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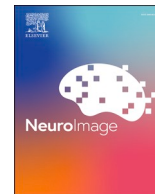
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Lithic industries, modern tools, and language: An evolutionary perspective through fMRI

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ABSTRACT

Tool use is a defining cognitive ability of the human species, relying on technical reasoning—a causal and analogical understanding of physical principles. Neuroarchaeological studies suggest that lithic tool use engaged a specialized frontoparietal network, which evolved into the left-lateralized network observed for modern tools. This network includes the left inferior parietal lobule, particularly the area PF, linked to technical reasoning, and the left inferior frontal gyrus, which is both involved in tool use and language. Since these latter two domains are based on hierarchical structuring, organizing embedded constraints, the common involvement of the left inferior frontal gyrus has been proposed as evidence of a co-evolutionary trajectory. Using fMRI, we investigated whether increasing mechanical complexity modulates frontoparietal activity and whether lithic and modern tools engage a common neural network. Participants performed a tool evaluation task, in which they assessed the functionality of both tool types across three levels of complexity designed to reflect embedded constraints. Our results revealed stronger functional connectivity between the left area PF and the left pars opercularis of the inferior frontal gyrus as mechanical complexity increased. The results also confirmed common activation for both tool types. By demonstrating that frontoparietal connectivity scales with complexity in tool evaluation, our study provides new insights into the neurocognitive foundations of tool use. These findings contribute to the broader discussion of a co-evolutionary relationship involving technical reasoning, tool making, and language, highlighting the role of hierarchical processing as a potentially shared computational principle.

1. Introduction

Humans uniquely excel at making tools and communicating complex information about them (Lieberman, 1993; Tomasello and Rakoczy, 2003; Stout, 2011; O'Madagain and Tomasello, 2022). This intertwining of technical skills and symbolic language characterizes human cognition and began evolving during the Paleolithic period (Gibson and Ingold, 1993; Pinker, 2010; Stout and Chaminade, 2012). Neuroarchaeology, combining archaeological insight with neuroimaging (Hecht and Stout,

2023), explores the neurocognitive foundations of this evolution. While the brain does not fossilize, lithic tools are valuable evidence of our ancestors' cognitive abilities. Producing these tools involved increasingly complex nested steps like selecting material, knapping, and adjusting gestures (Vaesen, 2012).

Lithic tools are often categorized by their association with different lithic industries. The Oldowan, dated between 2.5 and 2.9 Mya (Semaw et al., 1997, 2003; Plummer et al., 2023), is among the earliest lithic industries, marked by simple pebble tools produced by striking one

Laboratory website: <https://emc.univ-lyon2.fr/equipes/memoire-emotion-et-attention-mea/bryche-chloe>

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pebble against another to create a sharp edge (Braun et al., 2008; Bails and Dini, 2012). The Oldowan tradition continued until the emergence of the Acheulean industry, dated to between 1.5 and 1.76 Mya (Favreau, 2023), which persisted until 154,000 years ago. The Acheulean introduced significantly more complex production techniques, often associated with the handaxes—a well-known almond-shaped flint tool. Acheulean tool making involved multiple stages, including shaping and refining both sides of the stone to produce symmetrical and standardized forms like handaxes and cleavers, using complex materials such as siliceous. Acheulean tools are frequently compared to Oldowan tools as a case study highlighting the greater cognitive and technical demands of Acheulean production. By being complexified year after year and *Homo* after *Homo*, lithic tools can be thus interpreted as an enhancement of cognitive abilities (Renfrew and Zubrow, 1994; Coolidge and Wynn, 2016; Overmann and Coolidge, 2019), moreover when linked to our ancestors' cranial capacity augmenting (Neubauer, 2014; Toth and Schick, 2019). Tool making, defined by Shumaker et al. (2011) as the modification of an object to achieve a specific goal, and tool use, manipulating an object to effect environmental change, is thus a cognitive milestone reflected in lithic tools technology.

The neurocognitive basis of human tool use is supported mainly by the left hemisphere (Goldenberg and Hagmann, 1998; Johnson-Frey et al., 2005; Martin et al., 2016), even potentially among left-handed individuals (Króliczak and Frey, 2009; Goldenberg, 2013; Króliczak et al., 2016, 2021; Lesourd et al., 2020; Króliczak and Przybylski, 2024). The left inferior parietal lobe (IPL) is known to be involved in the selection, use, or even in the fabrication process of tools, whether they are familiar or not (Vingerhoets, 2008, 2014; Goldenberg and Spatt, 2009; Seiffert et al., 2025; Osieurak et al., in press). The intraparietal sulcus (IPS) aids in motor actions, coordinating hand-tool interactions (Tunik et al., 2007; Valyear et al., 2007), working in conjunction with premotor regions that support the mental representation of grasping actions (Jacobs et al., 2010; Martin et al., 2011). The lateral occipitotemporal cortex (LOT) supports representations of tools in both action-related and semantic contexts (Lesourd et al., 2023). The IPS, as well as the premotor areas and LOT, are also highlighted in neuroarchaeological studies on lithic industries, especially during tool making tasks or imagining making them (Stout and Chaminade, 2007; Stout et al., 2008, 2011). Neuroarchaeology broadly reports frontoparietal activity (Stout et al., 2015; Hecht et al., 2015, 2023), which is corroborated by research on modern tools and the implication of left inferior frontal gyrus (IFG) (Johnson-Frey, 2004; Goldenberg and Spatt, 2009; Wadsworth and Kana, 2011; Salazar-López et al., 2016; Seiffert et al., 2023; Króliczak and Przybylski, 2024). This frontal region is likely involved in planning, sequencing, and executing complex motor actions.

A network between the left IPL, particularly the area PF (Parietal F), and the left IFG has also been reported (Reynaud et al., 2016; E, 2019). Neuropsychological studies have shown that damage to the left area PF leads to tool use disorders (Goldenberg and Spatt, 2009; Martin et al., 2016). Therefore, some authors suggest that the left area PF may play a central role in the technical reasoning network (Federico et al., 2022). Technical reasoning refers to a form of reasoning oriented towards the physical world, supporting tool use and tool making through both causal and analogical processes (Osieurak and Reynaud, 2020; Mangalam et al., 2022; Osieurak et al., 2023). Technical reasoning did not yet receive much attention from neuroarchaeology, whereas several neuroarchaeological studies present a common activity for the left area PF (Bryche et al., 2024). While this area seems strongly related to technical reasoning, its connectivity with the left IFG still needs further investigation to understand better its role (E. Reynaud et al., 2019).

The left IFG, better known as Broca's area, is more often associated with language, a capacity that also uniquely evolved along the human lineage. Language is defined as a symbolic system that enables the transmission of complex information based on interrelated components that are logical and structured following specific principles (Pinker, 1994; Cancho and Solé, 2001). The left IFG, as part of a frontotemporal

network, is essential for modern language production. Its pars opercularis is involved in syntactic processing, while the pars triangularis supports lexical-semantic processing, with connections to the temporal cortex for language comprehension (Friederici et al., 2017). Some have argued that language and tool use share computational processes in handling complex hierarchical structures (e.g., Greenfield, 1991), suggesting a co-evolution scenario of their neurocognitive bases (Frey, 2008; Uomini and Meyer, 2013). Thus, a shared left IFG activity for both modern tools and language tasks has been reported (Higuchi et al., 2009; Thibault et al., 2021). Neuroarchaeological studies have also reported an activity in the left IFG in lithic tools tasks (Stout et al., 2011, 2015; Putt et al., 2019).

The goal of the present study was twofold. First, we aimed to provide insight into the shared neural substrates underlying language and tool use. Since a frontoparietal network appears to be involved in both tool-related tasks and language processing and given that both rely on complex hierarchical structures organized by precise rules, we hypothesized that the left IFG would activate during tasks with embedded constraints, whether related to language or tools (e.g., relative clauses, or considering both material and velocity). To test it, we designed an fMRI protocol where participants evaluated visual stimuli of tools with increasing complexity, requiring considering progressively more embedded constraints. The evaluation involved a split screen with four tools on each side, and participants were tasked with choosing the side displaying the more significant number of functional tools (Fig. 1). In other words, our task targets the conceptual step of tool use as participants did not have to use tools, but to assess their effectiveness. Three features varied for each stimulus; some of them were relevant for deciding whether the tools could work or not (e.g., absence vs presence of teeth on the saw blade), and others were irrelevant (e.g., the color of the saw AND the presence vs absence of a hole in the blade). The number of embedded mechanical constraints reflected three levels of difficulty, with fewer irrelevant features as complexity increased.

