron emission tomography, for example. The initial hypothesis was that the modern
111 cognitive processes involved in the current use of lithic tools and the associated brain
112 activity could be analyzed to produce new hypotheses about, among other things, the
113 emergence and evolution of these abilities in Paleolithic hominins. A new disciplinary
114 field was created: neuroarchaeology.

115 Colin Renfrew and his colleagues published several articles in a dedicated thematic
116 journal in 2008, presenting the idea that it would seem relevant to bring neuroscience
117 and archaeology together (Renfrew et al., 2008). Lambros Malafouris and Colin Renfrew
118 (2008) followed suit, a few months after publishing their first articles on the need for
119 interdisciplinarity between archaeology and neuroscience. Lambros Malafouris (2013)
120 explored the concept of the "longue durée," highlighting the interconnectedness of the
121 human body, technology, and brain over extended periods of time. He suggested that
122 these elements engage in co-evolutionary processes, where changes in one domain
123 influence and are influenced by developments in the others. Thus, Malafouris (2010;
124 2019; 2023) proposed insights into how the material and cognitive aspects of human
125 existence evolved in tandem shaping our interactions with technology and the
126 environment across millennia.

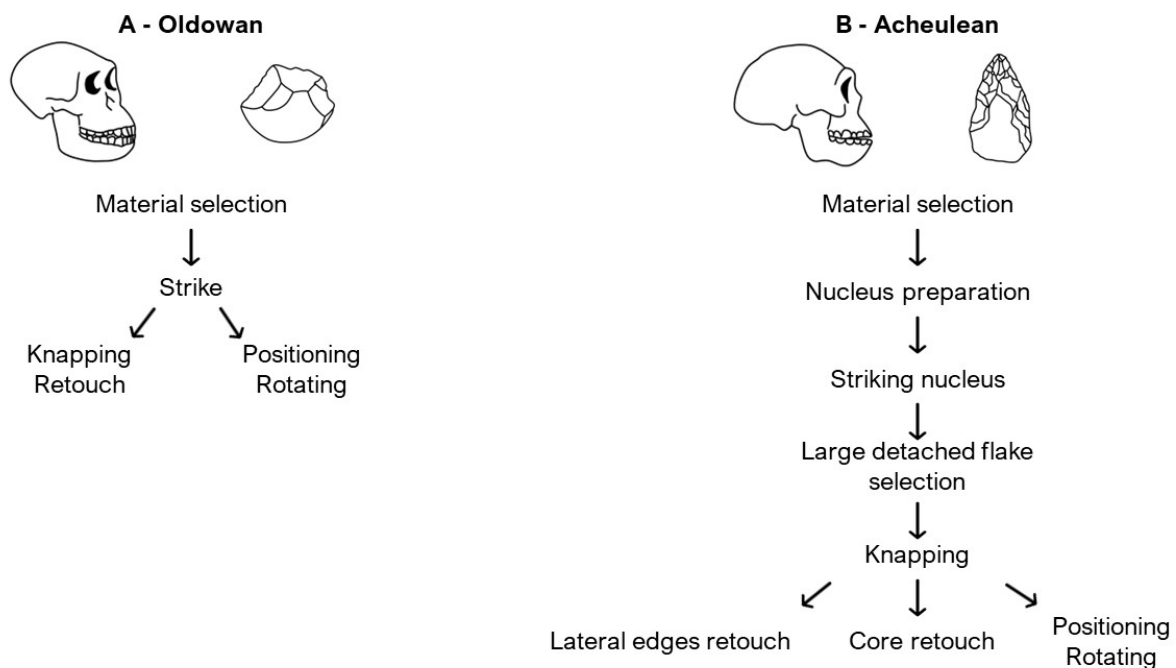
127 **3. From stone tools to neuroimaging stimuli**

128 **3.1. Oldowan and Acheulean**

129 Lithic industries offer a well-known study case to illustrate the cognitive evolution
130 of the genus *Homo*. Tools and associated hominin fossils have been found on the same
131 excavation sites (Schick et al., 2006; Mussi et al., 2023), which leads to characterize lithic
132 industries specific to certain representatives of the genus *Homo*. They do not elucidate
133 debates about which species made what type of stone tools because a fossil and a tool are
134 discovered simultaneously; it could be a different scenario explaining such a discovery,
135 including different species. Nevertheless, stone tools provide valuable information on the
136 technological evolution of humankind (Wynn et al., 2021). The progressive
137 complexification of lithic industries over time, in conjunction with the expansion of the
138 cranial capacity, is considered a privileged source of knowledge on the cognitive evolution
139 of our species. Even though our evolution is not linear, it is often illustrated with the
140 vulgarized association between tools and hominin remains, especially the skull, to
141 exemplify how, even without the actual knowledge we have about the human brain, the
142 first paleoanthropologists have been able to conjecture about our cognitive evolution. For
143 instance, we might use the association between *Homo habilis* and *Homo erectus* (Figure 1)
144 to illustrate the cranial expansion on the one hand. On the other hand, we can illustrate
145 the increasing complexity of technology by comparing Oldowan and Acheulean
146 technologies.

147 Lithic industries can therefore be characterized and referenced by their creator (i.e.
148 which *Homo* for which period) and by technology (i.e. which form for which use). Not all
149 *Homo* created and perfected the same tools. The Oldowan, dated from 2.9 or 2.6 Ma to 1.5
150 Ma BC, is considered one of the earliest technocomplexes. Associated with the culture of

151 pebble tools, chopping tools are produced by striking two pebbles against each other, with
 152 several flakes detached from the cut pebble to create a sharp edge (Braun et al., 2008;
 153 Bails & Dini, 2012). The latter can be either unifacial in which case it is called a chopper,
 154 or bifacial in which case it is called a chopping tool according to Lumley's classification
 155 (Schick et al., 2006) (Figure 1). The Oldowan was then followed by the Acheulean, dated
 156 from 1.76 Ma or 1.5 Ma ago (Diez-Martín et al., 2015; Favreau, 2023), depending on
 157 estimates, up to 154,000 years BC. The handaxe is the tool commonly associated with the
 158 Acheulean technocomplex. The manufacturing process became more complex than in the
 159 Oldowan period (Figure 1), and new stages in the production of stone tools appeared,
 160 giving the Acheulean period its traditional image of technological innovation. Two main
 161 families of tools are distinguished: handaxes on the one hand and cleavers on the other.



162

163 **Fig. 1** Illustration of simplified operation chains to compare Oldowan to Acheulean production's complexity. Simplified
 164 operation chain for: (A) chopping tool's production associated with Oldowan illustrated with a *Homo habilis* skull
 165 representation and a chopping tool representation; (B) Handaxe's production associated with Acheulean illustrated
 166 with a *Homo erectus* skull representation and a handaxe representation.

