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Cognitive abilities and identity of Early Pleistocene (2.6-0.8 million years) stone-tool makers, an overview

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Context

To understand the evolution of higher-order cognitive functions, such as the planning involved in tool-making, researchers must draw inferences from contemporary human and non-human primate studies and apply these insights to fossil and archaeological records. This approach, while insightful, faces the challenge of direct evidence. The evolution of the brain and its cognitive functions remain one of the foremost scientific challenges in this field (de Sousa et al., 2023), largely because it is impossible to observe the functional brain activity of extinct hominin species directly.

The evolutionary history of our ancestors and their techniques has become considerably more complex over the last twenty-five years thanks to new methods of analysis and new archaeological and palaeoanthropological discoveries (Figure 1), and therefore, exploring the link between the lithic assemblages and the Early Pleistocene (2.6-0.8 Ma) stone-tool makers could be challenging.

Brain activation processes during Oldowan and Acheulean production: an overview

Various researchers have explored the relationships between stone-tool making and brain function through the analysis of brain activation processes during Oldowan and Acheulean tool production. In this perspective, diverse methods of functional brain imaging have been used, for example, fluorodeoxyglucose positron emission tomography (FDG-PET)¹, functional magnetic resonance imaging² and image-based functional near-infrared spectroscopy³. The purpose of this research was to discuss which brain regions are the most active during these stone tool productions using different techniques: free-hand percussion⁴ and bifacial shaping⁵, which are mainly used by Oldowan and Acheulean stone-tool makers, respectively.

¹ FDG-PET, with isotope tracer (e.g. Stout et al., 2000; Stout & Chaminade, 2007; Stout et al., 2008).

² fMRI, where the subjects watch videos and are asked to make judgments about predictions of tool-making action outcomes (e.g. Stout et al., 2015).

³ fNIRS is a neuroimaging technique that measures changes in oxygenated and deoxygenated haemoglobin in the cortex.

In their protocols, the participants learn to make Oldowan and Acheulean stone tools (e.g. Putt, Wijekumar, Franciscus & Spencer, 2017).

⁴ Debitage with multidirectional flaking, the hammerstone is held by the dominant hand and the core is maintained by the non-dominant hand without the help of an anvil.

⁵ Consists of shaping a stone into a handaxe or cleaver and maintaining a sharp edge along the entire piece.

In these experimental setups, participants with varying levels of expertise (from novices to experts) engage in tool-making tasks or watch videos related to these processes.

In their 2000 study, using FGD-PET with one expert subject, Stout and collaborators (Stout, Toth, Schick, Stout & Hutchins, 2000) discovered that different regions of the cerebral cortex involved in the processing of sensory (visual and somatosensory) and motor information, as well as the cerebellum involved in the integration and control of motor activity were activated (Figure 2). Interestingly, cortical regions associated with high-level planning were not activated during Oldowan debitage.

In a subsequent study by Stout and Chaminade (2007), which involved six right-handed novice subjects during Oldowan production, additional regions were found to be active, i.e., the rostral intraparietal sulcus and ventral premotor cortex, which are involved in visuomotor function, as well as the interface between the perceptive and motor systems for controlling arm and eyes movements in motor control. See Figure 2.

The brain activation data from these studies indicate that the initial stages of acquiring Oldowan debitage skills primarily focus on perceptual-motor adaptation to task constraints. Since there is no activation of the ventro and dorsolateral cortex, the authors (Stout & Chaminade, 2007) consider that there is no high planification during Oldowan tool production.

Conversely, during the production of Acheulean handaxes with three expert subjects, a specific area of the brain, closely associated with decision-making processes (the right inferior prefrontal cortex, Brodmann Area 45 (BA 45)), shows significant activation (Stout, Toth, Schick & Chaminade, 2008). According to the authors, the activation of the ventrolateral prefrontal cortex, but not of the dorsolateral prefrontal cortex, known for its role in working memory, indicates that Acheulean shaping primarily involves cognitive processes for coordinating hierarchically organized ongoing action sequences.