We expected to see significantly increasing activity in the left IFG following the increasing complexity, which refers to the level of embedded constraints. More precisely, we hypothesized that this activation would be stronger in the pars opercularis, given its greater involvement in syntax processing, than the pars triangularis which is known to be more engaged in lexical-semantic processing. We initially intended to explore this aspect with a region of interest (ROI) approach based on an additional language task used as a localizer. The participants of the present fMRI study performed this additional language task, which consisted of evaluating sentences containing action verbs. There were two experimental manipulations leading to four experimental conditions. Sentences could be (1) syntactically correct or not and (2) semantically correct or not. Thus, we expected that the pars opercularis would be more sensitive to the syntactic manipulation and the pars triangularis to the semantic manipulation. Our predictions on this task were not confirmed as we did not obtain any statistical difference between the four experimental conditions. As a result, for sake of clarity, we did not discuss further this language task below and added information about it in **Supplementary Materials**. In addition, this led us to conduct literature-defined ROI analyses.

The second objective was to determine whether this shared neural activation extends to both modern and lithic tools. While common activations have been observed across both tool types, to our knowledge, no study has directly examined the cerebral activity underlying both modern and lithic tools within a single task and unified design. Instead, comparisons are typically drawn between neural responses to lithic tools and previously reported findings on modern tools use, leading to potential inconsistencies in interpretability. To determine if lithic tools trigger the same neural responses as modern tools, we included both types of stimuli: modern tools and lithic tools. Based on neuroarchaeological literature, we expected comparable activity across conditions, particularly in the left IFG and IPL. We also anticipated shared activation in the left area PF between modern and lithic tools,

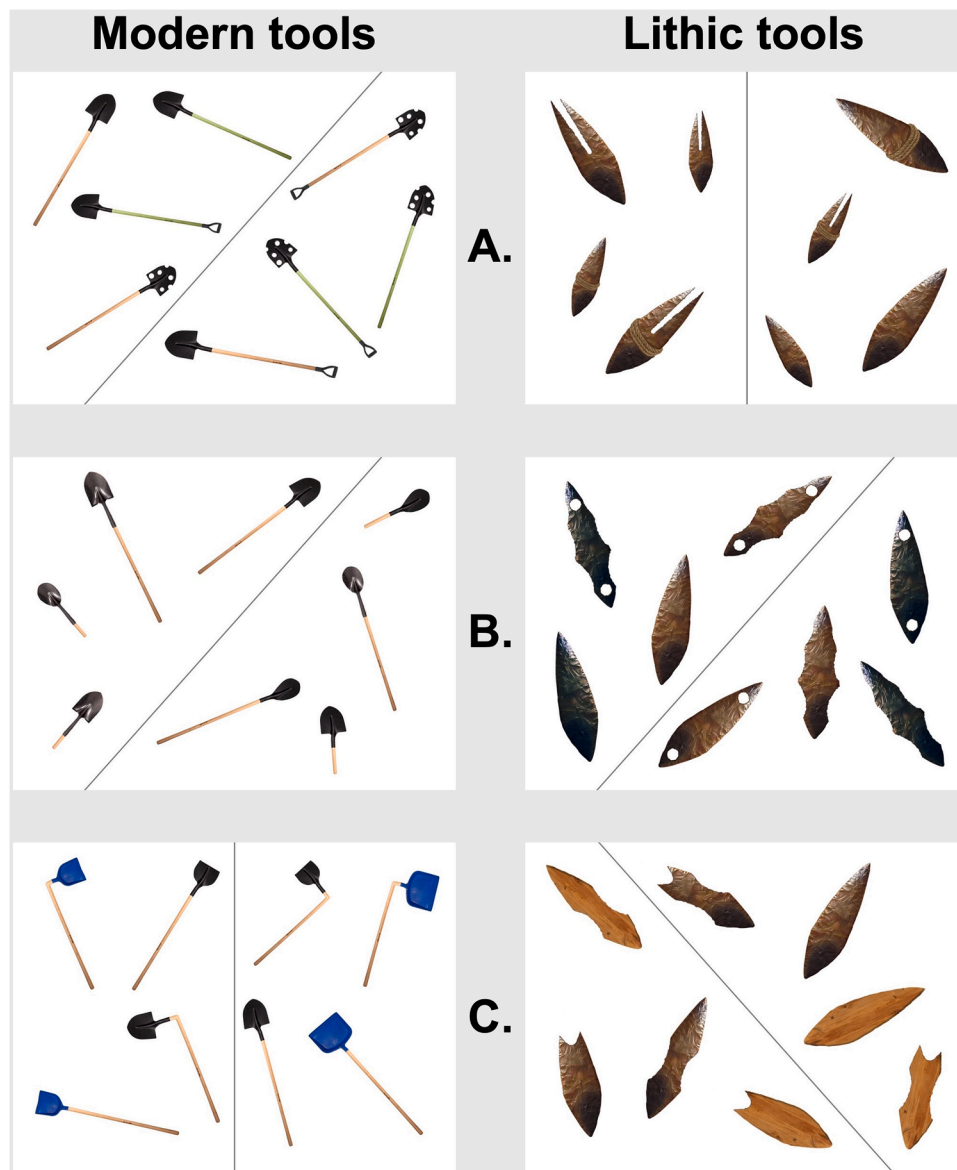


Fig. 1. Stimuli used in the behavioral and fMRI experiments, organized into two categories—modern tools and lithic tools—presented in separate columns. Within each category, (A) represents the lowest complexity level with one relevant feature embedded and two irrelevant features (correct response: Modern tools = left, Stone tools = right), (B) the intermediate complexity level with two relevant features and one irrelevant feature (correct response: Modern tools = left, Stone tools = left), and (C) the highest complexity level with three relevant features without irrelevant feature (correct response: Modern tools = right, Stone tools = right). The task consisted of choosing the side displaying the greater number of functional tools.

supporting further investigation into technical reasoning’s role in the cognitive evolution of the *Homo* genus. Similarly, activations are expected in additional regions known to be involved in tool use and observation, such as the IPS, LOTC, and premotor areas. However, these regions fall outside the primary scope of our study.

2. Behavioral experiment

Our experimental protocol required participants to look at pictures of modern and lithic tools and to determine whether they were functional or not based on relevant features. As modern humans are not familiar with lithic tools, we decided to create a “training” session to improve their knowledge about lithic tools and, as a result, decrease the complexity of the task for them. This training session consisted of two 30-minute sessions held within the same week. More detail is given below. To test the effectiveness of this training session, we first presented our experimental protocol with a group of participants who did

not take part in the fMRI experiment. This behavioral experiment also allowed us to investigate whether participants’ performance decreased as the degree of complexity increased.

2.1. Methods

2.1.1. Ethics

The study adhered to the principles of the Declaration of Helsinki and received approval from the French Ethics Committee of Saint-Étienne (ID-RCB N°: 2020-A02115-34). All participants provided informed consent after being fully briefed on the nature of the study and any potential consequences.

2.1.2. Participants

The study was conducted at the Laboratory for the Study of Cognitive Mechanisms, University of Lyon (Lyon, France). Recruitment was carried out through advertisements posted on campus and online social

platforms. No monetary compensation was provided. All participants were right-handed, reported no history of neurological or psychiatric disorders, and confirmed having no prior knowledge of lithic tools. A total of 20 participants aged between 18 and 28 were included in the behavioral experiment (female/male/non-binary gender: 18/2/0). Participants were randomly assigned to one of two groups: A training group, which received instruction on lithic tools production and use, and a control group, which did not receive any training.