167 Some authors often perceive the Oldowan period as representing a stasis in the
168 technological evolution of the genus *Homo* (Barsky, 2009), not because of its lack of
169 innovation and diversity but rather because it was in a state of equilibrium (Stout et al.,
170 2010). Its production patterns are considered simple, without sufficiently notable
171 technological innovation despite having lasted over 700,000 years. Its successor, the
172 Acheulean, have therefore be interpreted as a technological leap involving complex
173 production patterns (Figure 1), supposedly reflecting a cognitive, social; and biological
174 evolution of associated *Homo*, such as *Homo ergaster*, *Homo heidelbergensis* and even the
175 first *Homo sapiens idaltu*, all considered "larger-brained hominin" (Muller et al., 2017;
176 Toth & Schick, 2019). This is because handaxes imply opaque production gestures for a
177 person without prior knowledge. More than reverse engineering alone is needed to
178 understand how to produce this type of tool. This suggests a certain level of expertise is
179 required (Shipton & Nielsen, 2018; Alperson-Afil et al., 2020). Handaxes could, therefore,
180 have required not only better technical gesture practice but also over-imitation of the
181 learners (Rossano, 2017) or even a specific form of social transmission or learning
182 (Shipton, 2010). However, if learning how to produce a handaxe is more complicated than
183 learning how to produce a chopper, the actual production of the tool would also imply an
184 increase in cognitive capacity, for instance, working memory (Shipton et al., 2013; Muller
185 et al., 2023) and, more generally, executive functions (Adornetti, 2016; Ardila, 2018)
186 which will be discussed later. The transition between the Oldowan and Acheulean
187 technocomplexes could thus testify to an improvement in our ancestors' technical
188 cognition and ability to transmit, understand and manipulate information about stone
189 tools. If the tools have remained, unfortunately, the mind does not fossilize, so disciplines
190 such as neuroarchaeology seem a wise methodological choice to answer the questions
191 raised by the complexification of stone tools.

192 **3.2. Neuroimaging**

193 Introducing the new neuroimaging techniques into archaeological research
 194 represents a real challenge and a turning point for the discipline. It made it possible to
 195 explore the increasing complexity of Paleolithic tools from a new perspective. This is why
 196 stimuli used by neuroarchaeology experiments are generally associated with the
 197 Oldowan and Acheulean lithic industries, either independently (i.e., the stimuli are based
 198 only on the Oldowan or Acheulean) or comparatively (i.e., the stimuli are based on both
 199 types of industry). Table 2 offers an overview of the studies investigating the cerebral
 200 activity that reflects the cognitive processing associated with Oldowan and/or Acheulean
 201 stimuli.

Study	Industry type	Neuro-imagery technology	<i>n</i>	Longitudinal	Expertise level	Type of task	Stimulus type	Included in meta-analysis
Stout et al. (2000)	Oldowan	PET	1	no	Expert	Tool making Observation Imagination	Real tools	*
Stout & Chaminade (2007)	Oldowan	PET	6	yes	Trained novice	Tool making	Real tools	*
Stout et al. (2008)	Oldowan Acheulean	PET	3	no	Expert	Tool making	Real tools	*
Stout et al. (2011)	Oldowan Acheulean	fMRI	26	yes	Novice (11) Trained (10) Expert (5)	Observation Imagination Evaluation	Videos of tools	*
Hecht et al. (2014)	Oldowan Acheulean	sMRI dMRI	6	yes	Trained novice	Tool making	Real tools	
Stout et al. (2015)	Oldowan Acheulean	fMRI	6	yes	Trained novice	Observation Evaluation	Videos of tools	
Putt et al. (2017)	Oldowan Acheulean	fNIRS	31	yes	Trained novice	Tool making	Real tools	
Putt et al. (2019)	Oldowan Acheulean	fNIRS	33	yes	Trained novice	Tool making	Real tools	

Hecht et al. (2023)	Acheulean	sMRI dMRI	33	yes	Control (16) Trained novice (17)	Tool making	Real tools	
<i>PET: positron emission tomography; dMRI: diffusionl magnetic resonance imagery fMRI: functional magnetic resonance imagery; sMRI: structural magnetic resonance imagery; fNIRS: functional near-infrared spectroscopy</i>								

202 Brain imaging collects different types of data concerning brain activity or even brain
203 organization, depending on the technology used. The selection of regions of interest
204 depends on the hypotheses and thus guides both the choice of technology used and the
205 type of paradigm. For example, to observe the cerebral activity of the prefrontal cortex
206 during a task of evaluation of stone-tool images, then functional neuroimaging is
207 preferential. If, on the other hand, the aim is to observe the modification of brain
208 structures by making stone tools over time, then diffusion imaging would be preferable.
209 Combining the two can also be a very effective strategy in longitudinal studies, i.e.
210 involving different scans throughout the study (e.g., at 0 month, after six months and after
211 12 months). When analyzing the results obtained, contrasts in brain activity can be
212 observed, but this requires vigilance. This is where study replication becomes necessary
213 to find a similar pattern of brain activation depending on the area studied, the function,
214 and the type of task employed (i.e., image evaluation, mentalization, etc.). The more
215 studies find the same effects, the more confidently the hypotheses can be confirmed
216 because the difficulty of neuroimaging analysis lies in that significant activity in one area,
217 although correlated with the stimuli used, could be explained by different cognitive
218 processes simultaneously. This raises methodological issues that will be discussed
219 further below.

220 To collect brain imaging, different technologies are used. The most common is
221 functional magnetic resonance imaging (fMRI), a method that detects local changes in
222 blood flow to measure brain activity. There is also the positron emission tomography
223 (PET), another method that measures brain cell activity by injecting a weak radioactive

224 tracer. These techniques make it possible to obtain brain activity in relation to stimuli and
225 tasks (e.g., making a decision, performing a calculation). fNIRS (functional near-infrared
226 spectroscopy), a technique that analyzes brain activity by measuring its oxygenation
227 noninvasively, is also used. It is less sensitive to movement compared to MRI, where
228 participants must remain motionless. Similarly, EEG (Electroencephalography), another
229 noninvasive technique that measures brain activity, is widely utilized (Hecht & Stout,
230 2023; Yıldırım, 2023). It provides high temporal resolution and can capture rapid brain
231 activity changes, making it particularly effective in studying real-time cognitive processes.
232 These technological advances have enabled the neuroscience to gain a better
233 understanding of the areas involved in many modern neurocognitive processes in
234 general, and recently more specifically in the cognitive evolution of human beings.

235 Based on modern brains, neuroarchaeology using neuroimaging, therefore, seeks to
236 reconstruct the brain activity of the past. Before we explore the experimental
237 construction of this concept, it is important to understand the brain activity of modern
238 humans. Neuroarchaeology draws heavily on neuroimaging studies that examine the
239 brain's networks, particularly those involved in using modern tools. Studies in fMRI have
240 identified left-lateralized networks in the frontal, parietal, and temporal lobes (Johnson-
241 Frey, 2004; Johnson-Frey et al., 2005; Peeters et al., 2013; for a review, see Orban &
242 Caruana, 2014). Other neuroimaging techniques are also used. For example, Caruana, et
243 al. (2017) used stereo-electroencephalography (SEEG), an invasive version of EEG, to
244 record brain activity from 49 epileptic patients while observing modern tools and hand
245 actions. The design involved deconstructing actions into three key events: video onset,
246 action onset, and tool-object contact. The findings revealed that different brain regions
247 were selectively activated during these stages, with the left anterior supramarginal gyrus
248 (aSMG) showing specific activation for tool-action observation during the action event. By

249 understanding these modern networks, we can start to piece together how brain activity
250 might have evolved over time.

251 In neuroarchaeology paradigms, the stimuli used are usually photos or schematic
252 representations of stone tools, generally associated with Oldowan or Acheulean
253 technologies (Table 2). The transition between these two technocomplexes is thus
254 commonly associated with evolutionary changes, particularly neurocognitive ones, as
255 said previously. The *Homo* endocasts support these hypotheses to study the traces left by
256 the brain inside the skull (Bruner et al., 2014; Neubauer, 2014; Bruner, 2017; Pestana et
257 al., 2023). Traceology has also made it possible to understand the production processes
258 of different stone tools (e.g., chopper, handaxe, cleaver) associated with the Lower
259 Paleolithic and thus hypothesize that there was seemingly a need to call on more cognitive
260 resources. By bringing all these elements together, observing brain activity related to
261 stone tools' stimuli could provide a new data source. What is more, in the case of
262 comparative studies between Oldowan and Acheulean, the aim is to support the
263 neurocognitive bases behind the cognitive enhancement of our species and, hence, the
264 emergence of more complex technologies.