According to Stout and Chaminade (2012), an overlap between Oldowan and Acheulean is found in several cortical regions of the parietal lobe and the premotor cortex located in the frontal lobe. Regions specifically involved in Acheulean shaping can be found in the frontal cortex, and in particular in the right hemisphere homologue of anterior Broca's area (Stout & Chaminade, 2012) (Figure 2).

Using the fMRI method to identify activation during the observation of tool-making action with videos, Stout et al. (2015) observed that the prefrontal cortex shows greater responses during Acheulean than Oldowan debitage. This finding suggests that Acheulean shaping may involve more complex cognitive processes. According to their earlier work (Stout, Toth, Schick, Stout & Hutchins, 2000), Oldowan tool-making primarily requires coordination of visual attention and motor control, engaging motor and sensorimotor areas of the brain.

On the other hand, research by Putt (Putt, 2016; Putt, Wijekumar, Franciscus & Spencer, 2017), using the fNIRS method where participants learn to make Oldowan and Acheulean artefacts in either a verbal or nonverbal training context while carefully controlling the learning context, indicates that Acheulean tool-making involves not just motor control but also integrates higher-order motor planning, working memory, and auditory feedback mechanisms. This distinction between Oldowan and Acheulean tasks points to a possible evolutionary advancement in cognitive abilities and brain functions corresponding to these

two different stone tool-making technologies and brain functions corresponding to these two different stone tool-making technologies.

Who could be the stone-tool makers?

Another step in neuroarchaeology is to understand who the stone-tool makers were as well as possible perspectives in palaeoneurology. The conventional belief that *Homo* species only made the Oldowan artefacts is being questioned due to the presence of a temporal and geographical overlap with non-*Homo* species like *Paranthropus boisei*, *P. aethiopicus*, *P. robustus*, and *Australopithecus garhi* (Figure 1). Moreover, the skeleton of *Paranthropus*, exemplified by post-cranial elements, seems compatible with the anatomical features required for stone tool production, as noted by Domínguez-Rodrigo and colleagues (Domínguez-Rodrigo et al., 2013). Additionally, hand remains, initially allocated to *Homo habilis*, are now considered to belong to *Paranthropus* (Moyà-Solà, Kohler, Alba & Almécija, 2008). Therefore, the anatomical evidence supports the view that *Paranthropus* species were likely users and stone-tool makers. In addition, *Paranthropus* remains have been found together with Oldowan assemblages in some eastern African sites (Prat, 2023). Thus, Oldowan artefacts are associated not only with *Homo* species like *H. habilis* and *H. erectus/ergaster*, but also with *Paranthropus* (Figure 3). *Paranthropus* remains seem clearly more frequently associated than previously thought with lithic assemblages. This observation challenges the long-held view that tool-making is exclusive to the *Homo* genus. In addition, while the presence of *H. erectus* is mainly linked with Acheulean tools after 1.4 Ma, we can highlight evidence of their association with Oldowan tools in Africa and Eurasia (Prat, 2023). Moreover, the human-like cortical reorganization is not exclusive to the *Homo* genus. It was already evident 3 to 4 million years ago in species like *Australopithecus africanus*, with reorganization in the occipital and prefrontal cortical areas (Holloway & Kimbel, 2004; Beaudet et al., 2018). Such reorganizations are still debated for *Australopithecus afarensis* (e.g. Gunz et al., 2020; Holloway & Kimbel, 1986). Similar changes were observed in *Paranthropus robustus* (Holloway, 1972). Recent *Australopithecus* species like *Australopithecus sediba* (1.97 Ma) also show signs of this reorganization, particularly in the prefrontal cortex (Carlson et al., 2011). Additionally, Ponce de León et al. (2021) indicate that early African and Georgian hominins retained a great ape-like frontal lobe structure, but specimens from Africa and Asia younger than 1.5 Ma exhibit a human-like brain organization. This overview significantly broadens our understanding of early hominin behavior and tool-making skills. It paints a more intricate and nuanced picture of early hominin behavior and cultural evolution, underscoring a more complex narrative of early human evolution.

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