2.1.3. Training

The training sessions were conducted by C.B. and consisted of two 30-minute sessions held within the same week. Prior to the first session, participants completed a pre-training quiz to assess their baseline knowledge of lithic tools. The first session was conducted in the laboratory and focused on introducing participants to various types of lithic tools. Participants were provided with information on how these tools were produced and used, supplemented by hands-on interaction with real lithic tools and instructional videos. The training included explanations about the fabrication process and the functional purpose of the tools, as well as manipulation of different materials (e.g., flint vs. obsidian). At the end of this session, participants completed a second quiz to evaluate their immediate learning outcomes. The second session was conducted online and provided a more in-depth exploration of the same lithic tools introduced in the first session. Following this session, participants completed a third quiz to measure their retention and comprehension of the material. Later that week, participants returned to the laboratory to complete the behavioral task. Prior to this task, participants took a final quiz on lithic tools to assess their knowledge post-training. We analyzed the scores obtained on the initial quiz, before the stone tool training, and on the final quiz, after training, to assess whether participants demonstrated a genuine learning effect, as both quizzes were identical with a maximum score of 60 points. Participants did not have access to the correct answers from the quizzes until their final attempt, ensuring that they could not cheat and were required to apply what they had learned. To prevent reliance on visual recognition during the behavioral task, all visual materials used in the training (i.e., presentation slides, videos and quizzes) were distinct from those presented in the experimental task.

2.1.4. Behavioral task

Stimuli. The stimuli consisted of stimulus arrays; they can be accessed on OSF (<https://osf.io/4xbn6/files/osfstorage>). Each array contained eight tool images derived from a single original tool. Original tools were divided into two categories: modern or lithic. For each tool category, we selected eight distinct tools (Fig. 2), resulting in a total of 16 original (i.e., unmodified) images. Each tool was then digitally modified using ProCreate (v5.3) along two dimensions: **irrelevant modifications** (e.g., changes in handle color) and **relevant modifications** (e.g., adding holes to a shovel), with the latter rendering the tool less functional or entirely

unusable. These modifications were designed to create three levels of increasing complexity representing a gradient from simple to complex modifications; thus, the modifications were applied incrementally. At complexity level 1, a single relevant feature was modified (e.g., presence vs. absence of teeth on a saw blade) and two irrelevant features were modified (e.g., tool color and the presence vs. absence of a hole in the blade). At complexity level 2, two relevant features were modified simultaneously (e.g., presence vs. absence of teeth on the saw blade and short/ineffective vs. long/effective blade length), while only one irrelevant feature was modified. At complexity level 3, three relevant features were modified, and no irrelevant features were included. In each trial, the screen was bisected by a grey line, with four tool images presented on either side for a total of eight images (Fig. 2). Participants judged which side contained most highly functional tools; the side assignment was randomized. This resulted in a total of 48 stimulus arrays, with 24 for modern tools and 24 for lithic tools (i.e., 3 stimulus array * 8 original tools * 2 categories).

Procedure. Participants completed the behavioral task conducted on a computer running PsychoPy3 Experiment Builder (v2021.2.3) (Pierce et al., 2019). The task required participants to evaluate which side of the screen contained most functional tools (Fig. 1). Participants sat upright in front of the computer with their hands positioned on the keyboard to provide their responses. The behavioral task began with an instruction screen providing participants with detailed guidelines for the task. Following this, participants completed a brief training phase consisting of three practice trials to familiarize themselves with the procedure. The main task was divided into two parts: One focused on modern tools and the other on lithic tools, with the order of presentation counterbalanced across participants. The task comprised a total of 16 blocks, with 8 modern tools blocks and 8 lithic tools blocks. Each block contained three stimuli, from the same tool category (modern or lithic), presented across three levels of complexity. Both the order of complexity levels and the tool being displayed were randomized to avoid systematic biases. A 1000-ms fixation cross was displayed before each stimulus. Participants were instructed to respond as quickly as possible, but each stimulus remained on the screen for 20 s to ensure responses were recorded. This extended presentation time accommodated the pilot nature of the study, allowing confirmation that responses could consistently be made within an eight-second window, in preparation for the future fMRI experiment. Participants responded using a keyboard, pressing the "S" key for the left side and the "L" key for the right. After completing the first category (either modern or lithic tools), participants took a brief break before proceeding to the second category, which followed the same structure and procedure as the first. At the end of the task, participants completed a questionnaire about all the modern tools displayed during the experiment, in which they were asked to name each tool, indicate whether they had used it before, describe its functionality, and specify its typical use. All the 20 participants correctly identified 100 % of the modern tools and their intended purpose.

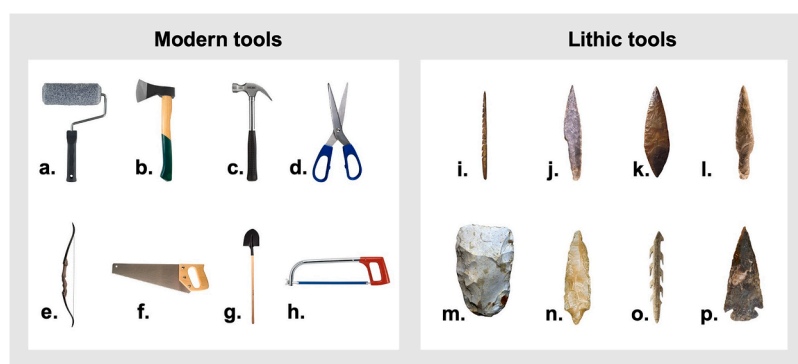


Fig. 2. Original tools used to create the stimuli arrays. On the left part for the modern tools: (a) roller, (b) axe, (c) hammer, (d) scissors, (e) bow, (f) wood saw, (g) shovel, (h) metal saw. On the right part for the lithic tools: (i) harpoon, (j) spear, (k) laurel, (l) dagger, (m) cleaver, (n) arrowhead, (o) harpoon, (p) arrowhead.

2.1.5. Statistical analyses

To assess the impact of training on learning, we used regression modelling in R (R Development Core Team, 2011) (lmerTest package; Kuznetsova et al., 2017) to fit a linear model with ‘Score’ as outcome variable and ‘Training session’ (Before versus After) as fixed effect, and ‘participant’s identity’ as random effect. We used the same model to test the effect of training on participants’ performance as a function of tool category with ‘Accuracy’ as outcome variable, ‘Training’ (Trained versus Control) and ‘Tool category’ (Modern versus Lithic) as fixed effects, and ‘participant’s identity’ as random effect. We also included the interaction between ‘Training’ and ‘Tool category’ in the model. We also used the same model with ‘Response time’ as outcome variable. To test the effect of complexity on participants’ performance as a function of tool category, we used regression modelling in R to fit a linear model with ‘Accuracy’ as outcome variable ‘Training’ (Trained versus Control) and ‘Complexity’ (Level 1 versus Level 2 versus Level 3) as fixed effects, and ‘participant’s identity’ as random effect. Here again, the model

included the interaction between ‘Complexity’ and ‘Tool category’. The same model was fitted with ‘Response time’ as outcome variable. Statistical significance was set at $p < 0.05$.

2.2. Results

2.2.1. Effect of training

The training sessions led to a significant improvement in quiz scores (Fig. 3f), demonstrating their effect on learning as analyses revealed a main effect of the Training Session ($F(1,9) = 103, p < .001$), with participants having better scores after the two training sessions (After estimate: 24.5; 95 % Confidence Interval [CI]: 19.54 to 29.45; $p < .001$). Concerning accuracy (Fig. 3a-b), the analyses revealed a main effect of Tool category ($F(1116) = 6.88, p = 0.010$), participants being better for modern tools than for lithic tools (Lithic estimate: -0.15 ; 95 % Confidence Interval [CI]: -0.23 to -0.07 ; $p < .001$). In addition, a Training*Tool category interaction was significant ($F(1116) = 5.84, p =$