265 One limitation often addressed is that neuroarchaeology studies are conducted on
266 modern human brains. Because premodern human brains may have had different
267 structural organizations, we need to combine the interpretation of endocasts (Holloway
268 et al., 2004; Holloway et al., 2009), artefact remains, and modern cerebral activity to
269 elaborate evolutive scenarios. However, although neuroarchaeological studies are not
270 sufficient in themselves to reconstruct the cognitive development of our species, they
271 have become an essential element in the interdisciplinary approach required for the study
272 of evolution.

273 **3.3. Methodology**

274 Although it is often considered that the current human brain is the heir to what
275 several hundred thousand years of evolution have produced (Sherwood et al., 2008),
276 modern humans do not daily use stone tools. It raises several fundamental points, such as
277 the participants' levels of “specific” expertise, “general” expertise or familiarity with stone
278 tools, thinking about the experimental design according to the hypothesis and, finally, the
279 validity of the results obtained.

280 The first point to address is the level of specific expertise of participants. Usually,
281 expertise implies a deep level of skill, knowledge, and proficiency gained through practice
282 acquired either through personal or academic experience, or because the experimental
283 protocol involves training of varying lengths (e.g., from a few hours to several months).
284 Several studies have explored the impact of expertise on stone knapping by comparing
285 naïve people to experts (Table 2). These studies have confirmed that the level of expertise
286 had an impact, by reporting increased brain activity in areas like the intraparietal sulcus
287 (IPS), premotor cortex, prefrontal lobe and regions involved in recognizing objects and
288 spatial awareness as they become more skilled (Stout, 2011; Stout & Chaminade, 2007;
289 Hecht et al., 2015). Thus, the level of expertise is an important aspect to consider but it
290 also depends on the task that will be asked of participants during the experiment. When
291 it comes to observing cerebral activity related to tools stimuli, several designs are
292 possible, each implying non-negligible specificities concerning the hypotheses. The task
293 may concern the evaluation of a tool, like defining the next necessary knapping to be
294 performed to obtain a specific technology. Or it may simply involve observing the tool in
295 action. The first step is, therefore, to clearly define the type of skill involved (i.e.,
296 observation/evaluation/understanding) and the level of expertise required for this.

297 The second point concerns the general expertise people can have with technical
298 activities. Evidence has demonstrated that the participant's general experience with tools
299 or DIY activities could influence their ability to learn, for example, how to produce stone
300 tools (Hecht et al., 2023). A frontotemporal network involving the left inferior frontal
301 gyrus (IFG) was positively associated with a brain organization favorable to the
302 production quality of tools of unknown technology, such as stone tools. This profitable
303 brain organization could be correlated with regular DIY practice. These prior skills,
304 impacting brain organization and the tool's quality produced, could also influence the
305 ability to process a task using tool-based stimuli such as those used in fMRI experiments.

306 The third point to address is the familiarity the participants have with stone tools.
307 Familiarity refers to a basic acquaintance or recognition of something, in our case, stone
308 tools. The level of expertise is generally confounded with the level of familiarity as experts
309 are necessarily familiar with stone tools whereas naïve people are generally also
310 unfamiliar with stone tools. Nevertheless, in some cases, the two variables can be
311 distinguished, leading to interesting research question. Even if humans are skilled
312 toolmakers, the fact remains that stone tools are no longer part of the daily panel of tools
313 actual humans use, which could make them opaque because they are unfamiliar. As seen,
314 this opacity could mean that naïve people would find it harder to understand how they
315 work, the physical principles on which they are based, and how to make and manipulate
316 them and would need some training (Geribàs et al., 2010; Pargeter et al., 2019). The
317 degree of familiarity has never been directly explored by neuroarchaeological studies.
318 Studies on modern tools has nevertheless provided interesting insights into the influence
319 of familiarity on tool processing (Vingerhoets, 2008). For instance, when a tool is
320 unfamiliar, there would appear to be an increase of PF area activity (Reynaud et al., 2016),
321 which is a brain area known to be involved in high-level tool-related cognitive processes

322 such as technical reasoning (see below). Thus, if naïve participants are asked to observe
323 a stone tool, it could be interesting to have them also perform the task on little-
324 known/used modern tools to ensure that lack of familiarity does not influence brain
325 activity and that participants are indeed calling on brain resources related to stone tool
326 observation and not something else.

327 In broad terms, this requires careful handling of the notion of familiarity and
328 expertise and, therefore, defining upstream of the protocol what is really being
329 questioned by the experiment. Is a good level of familiarity enough, or is it really a
330 question of expertise? This generally means distinguishing between novice, trained, and
331 expert. What is expertise for some may be no more than familiarity for others, so making
332 a clear methodological distinction between the different stages of familiarization and
333 acquisition of expertise might be necessary.

334 Finally, and more generally, neuroimaging implies a certain methodological rigor to
335 avoid falling into the trap of explanatory correlation. Applied to neuroarchaeology, this
336 means paying attention to several elements, such as the level of familiarity mentioned
337 above. Beyond that, and more generally, we also need to establish a homogeneity of
338 practices in terms of paradigm to guarantee the replicability of studies in the first instance
339 but above all of the results in the second. This raises several questions: What type of
340 representation should be used for stone tools, for example (i.e., diagrams, real photos,
341 video clips...), what type of analysis should be carried out, and what experimental design
342 should be used (i.e., block vs. event related)? Moreover, even when it comes to data
343 analysis, it is essential to be sure how to interpret the results. The activity of a specific
344 brain area can be triggered by different stimuli, as shown by the activity of the left IFG
345 that is retrieved both for language related stimuli or tool related stimuli. To address this,

346 study replication is a robust solution. That is, repeating a study with a high degree of
347 similarity to observe whether the same results are obtained. This can, and sometimes
348 must, be achieved by manipulating variables such as the type of population involved in
349 the study (i.e., archaeology students vs. students in other fields or rural vs. urban, etc.) or
350 the type of stimuli (i.e., video clips vs real pictures). While it is natural to pave the way for
351 neuroarchaeology by starting with unique studies, it is necessary for the discipline's
352 continuity that these studies do not remain unique. Indeed, a single study produces a
353 single result, even if firmly rooted in a rich theoretical context, and this result must be
354 interpreted in its uniqueness, i.e. with the uncertainty of being sure of finding this effect
355 in replication. Pioneering studies are aptly named: they are the reason for innovation in a
356 field and must now be supported by methodological enrichment. This is especially true
357 for a field such as neuroarchaeology, which aims to study the non-fossilizable brain
358 activity of our ancestors using a living modern brain. Indeed, this regularly gives rise to
359 fierce criticism of the integrity of the results obtained, which in turn calls for even greater
360 methodological vigilance (Hecht & Stout, 2023).

361 ***3.4. Beyond the brain***

362 Neuroarchaeology is multidisciplinary and often associated with disciplines that
363 study the brain in a rather direct way (e.g., neuroimaging, comparative anatomical
364 studies) to answer the methodological challenges brought by this complex scientific field.
365 However, studying the brain is not enough on its own, and combining new technologies
366 with neuroimaging would enable a circular dialogue between cognition and brain activity.
367 Eye-tracking technology might be the perfect example to illustrate this point.

368 This technology uses an adapted camera to follow a participant's gaze to obtain
369 several data types, such as pupil distance, fixation time, or the visual path explored. Visual

370 perception relies on specific neurocognitive bases associated with the frontoparietal
371 regions (Calhoun et al., 2001; Ganis et al., 2004), brain areas often interrogated by
372 neuroarchaeology. In addition, visual attention and spatial perception are important skills
373 for stone tools and, thus, for our evolution (Silva-Gago & Bruner, 2023). Mentioning this
374 example of technology here is pertinent, as it further fuels the various resources that
375 neuroarchaeology can call upon. Recent studies have shown interesting results when
376 participants observe stone tools that may be added to the brain evolution scenario (Silva-
377 Gago et al., 2021; Silva-Gago et al., 2022a).