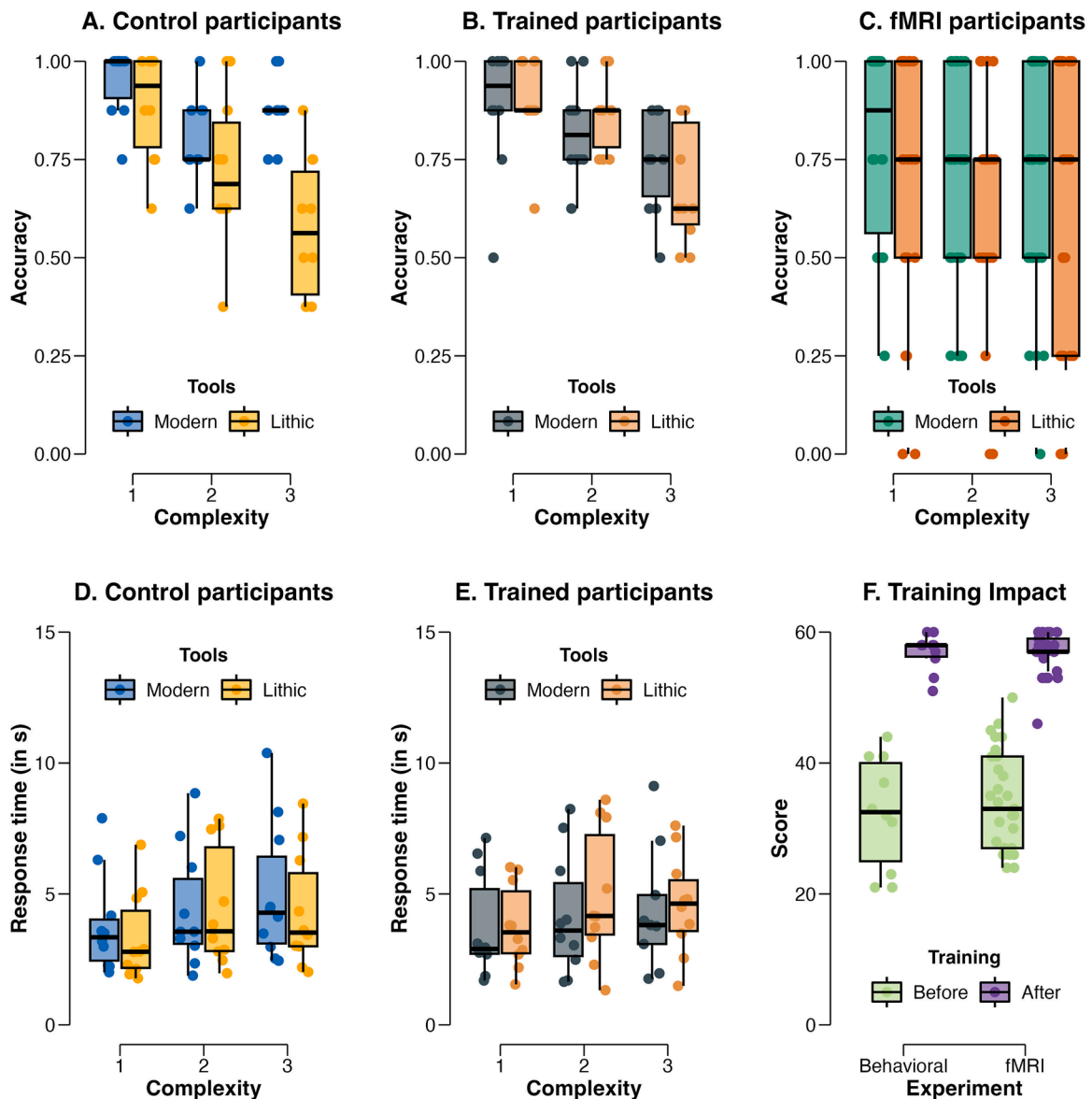


Fig. 3. Behavioral results of the behavioral and fMRI experiments. Accuracy (proportion of correct responses, range: 0 = 0 %, 1 = 100 %) as a function of complexity and tool category (Lithic versus Modern) in (A) control and (B) trained participants of the behavioral experiment and in (C) fMRI participants. Response time as a function of complexity and tool category (Lithic versus Modern) in (D) control and (E) trained participants of the behavioral experiment. (F) Quiz scores before and after training in behavioral and fMRI participants. Boxplots indicate the upper quartile, median and lower quartile, with whiskers extending to the most extreme data point that is no more than 1.5 times the interquartile range from the edge of the box. Bars represent the means and 95 % confidence intervals.

0.017). This interaction revealed that trained and control participants did not significantly differ from each other for modern tools (Trained estimate: -0.05 ; 95 % CI: -0.13 to -0.03 ; $p = .19$), whereas trained participants significantly obtained better performance than control participants for lithic tools (Trained*Lithic estimate: 0.14 ; 95 % CI: 0.03 to 0.25 ; $p = .017$). No significant results were reported for response time (all $p > 0.06$; Fig. 3d-e).

2.2.2. Effect of complexity

Concerning accuracy (Fig. 3a-b), the analysis revealed a main effect of Complexity ($F(1116) = 35.53$, $p < .001$) and a significant Complexity*Tool category interaction ($F(1116) = 6.51$, $p < .012$). More particularly, performance decreased for both modern and lithic tools as complexity increased (Complexity estimate: -0.05 ; 95 % CI: -0.09 to -0.01 ; $p < .018$) and this decrease was even greater for lithic tools than modern tools (Complexity*Lithic estimate: -0.08 ; 95 % CI: -0.14 to -0.02 ; $p < .012$). Concerning response time (Fig. 3d-e), a significant effect of Complexity was reported ($F(1,96) = 39.23$, $p < .001$), with slower response times as complexity increased (Complexity estimate: 0.55 ; 95 % CI: 0.32 to 0.77 ; $p < .001$).

2.3. Discussion

The results of the behavioral experiment revealed that our training was effective as trained participants obtained better performance than a control group for lithic tools. Moreover, this is further supported by the participants achieving significantly higher quiz scores after their training session. Therefore, we decided to employ the same training for fMRI participants. We also found a complexity effect as expected. No effect was found for response time. In broad terms, these results confirmed that our behavioral protocol could be used to test how participants deal with the increase of embedded constraints applied to modern versus lithic tools.

3. fMRI experiment

3.1. Methods

3.1.1. Ethics

The study adhered to the principles of the Declaration of Helsinki and received approval from the French Ethics Committee of Saint-Étienne (ID-RCB N°: 2020-A02115-34). All participants provided informed consent after being fully briefed on the nature of the study and any potential consequences.

3.1.2. Participants

The study was carried out in the Laboratory for the Study of Cognitive Mechanisms at the University of Lyon (Lyon, France) and at the Lyon Neuroimaging Department (CERMEP, Lyon, France). Participants were recruited at random through advertisements shared on social media platforms and from University Lumière Lyon II. Two weeks prior to the neuroimaging session (fMRI experiment), participants underwent a screening interview with a medical doctor to confirm eligibility. All participants were right-handed, had normal or corrected-to-normal vision, no reading impairments, and reported no history of neurological or psychiatric conditions. They also had to confirm having no prior knowledge of paleoanthropology or lithic industries. Participants in the fMRI experiment received a monetary compensation of 60€ for their participation. A total of 29 participants completed the fMRI experiment ($M_{\text{age}} = 24.88$, $SD = 3.72$, age range: 20 to 33; female/male/non-binary gender: 18/11/0). Inclusion criteria for the final sample required that head motion during scanning remained below 0.5 mm of displacement (measured as framewise displacement) between consecutive volumes for at least 90 % of the scan. No participants were excluded based on this criterion.

3.1.3. Training

The training procedure was the same as the one detailed above for the behavioral experiment. The only difference was that the behavioral experiment at the end of the week was replaced by the scanning session. We analyzed the scores obtained on the initial quiz, before the stone tool training, and on the final quiz, after training, to assess whether participants demonstrated a genuine learning effect, as both quizzes were identical with a maximum score of 60 points.

3.1.4. fMRI task

Stimuli. The stimuli used in the fMRI experiment were identical to those in the behavioral experiment, with the addition of a control task. For the control task, unmodified versions of the tools were used, with modern tools on one side and lithic tools on the other, resulting in 24 final stimulus arrays; they can be accessed on OSF (<https://osf.io/4xbn6/files/osfstorage>). Here, participants identified the side with the most tools in the same orientation, isolating perceptual alignment without assessing functional utility.