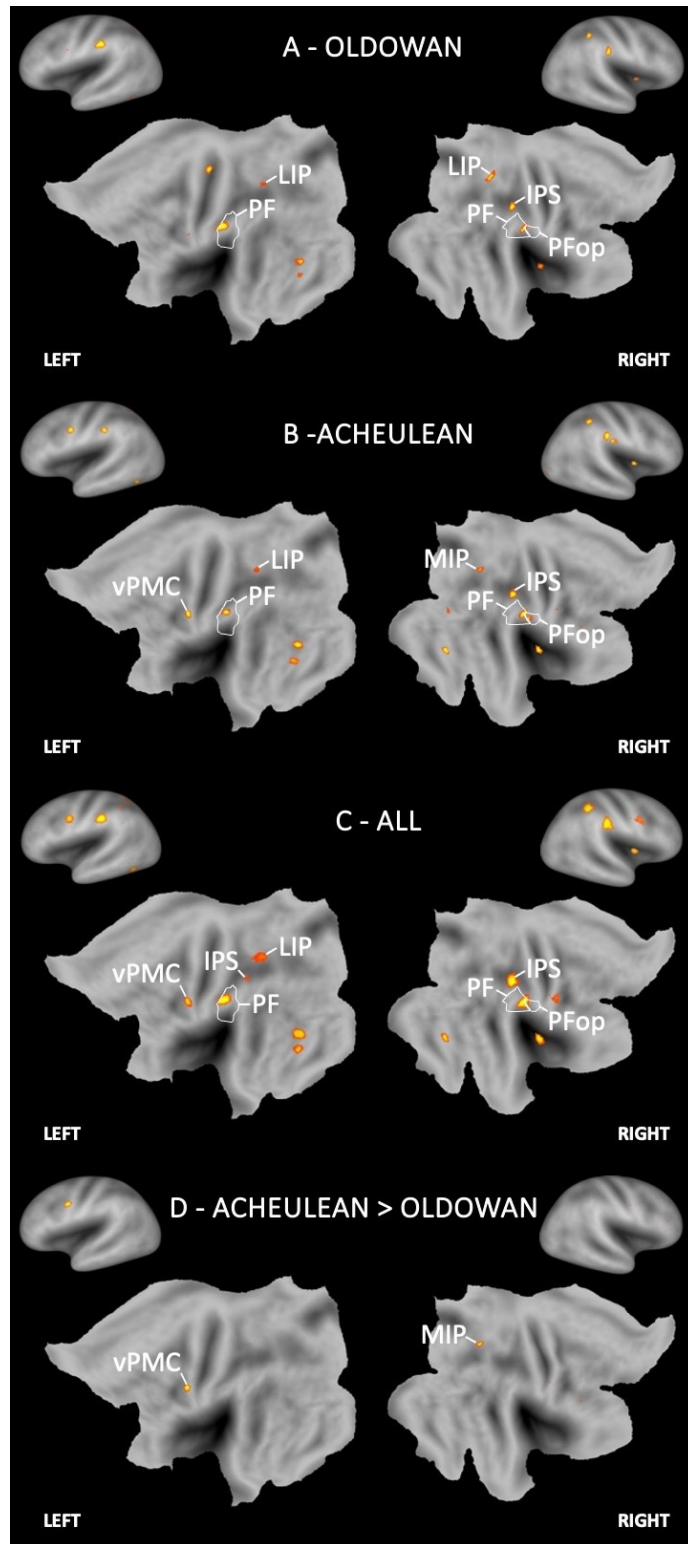
378 The famous dyad Oldowan and Acheulean is also found in eye-tracking research.
379 Observing differences in the visual exploration of these tools could help us to understand
380 the visuospatial cognitive prerequisites necessary for the transition between Oldowan
381 and Acheulean, and to correlate these results with neuro-imaging studies, particularly in
382 the fronto-parietal areas. Handaxes, based on a more complex composition, seem to
383 require more sustained exploration and visual attention (Silva-Gago et al., 2021). The
384 transition between these technologies would, therefore, not only rely on an enhancement
385 of executive functions but also on other skills, such as vision, beginning to be integrated
386 into evolutionary questioning. The question of expertise has also been addressed (Silva-
387 Gago et al., 2022b). When archaeologists observe stone tools, they treat them visually
388 differently than naïve people. Experts focus their attention directly on the knapped
389 regions, whereas naive people tend to concentrate on the tool's core. Experts, therefore,
390 concentrate more readily on the effective parts of the tools, indicating a certain need for
391 knowledge concerning the visual extraction of stone tool properties. From one technology
392 to another, from one level of expertise to another, different levels of cognitive process
393 recruitment seem to be involved, increasing in line with the growing complexity of stone
394 tools.

395 Above all, the results obtained are likely to fuel new hypotheses, particularly in
396 neuroimaging. For this reason, it is important that the use of these new technologies be
397 methodologically aligned with neuroimaging studies. The same precautions need to be
398 taken concerning the level of expertise of the participants, but also the type of stimuli and
399 tasks used. Unbiased exploitation of the results must be guaranteed by a methodological
400 consensus designed to clearly define the boundaries between speculation and hypothesis,
401 as well as between modernity and presumed evolution. Consideration of the
402 methodological constraints represented by the study of modern subjects in
403 neuroarchaeology must be made not only in the case of studies involving neuroimaging,
404 but indeed for any type of study involving a notable scientific contribution to the question
405 of the study of evolution. The recency of these different fields implies some readjustments,
406 but these will enable future research to be anchored in a multidisciplinary environment
407 where the homogeneity of practices can guarantee everyone the exploitation of data.

408 **4. Neuroarchaeology and cognitive functions**

409 As mentioned above, the use of neuroimaging is determined by the brain areas of
410 interest and the type of paradigm employed. Given the studies already carried out,
411 generally involving stimuli related to the Oldowan and/or Acheulean periods, it is
412 therefore relevant to focus on these specific case studies to understand the hypotheses of
413 neuroarchaeology concerning the evolution of the human brain. Among all the hypotheses
414 proposed to explain how the Oldowan to Acheulean transition could have occurred, we
415 will focus on three specific ones, each highlighting a specific cognitive function: executive
416 functions, language, and technical reasoning. While the two formers have received
417 support and discussion over the last decades (Coolidge & Wynn, 2001; Coolidge & Wynn,
418 2005; Stout & Chaminade, 2012; Ruck, 2014; Ardila, 2018), the latter, the technical

419 reasoning hypothesis, has never really been considered under this specific conception
420 (Osiurak et al., 2023a). We wish to introduce it, principally because it reunifies different
421 aspects of technical cognition, i.e., a cognitive domain that needs more investigation, as
422 stressed by some authors such as Wynn and colleagues (Wynn & Coolidge, 2014; Wynn
423 et al., 2016). We are also aware that other cognitive functions could have been discussed
424 here, such as intelligence, social cognition (Shipton & Nielsen, 2015; Lombard & Högberg,
425 2021), or visuospatial cognition (Bruner & Iriki, 2016; Bruner et al., 2018) that we have
426 partly discussed above in light of eye-tracking results. However, as these hypotheses have
427 not yet been investigated much using neuroimaging paradigms, we will focus here on
428 studies carried out in neuroarchaeology. The following three sections discuss how
429 neuroarchaeological studies have supported each of these three hypotheses by
430 presenting the key results obtained. We used a meta-analysis methodology on the
431 available neuroimaging studies to provide a synthetic view of the results. The results
432 are provided in Figure 2 (for the Methods, see Supplementary material). These results will
433 be discussed only with caution because the meta-analysis includes only a very small
434 number of studies: this meta-analytical approach is first and foremost a synthetic
435 representation of the data. Thus, the results of this meta-analysis are more descriptive
436 than inferential, as if we had merely reported on a brain map the activation peaks of the
437 study. The objective was to combine all the results obtained from different compatible
438 studies in neuroarchaeology (Table 2), which aimed to compare brain activity on tasks
439 involving Oldowan and/or Acheulean (Figure 2; for methods, see Supplementary
440 Information). Although the robustness of a more conventional meta-analysis could not be
441 found, it nevertheless seemed interesting to synthesize these results so as to compare
442 Oldowan and Acheulean and observe whether activations common to other cognitive
443 functions, such as language and technical reasoning, were found.