Procedure. In the scanner, stimuli were back projected onto a screen (60 Hz frame rate, 1024×768 pixels screen resolution) via an LCD projector (LX 501, CHRISTIE) and viewed through a mirror mounted on the head coil. Images on the screen had dimensions of 36×24 cm, corresponding approximately to $62^\circ \times 44^\circ$ of visual angle, based on an estimated viewing distance of 30 cm between the mirror and the participants' eyes. The task design included 18 blocks divided into three conditions: lithic tools, modern tools, and a control condition. Stimuli were divided into three increasing levels of complexity reported as one, two and three. Each block contained two or three different stimuli of the same type (i.e., modern or lithic) and a specific complexity level (e.g., three modern stimuli of complexity level two). To maintain experimental control, the order of blocks was pseudo-randomized: every two blocks with either modern or lithic stimuli were followed by a control block, and consecutive blocks of the same type were avoided, though blocks of the same complexity level could appear in sequence. The control block contained two or three different stimuli. In total, 48 stimuli were presented across all blocks randomly, with 16 different stimuli randomly picked per condition (i.e., lithic tools, modern tools or control). This design was repeated two times. Each block began with a 15-second fixation cross to ensure baseline stabilization. Each stimulus was displayed for 6 s, during which participants were instructed to produce a mental response. To recenter participants' gaze and prevent anticipatory shifts to other screen locations, a 500 ms fixation cross was presented between stimuli within each block. To minimize motor-related confounds in the fMRI signal and to maintain participant engagement, only the final stimulus of each block required a motor response. This design prevented anticipation effects and encouraged participants to mentally evaluate each item within the block. Thus, at the end of each block, participants were prompted to provide a motor response using a handheld remote. This prompt was indicated by a red square around the final stimulus, which remained on the screen for an additional 2 s even if the participants gave their response before the time limit, resulting in a total display time of 8 s for stimuli requiring a motor response. At the end of the task, outside of the scanner, participants completed a questionnaire about all the modern tools displayed during the experiment, in which they were asked to name each tool, indicate whether they had used it before, describe its functionality, and specify its typical use. All the 29 participants correctly identified 100 % of the modern tools and their intended purpose.

fMRI data acquisition. Imaging data were acquired on a 3T Siemens Prisma Scanner (Siemens, Erlangen, Germany) using a 64-channel head coil. Blood-Oxygen Level Dependent (BOLD) images were recorded with T2*-weighted echo-planar images (EPI) acquired with the multi-band sequence. Functional images were all collected as oblique-axial scans aligned with the anterior commissure-posterior commissure (AC-PC) line with the following parameters: 815 vol per run, 57 slices, TR/TE = 1400 ms / 30 ms, flip angle = 70° , field of view = 96×96 mm², slice

thickness = 2.3 mm, voxel size = $2.3 \times 2.3 \times 2.3$ mm³, multiband factor = 2. Structural T1-weighted images were collected using an MPRAGE sequence (224 sagittal slices, TR/TE = 3000 / 2.93 ms, inversion time = 1100 ms, flip angle = 8°, 224×256 mm FOV, slice thickness = 0.8 mm, voxel size = $0.8 \times 0.8 \times 0.8$ mm³).

Preprocessing of fMRI data. Structural T1-weighted images were segmented into tissue type (GM: grey matter, WM: white matter and CSF: cerebro-spinal fluid tissues) using the Computational Anatomy Toolbox (CAT12; <http://dbm.neuro.uni-jena.de/cat12/>) segmentation tool, to facilitate the normalization step. Functional data were analyzed using SPM12 (Wellcome Department of Cognitive Neurology, <http://www.fil.ion.ucl.ac.uk/spm>) implemented in MATLAB (Mathworks, Sherborn, MA). The first 3 EPI volumes were collected and discarded prior to the start by the scanner to allow for T1 equilibration effects. No slice-timing correction was applied. Preprocessing for univariate analyses included the following steps (1) 3D motion correction and linear detrending; (2) realignment to the mean EPI image with 6-head motion correction parameters and unwarping using topup (Andersson, Skare, and Ashburner, 2003); (3) co-registration of the individual functional and anatomical images; (4) normalization towards MNI template; and (5) spatial smoothing of functional images (Gaussian kernel with 5 mm FWHM).

3.1.5. Statistical analyses

fMRI analyses. For the first-level analysis, a general linear model was created using design matrices containing 7 regressors (explanatory variable), 6 for each condition (e.g., Tools = Lithic and Complexity = level 1) and 1 for the control condition, modeled as a boxcar function (with onsets and durations corresponding to the start of each stimulus of that condition) convolved with the canonical hemodynamic response function (HRF). Six regressors of non-interest resulting from 3D head motion estimation (x, y, z translation and three axis of rotation) were added in the design matrix. The model was estimated in each participant, also considering the average signal in the run. After model estimation, we computed the six simple contrasts at the first level (i.e., experimental conditions against control conditions) that were transferred to a second level group analysis (one sample *t*-tests) to obtain the brain regions activated for each level of Complexity (C1>Control, C2>Control, and C3>Control), and for each type of tools (Lithic > Control and Modern > Control). We present results maps with a significance threshold set at $p < .05$ with family-wise error (FWE) correction for simple contrasts. For the second-level analysis we also used the MRM toolbox (McFarquhar et al., 2016) to specify a repeated measures model with Tools (Modern and Lithic) and Complexity (C1, C2 and C3) as within-subject factors. No explicit baseline condition was included in the design, an implicit baseline was present, as the fixation cross displayed at the beginning of each block was not modeled. This technique allows for the unconstrained modelling of the variance-covariance structure of the data per-voxel, unlike SPM which assumes a single structure for the whole brain. Therefore, MRM should allow for more valid inference. The analysis was conducted voxel-by-voxel, applying a multivariate general linear model (GLM). Thresholding was performed at the cluster level using 5000 permutations to generate *p*-values that were corrected using family wise error (FWE) procedure at $p < 0.05$. The multivariate test statistic used was Pillai's trace. Statistical maps were visualized with the BrainNet Viewer (<https://www.nitrc.org/projects/bnv/>) (Xia et al., 2013).

ROI/seed selection. A total of 3 spherical seeds (radius = 5 mm), located in the left hemisphere, were created in the MNI atlas space (Fig. 6a). To ensure the independence of ROI selection from ROI testing, we initially intended to use ROIs derived from our own language task. However, since this was not possible, we relied on literature-defined ROIs based on previous research on language and tool use. The PF area has been associated with technical reasoning skills, an ability that enables people to use tools to solve problems based on mechanical knowledge (PF: $x = -60$, $y = -34$, $z = 46$) (Reynaud et al., 2016;

Federico et al., 2023; Osiurak et al., in press). We selected BA44 and BA45 as ROIs due to their distinct yet complementary roles in language and action-related processing. BA44 is primarily involved in hierarchical motor planning and syntactic structuring, making it particularly relevant for both tool use and language production. In contrast, BA45 is more engaged in semantic processing and integration, supporting higher-level conceptual understanding. Given our study's focus on the overlap between tool-related cognition and language, these ROIs allow us to investigate their respective contributions to technical reasoning and linguistic structuring (BA44: $x = -52$, $y = 5$, $z = 29$; Reynaud et al., 2016; BA45: $x = -42$, $y = 29$, $z = 5$; (Thibault et al., 2021).

ROI-to-ROI functional connectivity analysis. Analyses of fMRI data were performed using the CONN Toolbox (version 22.v2407; Whitfield-Gabrieli and Nieto-Castanon, 2012; Nieto-Castanon and Whitfield, 2022). In addition, functional data were denoised using a standard denoising pipeline (Nieto-Castanon, 2020) including the regression of potential confounding effects characterized by white matter timeseries (5 CompCor noise components), CSF timeseries (5 CompCor noise components), SPM_covariates regressors (6 components), session and task effects and their first order derivatives (14 factors), and linear trends (2 factors) within each functional run, followed by bandpass frequency filtering of the BOLD timeseries (Hallquist et al., 2013) between 0.008 Hz and 0.09 Hz. CompCor (Behzadi et al., 2007; Chai et al., 2012) noise components within white matter and CSF were estimated by computing the average BOLD signal as well as the largest principal components orthogonal to the BOLD average within each subject's eroded segmentation masks. Then, Seed-based connectivity maps (SBC) and ROI-to-ROI connectivity matrices (RRC) were estimated characterizing the patterns of functional connectivity with BA45, BA44, and PF. Functional connectivity strength was represented by Fisher-transformed bivariate correlation coefficients from a weighted general linear model (weighted-GLM; Nieto-Castanon, 2020), defined separately for each pair of seed and target areas, modeling the association between their BOLD signal timeseries. Individual scans were weighted by a boxcar signal characterizing each individual task or experimental condition convolved with *An spm* canonical hemodynamic response function and rectified. Group-level analyses were performed using a General Linear Model (GLM; Nieto-Castanon, 2020). For each individual voxel a separate GLM was estimated, with first-level connectivity measures at this voxel as dependent variables (one independent sample per subject and one measurement per task or experimental condition, if applicable), and groups or other subject-level identifiers as independent variables. Voxel-level hypotheses were evaluated using multivariate parametric statistics with random-effects across subjects and sample covariance estimation across multiple measurements. Inferences were performed at the level of individual clusters (groups of contiguous voxels). Cluster-level inferences were based on parametric statistics from Gaussian Random Field theory (Worsley et al., 1996; Nieto-Castanon, 2020). Results were thresholded using a combination of a cluster-forming $p < 0.001$ voxel-level threshold, and a familywise corrected *p*-FDR < 0.05 cluster-size threshold (Chumbley et al., 2010).

Behavioral analyses. To assess the impact of training on learning, we used regression modelling in R (R Development Core Team, 2011) (lmerTest package; Kuznetsova et al., 2017) to fit a linear model with 'Score' as outcome variable and 'Training session' (Before versus After) as fixed effect, and 'participant's identity' as random effect. To evaluate the accuracy of motor responses recorded during the scanning session, we used the same model with 'Accuracy' as outcome variable, 'Tool category' (Modern versus Lithic) and 'Complexity' (Level 1 versus Level 2 versus Level 3) as fixed effects, and 'participant's identity' as random effect. Statistical significance was set at $p < 0.05$.

3.1.6. Pre-registration

The hypotheses, methods and analyses were preregistered on OSF (<https://osf.io/ufwc5>).

3.2. Results

3.2.1. Behavioral results

The training sessions had a significant impact on scores (Fig. 3f), as analyses revealed a main effect of the Training Session ($F(1,28) = 273.03, p < .001$), with participants having better scores after the two training sessions (After estimate: 22.90; 95 % Confidence Interval [CI]: 20.2 to 25.70; $p < .001$). Concerning the responses made in the scanner (Fig. 3c), the analysis revealed that participants were better for modern tools than for lithic tools (Lithic estimate: -0.11 ; 95 % CI: -0.35 to 0.12 ; $p = .38$), but this difference was not significant ($F(1152) = 0.79, p = .38$). The performance also decreased as complexity increased (Complexity estimate: -0.05 ; 95 % CI: -0.13 to 0.02 ; $p = .19$), but again this effect did not reach significance ($F(1152) = 2.33, p = .13$). The interaction Complexity*Tool category was not significant ($F(1152) = 0.12, p = .74$). In broad terms, we found a pattern of results that was consistent with the one obtained in the behavioral experiment. However, the effects were not significant. As explained above, the participants of the fMRI experiment had only to produce a response for the last stimulus of the block. Therefore, the lack of significance certainly resulted from the little number of responses that fMRI participants had to make for each level of complexity and for each category of tools (i.e., 4 responses for Modern tools with a level 1 of complexity, 4 responses for Modern tools with a level 2 of complexity, and so on), which decreased the statistical power of our analyses.

3.2.2. fMRI results

The results of the simple contrasts for each level of Complexity and Tools are shown in Fig. 4. The contrast between each level of Complexity and control condition (Fig. 4a), as well as for each level of Tools against control condition (Fig. 4b) revealed significant brain activations in bilateral IPS, bilateral IFG and bilateral temporal occipital fusiform cortex and other brain areas including the left area PF.

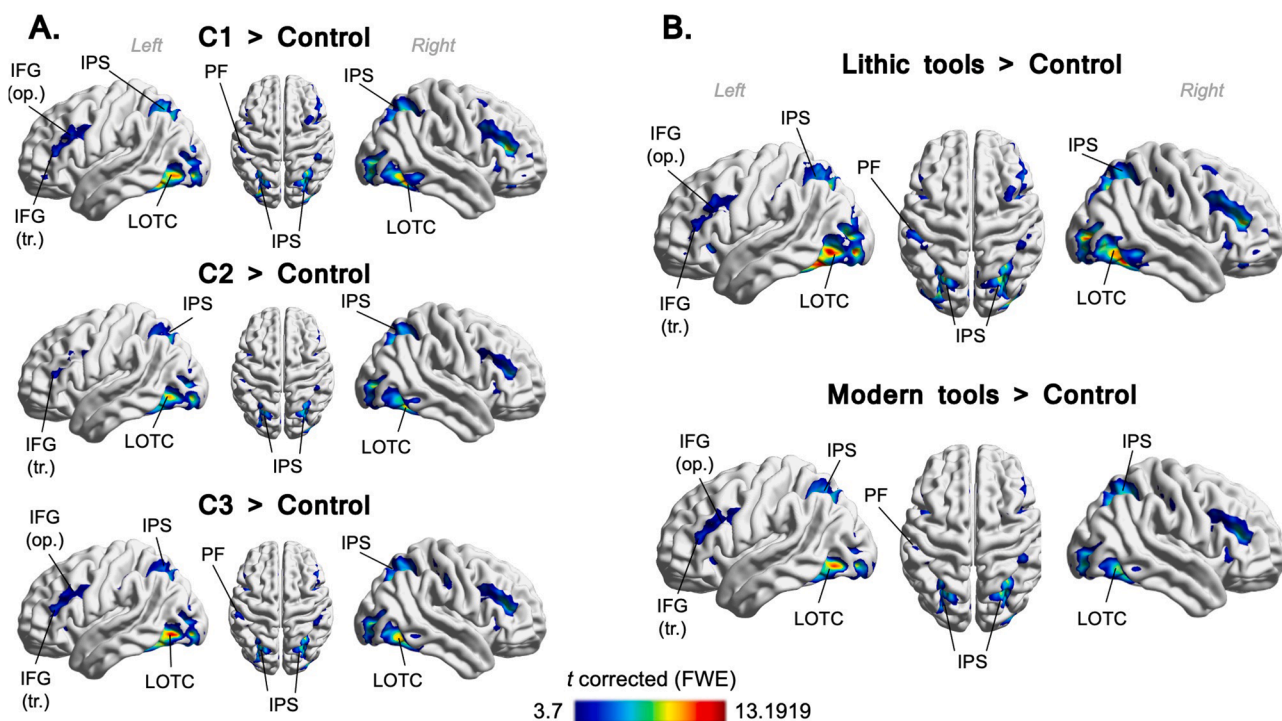


Fig. 4. Statistical maps for the contrasts between Complexity and control condition (A): C1>Control (threshold of spatial extent = 73), C2>Control (threshold of spatial extent = 91), C3>Control (threshold of spatial extent = 64); and (B) between Tools and control condition: Lithic>Control (threshold of spatial extent = 70) and Modern>Control (threshold of spatial extent = 63). Statistical maps are projected on an ICBM MNI template and FWE-corrected ($p < .05$) for multiple comparisons across the whole-brain at the cluster level. Left, left hemisphere; Right, right hemisphere; IFG, inferior frontal gyrus (op., opercular part; tr., triangular part); IPS, intraparietal sulcus; LOTC, lateral occipital temporal cortex; PF, parietal area F.

The results of the repeated-measures ANOVA with Tools and Complexity as within-subject factors are shown in Fig. 5. We found a main effect of Complexity (Fig. 5a), indicating that as complexity increases, regardless of the type of tools, activity decreases in bilateral angular gyrus. There was no significant interaction between Tools and Complexity. We also found a main effect of Tools (Fig. 5b), with lithic tools being associated with greater activity compared to modern tools in the bilateral LOTC, and left area PF.