444

445 **Fig. 2** Meta-analysis results with stone tool stimuli. (a) Oldowan: Set of activations for the Oldowan condition;
 446 (b) Acheulean: Set of activations for the Acheulean condition; (c) All: Set of activations for both conditions; (d)
 447 Acheulean > Oldowan: Contrasting superior activations for the Acheulean condition compared with the Oldowan.
 448 Abbreviations: vPMC, ventral premotor cortex; IPS, intraparietal sulcus; LIP, lateral intraparietal area; MIP, medial
 449 intraparietal area; PF, parietal area F; PFop, parietal area Fop.

450 **4.1. Executive functions**

451 *Background.* Executive functions are associated with a diverse range of skills such
452 as planning, working memory, inhibition, mental flexibility, and action initiation and
453 control (Chan et al., 2008). Mainly affiliated with the frontal lobe, executive functions
454 engage other brain areas such as the parietal lobes (for review, see Alvarez & Emory,
455 2006). We will focus on working memory, the ability to manipulate information to work
456 with it (Alloway & Copello, 2013). The associated areas generally involve fronto-parietal
457 activity, with a special emphasis on the dorsolateral prefrontal cortex (Eriksson et al.,
458 2015; for a review, see Chai et al., 2018). We will also focus on another cognitive capacity,
459 cognitive control, which also mainly recruits the dorsolateral prefrontal cortex (Miller,
460 2000; Badre et al., 2009). Cognitive control is associated with pursuing goals, particularly
461 high-level ones (Miller & Cohen, 2001; Friedman & Robbins, 2022). While executive
462 functions and cognitive control are closely related, they are not necessarily
463 synonymous. Executive functions are a broader term encompassing various cognitive
464 processes involved in goal-directed behaviour. In contrast, cognitive control focuses
465 explicitly on the regulation and management aspects of these processes. Neuroimaging
466 studies have made significant strides in distinguishing between cognitive control and
467 executive functions (Niendam et al., 2012). However, the distinction is often subtle and
468 depends on the specific tasks being examined.

469 *Rationale.* The increasing complexity of lithic industries might, among other things,
470 reflect an enhancement of executive functions (Wynn, 2002; Vaesen, 2012). Working
471 memory is often highlighted when discussing the various executive functions involved in
472 the rise of our species (Martín-Loeches, 2010). For example, it could have helped to
473 engage in activities requiring complex planning, such as tool making (Figure 1) or hunting

474 with artefacts (Haidle, 2010). The ubiquity in the cognitive debate on the evolution of our
475 species can be explained by the fact that working memory is generally associated with an
476 idea of "modern thinking" (Coolidge & Wynn, 2005). Thus, from an empirical point of
477 view, lithic tools suggest that their complexification may have been supported by
478 enhanced working memory skills especially when it comes to Upper Paleolithic composite
479 tools (Haidle, 2010; Lombard & Haidle, 2012). Because of their great complexity,
480 composite tools, made by combining multiple materials or components to achieve a
481 specific function or purpose, rely on an enhanced working memory to manipulate
482 different elements at the same time. Those tools rely on production patterns that
483 interweave several elements simultaneously, unlike the first stone tools, which did not
484 involve many elements. However, this enhancement of working memory, although more
485 easily illustrated by Upper Paleolithic tools, may already have been necessary to
486 transition from Oldowan to Acheulean (Uomini, 2017). Cognitive control is also
487 questioned as having played an important role in the cognitive rise of the genus *Homo*
488 (Faisal et al., 2010; Stout, 2010). The remains of lithic industries can be again interpreted
489 as requiring more cognitive control as they become more complex because this growing
490 complexity could be based, for example, on better planning capabilities as production
491 schemes become more entangled. Generally, in the comparison between two large
492 technocomplexes following one another, enhanced executive functions are inferred in
493 Paleolithic tool makers.

494 *Evidence.* A pioneering study was first carried out on the Oldowan only with a single
495 subject expert in the production of stone tools (Stout et al., 2000). Few years later, a
496 second longitudinal study (Stout & Chaminade, 2007) focused on trained novices. Both
497 studies used PET. The main activations observed were in the IPS, with an increase in
498 activity in novices once trained, the premotor cortex, as well as areas involved in object

499 recognition in the lateral occipital cortex and visuospatial cognition. A lack of activation
500 of certain brain areas related to executive functions was reported, notably in task
501 prioritization and high-level goal pursuit. These initial findings seemed to corroborate the
502 idea that the Oldowan industry would engage simple production patterns since there is a
503 non-significant frontal lobe activation suggesting weak recruitment of executive
504 functions. These findings were complemented by another study (Stout et al., 2008), in
505 which PET scans were this time on expert subjects, who were asked to produce separate
506 Oldowan and Acheulean tools. One of the main differences observed for the Acheulean,
507 apart from a pronounced lateralization in the right hemisphere, was the increased activity
508 of the right inferior prefrontal cortex, certainly testifying to a greater need to regulate
509 complex actions.

510 Another longitudinal study in fMRI, was conducted while maintaining a comparative
511 methodology between Oldowan and Acheulean (Stout et al., 2015). Participants were
512 trained for two years to make both tools, during which three brain imaging sessions were
513 scheduled, i.e. before, during, and after the two years of training. Participants were asked
514 to evaluate video stimuli presenting lithic tools either by indicating whether the next
515 knapping indicated was correct according to the technology (strategy), or by indicating
516 whether the next knapping indicated on the video would indeed produce a specific type
517 of flake (prediction). The results obtained were consistent with previous studies, notably
518 showing increased activity in the right inferior frontal gyrus for the Acheulean compared
519 with the Oldowan, and in its left counterpart depending on the task and imaging date
520 compared with training. Acheulean would involve more executive control than Oldowan,
521 thus engaging more activations of the dorsolateral prefrontal cortex. fNIRS studies have
522 also proposed new hypotheses, still looking at the contrast between Oldowan and
523 Acheulean, focusing on working memory (Putt et al., 2017; Putt et al., 2019). In the first

524 study (Putt et al., 2017), participants were divided into groups receiving either verbal or
525 nonverbal instruction and underwent seven training sessions. The study found that
526 Acheulean tool making activated brain regions related to working memory, motor
527 planning, and multisensory integration, indicating higher cognitive demands than
528 Oldowan tool making, notably in the dorsolateral prefrontal cortex. A following study
529 (Putt et al., 2019) corroborated this finding, suggesting that the cognitive complexity
530 required for Acheulian tool production was a significant step in human cognitive
531 evolution.