ROI-to-ROI functional connectivity. The modulation of FC according to Tools and Complexity among the three ROIs of interest is represented in Fig. 6. We found a significant modulation of functional connectivity between the pars opercularis of the left IFG and PF, $F(6,23) = 9.29, p_{FDR} < 0.001$.

The results of the mixed-effects model on connectivity values, with Complexity, Tools, and their interaction as fixed effects, and participants as a random effect, are also presented in Fig. 6. We found a significant interaction between Complexity and Tools, $F(1142) = 4.23, p = 0.040, \eta_p^2 = 0.03$ (Fig. 6c), suggesting that the functional connectivity between the pars opercularis of the left IFG and PF increased as a function of complexity for modern tools, but not for lithic tools.

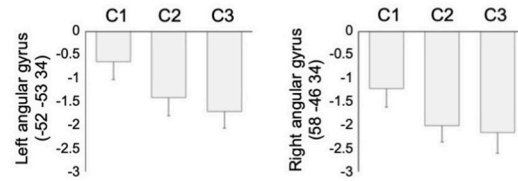
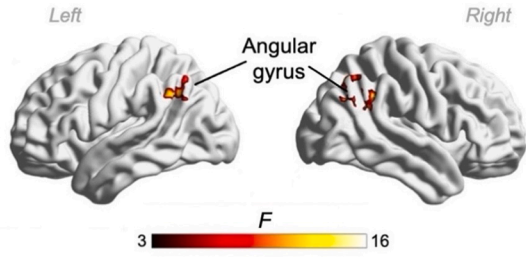
4. Discussion

The first goal of the present study was to investigate the potential shared neural substrates underlying language and tool use, focusing on the activity of the left IFG, particularly its pars opercularis. The second goal was determining how much the modern and lithic tools networks overlap. The following sections address how our results provide insight into these questions.

4.1. Tool use and language

The link between tool use and language is not new in the

A. Main effect of Complexity



B. Main effect of Tools

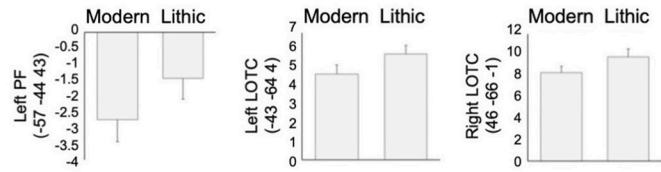
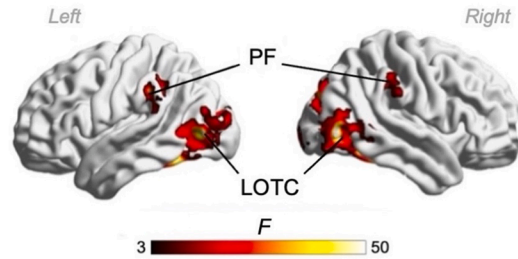
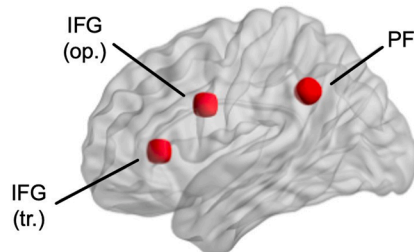
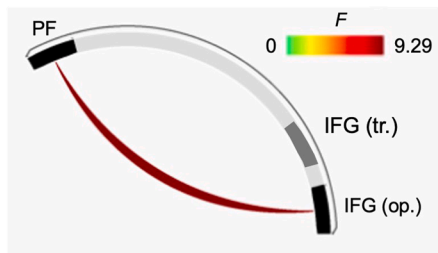


Fig. 5. Brain regions showing (A) a main effect of the factor Complexity (C1, C2 and C3) and (B) a main effect of the factor Tools (Modern and Lithic). Left, left hemisphere; Right, right hemisphere; LOTC, lateral occipital temporal cortex; PF: parietal area F.

A. The ROI seeds



B. Functional Connectivity Modulation by Tools and Complexity



C. Connectivity Values in LMM with Tools and Complexity

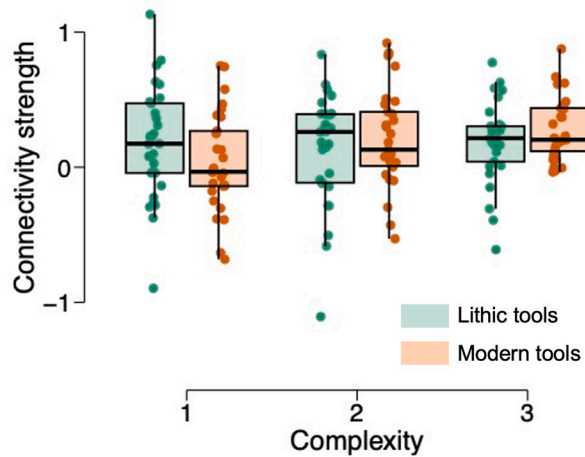


Fig. 6. Results of the ROI-to-ROI functional connectivity analysis. (A) The 3 ROI seeds considered in the ROI-to-ROI analysis. (B) Significant functional connectivity modulation according to Tools and Complexity ($p_{FDR} < 0.05$, two-sided), the color scale represents the F-values associated with these effects. (C) Individual connectivity values entered in a linear mixed model (LMM) with Tools and Complexity as within-subject factors. IFG, inferior frontal gyrus (op., opercular part; tr., triangular part); PF, parietal area F.

psychological, neuroscientific, and archaeological literature. Here we examined whether the left IFG and particularly its pars opercularis could show an increasing activity when participants had to process tool stimuli that increased in terms of embedded constraints. Our predictions were confirmed by the functional connectivity analyses, which revealed an increasing functional connectivity between the left area PF and the pars opercularis of the left IFG as the complexity increased. This increasing functional connectivity was not reported between the left area PF and the pars triangularis of the left IFG. The main conclusion that can be drawn from our results is that the pars opercularis but not the pars

triangularis may be the key region that the left IFG shares with the tool use network. This result confirms the neuroscientific literature on language that has shown that the pars opercularis is more engaged in action-related sentences and syntactic processing whereas the pars triangularis is more involved in semantic processing (Crozier et al., 1999; Rodd et al., 2015; Enge et al., 2020; Zaccarella et al., 2021). Here, the increasing activity of the pars opercularis suggests that this region plays a key role in nesting several physical constraints inside the same object, such as its shape and material, in order to make it suitable for a specific mechanical problem. This is similar to syntactic processing, which can

require nesting within a single world with different constraints, such as plurality and gender. In other words, the pars opercularis could play a nesting role by integrating different constraints to solve a specific problem. Interestingly, this nesting role has also been suggested in the field of mathematics, in which it was shown that the functional connectivity between the left IPL and the left IFG could be modulated by the complexity of calculations (Nakai and Sakai, 2014). This nesting role must not be confounded with a planning role that consists of solving a sequential problem to optimize time and that is commonly associated with a more anterior prefrontal activity. This conclusion must be tempered in two respects. First, we hypothesized an increase activity of the pars opercularis as the complexity increased. However, the whole-brain analyses did not confirm this aspect. Taken together with the functional connectivity results, this suggests that the pars opercularis might always be engaged to monitor the constraints to be embedded, so the change might more concern its connectivity with other brain areas than its activity itself. Future work is needed to confirm this finding. Second, our results on the distinction between the pars opercularis and the pars triangularis are based on literature-defined ROI analyses because of unexpected results obtained on our language tasks. Our results would have been more straightforward and solid if we could have used this language task as a localizer, allowing us to directly link the left IFG activity in syntactic versus semantic processing and our tool task. Future work is also needed to reproduce our findings with an effective language task as a localizer.