532 Our meta-analysis revealed non-significant dorsolateral prefrontal lobe activity for
533 the Oldowan. On the other hand, the meta-analysis showed more significant ventral
534 premotor activity for the Acheulean compared to the Oldowan condition, while the
535 Oldowan compared to Acheulean condition did not show any brain activation. This
536 corroborates the idea that Acheulean effectively relies on some greater neuro-cognitive
537 recruitment than Oldowan. These findings seem to be partially consistent with the
538 hypothesis of an enhancement of executive functions, particularly the cognitive control
539 and planning, during the paleolithic period. Earlier theories that predate
540 neuroarchaeology, with their emphasis on the frontal lobe, have thus found fertile ground,
541 thanks to the addition of neuroscience to evolutionary questioning, to extend hypotheses
542 concerning the specific evolution of this brain structure.

543 ***4.2. Language***

544 *Background.* Human language refers to an idea of voluntary communication based
545 on interconnected units that make sense and are organized according to precise rules
546 (Cancho & Solé, 2001). Accurately estimating the emergence of modern language is a
547 delicate task. Depending on the theoretical context, the estimate can vary, leaving room

548 for debate. Some estimates date it as having appeared between 100,000 and 350,000 BC
549 (Raffler-Engel et al., 1991; Perreault & Mathew, 2012). However, recent work on the need
550 for certain forms of teaching to transmit and maintain the technical gestures already
551 necessary for Oldowan is pushing back the boundaries of how language evolution can be
552 perceived (Arbib, 2012; Gärdenfors & Högberg, 2017; Barham & Everett, 2021). Thus,
553 language could have taken root as early as the Lower Paleolithic in much simpler forms,
554 such as gestural and/or verbal protolanguage, without the need for a complex syntactic
555 and symbolic system. Nevertheless, there is also discussion that language would not
556 necessarily have been a supporting modality for our species' early technological evolution
557 (Putt, 2023). The first lithic industries could have spread without a transmission vector
558 comparable to language as we understand it today (Putt et al., 2014; Putt et al., 2017).
559 However, this still implies the need for further research about the link between language,
560 or at least transmission modalities, and the technical and cognitive evolution of our
561 species.

562 Thus, other scenarios can also be considered, in which toolmaking and speech
563 production are not as tied as a scenario of co-evolution might suggest. Malafouris's
564 material engagement theory (2013) presents a different viewpoint from the traditional
565 symbolic and language-based approaches. This theory suggests that cognition is not
566 limited to the brain but extends through the interaction between humans and their
567 material surroundings. It emphasizes how early toolmaking can be seen as a form of
568 embodied cognition. This perspective challenges the idea that speech and toolmaking are
569 closely linked. Instead, it suggests that tools are not just products of cognitive
570 representation but actively shape human thought and behavior. Additional support for
571 this perspective is found in Hodgson's research (2012, 2015, 2023), which expands on the
572 material engagement theory by illustrating how early humans' interaction with physical

573 objects, such as tools, played a crucial role in cognitive evolution. Hodgson and colleagues
574 have suggested that the act of making tools may not necessarily indicate the development
575 of linguistic or symbolic thinking, but rather emphasizes the cognitive importance of
576 engaging with material objects. These ideas challenge the co-evolution theory of tools and
577 language, suggesting that we must consider the physical aspect of tool making and the
578 complex interactions involved. They emphasize the material complexity during the
579 Paleolithic, which cannot be solely attributed to a proto-symbolic or syntactic system.
580 Tools and language may have evolved together, but the material engagement theory
581 reminds us that it is essential to recognize the environmental and material factors that
582 influenced each skill, similarly or differently.

583 Although there are still active debates about how and why language emerged in our
584 ancestors' brains, we better understand how these processes function in the modern
585 human brain. The left IFG is involved in active modern language production, but
586 upstream, anchored in a frontotemporal network. Divided in three parts, the pars
587 opercularis would serve syntactic processing, while the pars triangularis would support
588 lexical-semantic processing, with connectivity with the temporal cortex involved in
589 language comprehension (Friederici et al., 2017). Thus, the human brain areas associated
590 with language generally are the left IFG in the frontal lobe and Wernicke's area in the
591 temporal lobe. However, the neurocognitive basis of language can be part of a wider
592 network. For example, language production requires the involvement of motor areas,
593 among others (Lieberman, 2002). When talking about language in the brain, we need to
594 be careful about which skill we are referring to, whether we are talking about
595 comprehension or production, because the neurocognitive networks involved can differ.

596 *Rationale.* Language is generally perceived as a skill that has played a decisive role
597 in the evolution of humankind (Tattersall, 2018). Associated with human thought and
598 intelligence (Carruthers, 2002), language is used to express ideas, communicate, and
599 exchange around symbolic systems. Micro-society experiments have been examined the
600 importance of communication and language in the transmission of technical content. In
601 such experiments, participants can be organized into linear chains of participants as in
602 the telephone or whispers game, so that each participant represents a generation
603 (Mesoudi & Whiten, 2008). The first participant performs a task and can then transmit
604 information to the second participant in the chain, and so on. Micro-society experiments
605 have shown that the use of verbal or gestural communication enables a better
606 accumulation (or a slower decline) of technical solutions (Castro et al., 2004; Morgan et
607 al., 2015; McGuignan et al., 2017). However, what interests us here is individual
608 production less than peer-to-peer transmission. As such, language could play a decisive
609 role in modulating the inner thought that regulates activities (Luria, 1958). In addition,
610 parallels have been drawn between the construction of a sentence, which must respect
611 orthographic and grammatical rules, and the production of a tool, which must respect
612 logical hierarchical planning that also adheres to rules (Holloway, 1969; Stout et al., 2021;
613 Arbib et al., 2023). Language and tools could, therefore, be based on common
614 neurocognitive foundations, giving rise to a scenario of cognitive co-evolution (Stout et
615 al., 2008; Stout et al., 2021; Osiurak et al., 2021a).

616 *Evidence.* The interest for the link between language and tools has been supported
617 by neuroarchaeological studies that have found brain activity in the left IFG while the
618 stimuli were about stone tools but not language related (Stout et al., 2011; Stout et al.,
619 2015; Putt et al., 2019). The overlap of cerebral activations in the left IFG between
620 language and tools therefore prompts us to question the role of this area, both in terms of

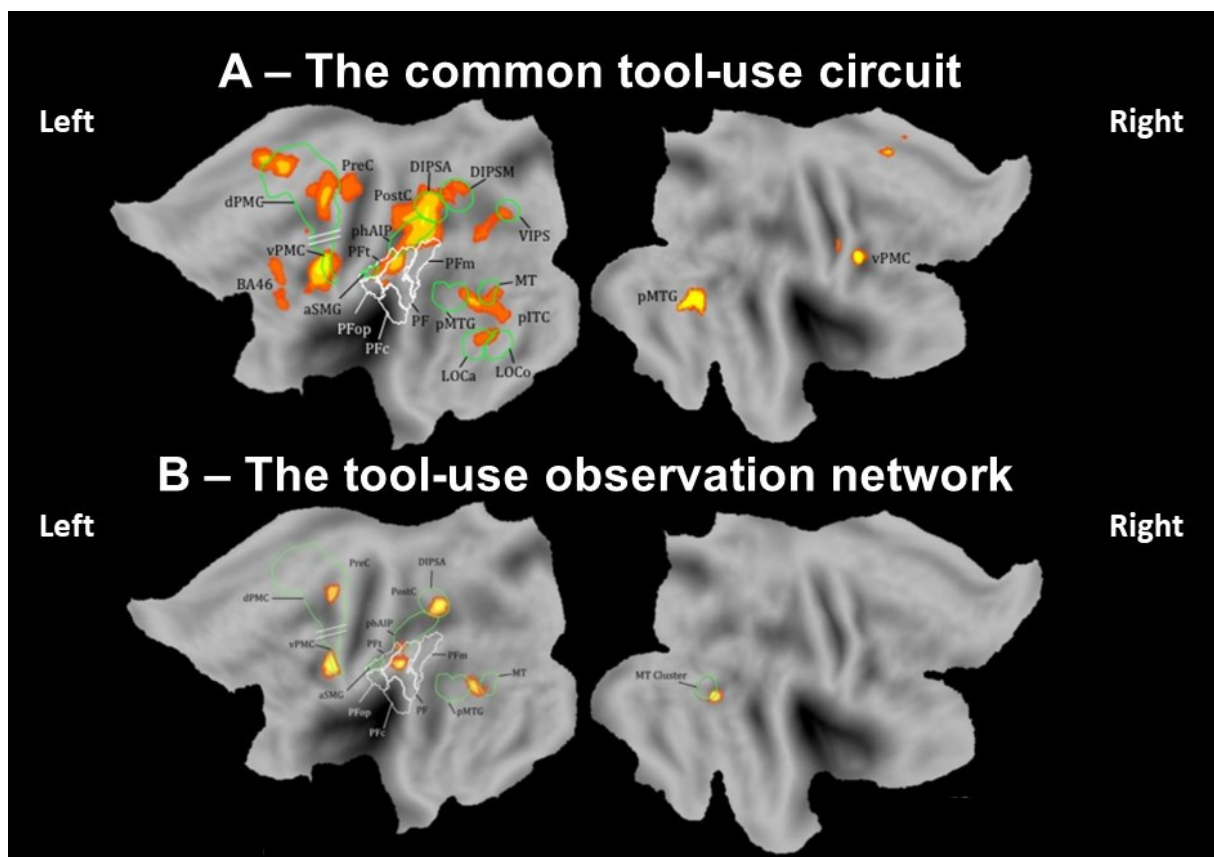
621 its emergence and importance in our cognitive evolution, and in terms of its role in the
622 specific skills involved in lithic industries, but also in verbal communication. A
623 neuroimaging study was conducted to compare the cerebral activity in tasks involving
624 modern tools and language (Higuchi et al., 2009). The results revealed overlapping
625 activation in Broca's area, associated with the left IFG, for both types of tasks, leading the
626 authors to conclude that language and tool use share computational processes in the
627 processing of complex hierarchical structures common to these skills.

628 The association of this area with language-related functions or task prioritization
629 reinforces the interest in further investigating the relationship between tools and
630 language (Uomini & Meyer, 2013). Various studies have revealed overlapping activation
631 of language-related brain areas when making or observing lithic industries, particularly
632 in the left IFG as well as in its right counterpart (Stout & Chaminade, 2007; Stout et al.,
633 2008; Stout et al., 2011; Putt et al., 2017; Putt et al., 2019). The present meta-analysis
634 confirmed these findings by revealing the activation of the left IFG, which was more
635 pronounced for Acheulean stimuli than Oldowan stimuli (Figure 2). This finding
636 corroborates the potential increasing involvement of “syntactic” computational processes
637 in the processing of stone tool stimuli as their complexity increases (Greenfield, 1991;
638 Stout et al., 2000; Stout et al., 2007; Stout et al., 2008; Stout et al., 2011).

639 **4.3. Technical reasoning**

640 *Background.* Technical reasoning is a form of reasoning that is oriented towards the
641 physical world (Osiurak & Reynaud, 2020; Mangalam et al., 2022; Osiurak et al., 2023b).
642 It is both causal (prediction of future events) and analogical (transfer from what is learnt
643 from one situation to another). It is based on mechanical knowledge, which refers to non-
644 declarative knowledge about abstract physical principles such as lever or cutting.

645 Technical reasoning is thought to support tool use and tool making as well as allowing
646 individuals to acquire new technical content from social learning (Osiurak et al., 2021b;
647 Osiurak et al., 2023b). In broad terms, technical reasoning is at work not only in asocial
648 context but also in social contexts such as when people observe others using tools. The
649 area PF (parietal area F) within the left inferior parietal lobe is central to the technical-
650 reasoning network, notably because neuropsychological studies have documented that
651 damage to the left area PF produces tool-use disorders in neurological patients
652 (Goldenberg & spat, 2009; for review, see Osiurak & Reynaud 2020) since the left parietal
653 lobe is involved in tool use. Two meta-analyses carried out on studies involving the
654 understanding (Reynaud et al., 2016) or observation (Reynaud et al., 2019) of tools using
655 brain imaging (fMRI or PET) have supported the interest of the approach based on
656 technical reasoning, but also highlighted the importance of certain brain areas (Figure 3).
657



658

659 **Fig. 3** Meta-analysis results with modern tool stimuli. (a) Meta-analysis results for “the common tool-use circuit”,
660 Reynaud et al., 2016. (b) Meta-analysis results for “the tool-use observation network”, Reynaud et al., 2019.
661 Abbreviations: vPMC, ventral premotor cortex; dPMC, dorsal premotor cortex; PreC, precentral cortex; PostC,
662 postcentral cortex; phAIP, putative human homologue of the anterior intraparietal area; DIPSA, dorsal IPS anterior;
663 DIPSM, dorsal IPS medial; vIPS, ventral IPS; PFt/aSMG, anterior portion of supramarginal gyrus, which largely overlaps
664 with the cytoarchitectonic area PFt of SMG; PF, PFm, PFt, PFop and PFm, cytoarchitectonic areas of SMG; pMTG,
665 posterior middle temporal gyrus; pITC, posterior inferior temporal cortex; LOCa, LOCo, occipital cortex; MT, MT cluster,
666 middle temporal cluster.

667 The results reported in these meta-analyses are based on studies that presented
668 participants with different types of stimuli (i.e., video clips or photos) involving modern
669 tools. Participants were asked either to understand the use of the tool presented or to
670 observe its use. These meta-analyses reported similarities in the activity of the area PF
671 between tool observation and tool use. Not only would the PF area, therefore, have a role
672 to play in tool use, understanding, and observation, but the authors concluded more
673 specifically that this region may be central in the cerebral network supporting technical
674 reasoning. The left IFG is also commonly reported. However, its role in the technical-
675 reasoning network remains to be explained since patients with only frontal lobe lesions
676 have no difficulties in using tools appropriately (Goldenberg & Spatt, 2009).

677 *Rationale.* The role of technical, more usually called causal (Heyes, 2023), reasoning
678 in the lithic production process has received not as much attention from archaeologists
679 compared to other cognitive processes such as symbolic thinking (Wynn & Coolidge,
680 2014; Wynn et al., 2016). Nevertheless, the archaeological literature is far from silent on
681 this aspect. For instance, causal reasoning has already been shown to support the
682 production of stone tools (Wadley, 2013; Haidle, 2014), which in turn promotes the
683 development of causal reasoning. A seven-grade model has been proposed (Gärdenfors &
684 Lombard, 2018; Gärdenfors & Lombard, 2020) to reflect the increasing complexity of
685 causal reasoning from early hominins to modern humans. This model suggests that this
686 progression highlights how humans evolved from understanding direct physical effects

687 (e.g., individual actions causing outcomes) to comprehending abstract causal networks,
688 such as predicting unobservable causes and applying causal knowledge across domains.
689 The model emphasizes that advanced levels of causal cognition, including speculative
690 tracking and causal grammar, were decisive during humankind's evolution. Added to this,
691 it is also necessary to address the issue of analogical reasoning, which can be seen as a
692 higher level of reasoning, enabling knowledge to be transferred from one situation to
693 another. Introducing the question of technical reasoning here aims to reunite the issues
694 of causal and analogical reasoning around a more particularly technical content, notably
695 concerning tools. The idea is that we can apply our knowledge of how modern humans
696 produce and use actual tools to stone tools through the prism of technical reasoning.

697 Evidence also supports the idea that early stone tool making reflected the
698 exploitation of causal physical relations. For instance, at the Gona site in Ethiopia,
699 statistical research on the number of lithic tools found (mainly Oldowan type) with the
700 rocks used as the main material showed significant selectivity between several types of
701 volcanic rock (Stout et al., 2005). Of more than 800 artifacts recovered, rhyolite and
702 trachyte were the most cut volcanic rocks, compared to basalt, while basalt deposits were
703 more numerous. There was, therefore, a selection of material related to rock type,
704 percentage of phenocrysts and surface mass, as these characteristics have been shown to
705 influence the quality and ease of knapping. Despite the ease of access to basalt, the choice
706 of material was not based on availability but on quality, which would imply reasoning
707 based on physical principles. The fact that several volcanic rocks corresponding to the
708 same selectivity criteria were preferentially used may point to this idea of not only causal
709 reasoning (i.e. they will be easier to carve/make a better tool) but also analogical
710 reasoning (i.e. this rock resembles another that is easy to cut, then it will be too/the tools
711 will also be more efficient) supporting the question of technical reasoning in the cognitive

712 evolution of the genus *Homo*. Beyond the selectivity of materials, there was also the fact
713 that some materials could be transported over long distances (Harris & Isaac, 1976),
714 reflecting a desire to move them strategically (Toth, 1985). Evidence also indicates that
715 stone knapping is based on the exploitation of functional parameters that the knappers
716 must understand (Bril, 2010). Thus, technical reasoning could have played a decisive role
717 in our ancestors' ability to develop more complex stone tools, especially after the
718 Oldowan, indicating an increase in specific cognitive skills. Moreover, they may have
719 developed ancillary skills, such as transmitting technical content through language and
720 better teaching methods.

721 *Evidence.* For the moment, the question of technical reasoning has received little or
722 no interest from neuroarchaeology concerning the cognitive evolution of our species.
723 Unlike modern tools, neuroimaging studies of stone tools have not yet focused on
724 technical reasoning. Yet, the results of our meta-analysis showed a common activity
725 across all studies at the level of PF (Figure 2), which could corroborate the idea that stone
726 tools might involve technical reasoning. Obviously, there must be more than technical
727 reasoning to explain the transition from Oldowan to Acheulean. Nevertheless, it does
728 enable us to understand the prerequisites of technical cognition that made this transition
729 possible. From there, we can cross-reference hypotheses concerning the need for
730 technical cognition and language to understand the complexification of stone tools. An
731 fNIRS study showed that the left IFG was more involved in Acheulean than Oldowan stone
732 (Putt et al., 2019). Put into perspective, this opens the way to two hypotheses.

733 The first is that stone tools are based on interlocking technical characteristics (e.g.
734 an arrowhead must be symmetrical, have a peduncle, be sufficiently fine and sharp, etc.)
735 and must respect hierarchical rules concerning production processes, use and general

736 properties. These technical characteristics presuppose the need to manage both the
737 combination and the management of the constraints that this implies, such as not cutting
738 one part before another. An amodal process, mainly supported by the left IFG, could be
739 called upon to enable this interweaving of rules and constraints, involving both neuro-
740 cognitive bases associated with language and technical reasoning. The second hypothesis
741 is that language serves to temporarily keep in mind the different technical characteristics
742 to be respected and to regulate the technical reasoning that will enable them to be
743 combined. Generally speaking, the link between tools and language has already been
744 explored in neuropsychology with regard to the modern brain, but it could also be of
745 particular interest for understanding the cognitive evolution, perhaps joint, of these
746 cognitive skills.

747 A community of networks between modern and lithic tools can be observed (Figures
748 2 and 3), which suggests a need for further investigations into technical reasoning and its
749 implication in stone tools' complexification. The fact that left PF shows an activation for
750 lithic industries stimuli raises questions about technical reasoning. This reasoning is non-
751 verbal and based on physical principles, using both causal and analogical reasoning
752 (Osiurak & Reynaud, 2020), for which the left PF area seems to play a crucial role.
753 Inferring the presence of technical reasoning in the Paleolithic can be supported by
754 paralleling modern activations concerning stimuli based on lithic industries, but also
755 thanks to the stone tools themselves. However, technical reasoning seems to be essential
756 for the use of modern tools. Then, it should be just as much so for lithic tools since they
757 also require knowledge of physical properties (Stout & Chaminade, 2007), enabling the
758 selection of efficient cutting gestures, as well as material orientation or knapping velocity.

759 **5. Conclusion**

760 New technologies, particularly neuroimaging, offer paleoanthropology and the
761 general study of human evolution new avenues to explore and to explain our cognition
762 evolution. The transition between the Oldowan and the Acheulean is often seen as a
763 cognitive enhancement that made the complexification of lithic tools possible (Vaesen,
764 2012; Stout et al., 2014), particularly in terms of executive functions (Wynn, 2002;
765 Coolidge & Wynn, 2016). The enhancement of the executive functions would notably have
766 enabled access to better task planning (Stout et al., 2010), necessary for Acheulean,
767 greater working memory capacity (Putt et al., 2019), as well as more executive control
768 (Hecht et al., 2015). Previously presented studies using neuroimaging to compare brain
769 activity in relation to these industries supported the notion that Acheulean would indeed
770 require more executive function (Salagnon et al., 2020). They have also revealed the
771 activation of language-related areas, notably in the IFG. Studies involving modern tools
772 and language have also presented activations in this area (Higuchi et al., 2009), thus
773 questioning its specificity in language development. However, the parietal lobes could
774 also have played a key role in visuospatial cognition (Bruner, 2018; Bruner et al., 2023).
775 Although eye-tracking is a promising technology for understanding the evolutionary role
776 of visuospatial cognition, future work combining neuroimaging and eye-tracking based
777 on stone tool stimuli could enrich current debates. This also offers the opportunity to look
778 at other dimensions of human evolution, such as the emergence of art (Hodgson, 2006;
779 Wisner et al., 2023) or even more complexed tools, like spears (Williams et al., 2014),
780 which are also beginning to benefit from an approach using neuroimaging and eye-
781 tracking techniques.

782 The frontal lobe seems often emphasized, future neuroarchaeology may focus on
783 new regions of interest such as a fronto-parietal circuit. Indeed, technical reasoning
784 associated with the parietal lobe and a fronto-parietal network (Reynaud et al., 2016;
785 Reynaud et al., 2019) could have played a decisive role in the complexification of lithic
786 tools. The hypothesis of this type of technical cognition, present as early as the Paleolithic,
787 has yet to receive much attention. Being essential for lithic tools since they also require
788 knowledge of physical properties enabling the selection of efficient knapping gestures, as
789 well as material orientation or knapping velocity (Stout & Chaminade, 2007). Thus, the
790 development of technical reasoning could also be of interest in the cognitive potential that
791 enabled hominins to improve their tools.

792 Therefore, new regions of interest may need to be considered or reconsidered to
793 explain the cognitive evolution of our species while taking care of the methodological
794 challenges this represents. Observing a homogeneity of hypotheses and a logical continuum
795 in the activation of the frontal lobe and the left inferior parietal lobe would be interesting, as it
796 could help identify the structures that played a crucial role in our cognitive and cerebral
797 development. These structures are key not only for the use of more complex tools but also for
798 language, given that they appear to share some neural activity. However, recent fields such as
799 neuroarchaeology raise several methodological issues. Therefore, the scientific
800 community sensitive to this discipline will need to work together to ensure consistency
801 of practice. Replicability of studies and, above all, of results, paradigms consistent with
802 the crossroads between the past and modernity, and the theoretical frame of reference
803 are just some of the non-exhaustive points that need to attract and maintain the attention
804 of the researchers concerned.

805

806 **References**

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