Beyond the role of the left IFG in complexity, we obtained an unexpected finding on this aspect as the main effect of complexity was characterized by decreasing bilateral activation in the supramarginal gyrus (SMG) and the angular gyrus (AG). Concerning the SMG, this could have reflected a decreasing involvement of anterior SMG regions such as the left area PF or Pft (Parietal Ft) due to increasing demands on technical reasoning, visuomotor integration, or action representation more generally (Johnson-Frey, 2004; Peeters et al., 2013; Reynaud et al., 2016). This interpretation, which does not make sense because it describes an inverse relationship, is hardly convincing because the activation pattern is more posterior to the aforementioned parietal areas, closer to AG. AG is considered as a key brain region for semantic processing (e.g., Binder and Desai, 2011; Kuhnke et al., 2023). However, it has also been found that AG activity is linked to task complexity, with less AG deactivation for easier conditions (Humphreys and Lambon Ralph, 2017; Humphreys et al., 2021). The results shown in Fig. 5a are consistent with this, demonstrating a decrease in AG activation as complexity increases. The reported negative value could suggest a progressive AG deactivation with increasing complexity. However, this negative value should not be interpreted as evidence of deactivation, as the analysis only tested the effect of complexity. In fact, to confirm the presence of a deactivation, it is necessary to demonstrate that AG is more active in the control condition than in the experimental conditions. We conducted this analysis (see **Supplementary Materials**), which confirmed that AG is indeed more active in the control condition compared to the experimental conditions. In sum, our pattern of results is perfectly consistent with the aforementioned findings, which corroborate the effect of complexity reported in our study. It also supports the idea that AG might be a domain-general region as we reported here for a “non-semantic” task (Humphreys et al., 2021).

4.2. Modern and lithic tools

Although modern and lithic tools can serve similar purposes, such as cutting, their shapes and graspable properties differ significantly. In addition, lithic tools differ from modern tools simply because we are less familiar with them. Although the participants here received a training about lithic tools, we can consider that familiarity remains the key characteristic distinguishing modern from lithic tools. Our findings revealed that both modern and lithic tools elicited the classical tool use network, with the recruitment of parietal, frontal, and temporal regions.

We also found a modulation of this network according to the tool type. This modulation did not concern any pars of the left IFG, which confirms its sensitivity to complexity and not to “unfamiliarity”. Likewise, although AG is not commonly associated with the tool use network, it was not affected by the tool type modulation, confirming its sensitivity to complexity and not to “unfamiliarity”. More relevant to our concerns, we observed a greater recruitment of the SMG for modern than lithic tools. This recruitment targeted brain regions located anteriorly in the SMG such as the left area PF. This is consistent with studies that have shown that the left SMG is more specifically recruited when the tool use task is unfamiliar (Vingerhoets, 2008; Reynaud et al., 2016; Seiffert et al., 2025; Osiurak et al., in press). Taken together, these findings suggest that lithic tools in modern humans could put higher demands on cognitive processes underlying tool use, such as technical reasoning, perhaps for evaluating their mechanical properties relative to the physical constraints. Our results also revealed bilateral activity in the middle temporal gyrus (MTG), with stronger activation for lithic tools. The left MTG, particularly its posterior portion, is well-documented as a key region within the semantic and conceptual network for tool use knowledge (Ramayya et al., 2010; Lausberg et al., 2015). Despite participants’ prior training about lithic tools, the increased activation in the left MTG for those lithic artifacts likely reflects the greater conceptual demands of their unfamiliarity. This heightened activity supports the construction of a contextual representation of tool use, facilitating the cognitive processing of these less familiar objects (Andres et al., 2013). The right MTG, while less frequently discussed, has been identified as critical in storing conceptual knowledge required to associate tools with their corresponding actions (Stout et al., 2015; Putt et al., 2017; S. S. J. 2019). Our findings are also aligned with this view by demonstrating overlapping activity for modern and lithic tools and highlighting the MTG’s role in integrating conceptual representations across diverse tool types.

4.3. Evolutionary implications

The anterior SMG’s unique evolution and absence in non-human primates (Peeters et al., 2009; Orban, 2016) underscore the pivotal role of the parietal lobe in human-specific tool use networks. Its specialization reflects the increasing demands of tool making and use, mirroring the progression of lithic technologies (Stout et al., 2008; Hecht et al., 2023). This region grew in volume during the Paleolithic and underwent increasing functional specialization, as evidenced by fossil endocasts and modern neuroimaging studies (Bruner, 2010; Bruner and Iriki, 2016).

Additionally, the expansion of the frontal lobe (Bruner, 2004; Sherwood et al., 2008), especially its inferior regions, further supports the idea that increasing cognitive demands for tool making and complex communication played a crucial role in shaping the human brain. Modern human brains exhibit a better structural specialization in the left IFG compared to great apes, which may enhance neural connectivity and processing efficiency for language (Shenker et al., 2008). Moreover, the left IFG area shows a unique leftward asymmetry in humans, supporting its role in specialized linguistic functions (Cantalupo and Hopkins, 2001; Sherwood et al., 2003).

Finally, the functional connectivity between the left area PF and the pars opercularis of the left IFG represents a cornerstone of the technical reasoning network, supporting the coordination of physically oriented causal reasoning and possibly symbolic representation. This network underscores the overlap between tool making and linguistic abilities, reinforcing the hypothesis that shared cognitive demands shaped human evolution. This overlap may reflect co-evolutionary processes, where the demands of increasingly complex tool making and symbolic communication mutually shaped the development of this frontoparietal network. This dual role reinforces the idea of the co-evolution of tool use and language, as both rely on shared computational processes for handling complex structures (Higuchi et al., 2009; Stout and Chaminade, 2012).

Previous work has highlighted the importance of a frontoparietal network in acquiring lithic tools making skills by modern humans (Hecht et al., 2015). Beyond its role in technical reasoning, evidence suggests that human frontoparietal networks exhibit a unique organization compared to non-human primates (Mars et al., 2011). These networks do not align with any known resting-state networks in monkeys, suggesting an evolutionary divergence in functional organization. Additionally, these regions are situated in brain areas that underwent the most significant cortical expansion (Van Essen & Dierker, 2007). The specificity of these networks in humans has been linked to higher-order cognitive abilities, including behavioral control, intelligence, procedural and abstract reasoning, as well as tool use and logical inference (Duncan et al., 2000; Dehaene et al., 2003; Frey, 2008; Passingham, 2009). These functions are central to problem-solving, innovation and language, supporting the idea that frontoparietal specialization played a critical role in the evolution of tool-related cognition and communication.

4.4. Limits

One limitation of the present design lies in the difficulty of fully isolating tool-related cognitive processes from other high-level demands such as attention and working memory. Although the control condition was constructed to minimize functional reasoning, we cannot completely rule out the possibility that participants engaged in incidental processing of tool function. In addition, the observed activation pattern was not strictly left-lateralized, diverging from earlier findings in studies using tasks focused on naming or familiar tool use. However, this does not necessarily contradict the existing literature in neuroarchaeology (e.g., Stout et al., 2011). Our findings may thus reflect the cognitive demands of reasoning about tool function, rather than semantic retrieval. Future work should further disentangle these cognitive components by implementing additional control conditions and by systematically manipulating task complexity and functional ambiguity.

5. Conclusion

Neuroarchaeology, integrating fossil evidence, Paleolithic artifacts, and modern neuroimaging, requires a rigorous methodological approach. While modern tools use is well-documented in neuropsychology and neuroscience, neuroarchaeology cannot rely solely on this literature. Assuming that lithic tools engage the same neural circuits as modern tools solely due to their evolutionary precedence is an oversimplification. To address this, our study directly compared modern and lithic tools within the same design, confirming that both engage overlapping brain networks, particularly the IPL/SMG and PF, as well as a functional connectivity with the pars opercularis of the left IFG.

The modern human brain is the product of intricate co-evolutionary processes, where environmental pressures shaped neural development, while the brain's evolving capabilities transformed how our ancestors engaged with their surroundings (Malafouris, 2010, 2013; L., 2019). The technological evolution of humans is often attributed to their tool making abilities and communication skills (Ruck, 2014; Schillinger et al., 2015; Barham and Everett, 2021). Our findings support the hypothesis of an evolutionarily specialized frontoparietal network with the connectivity between the left area PF and the pars opercularis of the left IFG, critical for both tool use and language. Moreover, this network appears to rely on uniquely human brain structures, such as the anterior SMG, which is absent in non-human primates (Peeters et al., 2009; Urban, 2016). This further supports the idea that the specialization of the frontoparietal network played a key role in shaping the cognitive capacities that define *Homo sapiens*.

Code and data availability

The codes and data that support the findings of this study are

available at <https://osf.io/4xbn6/files/osfstorage>.

CRediT authorship contribution statement

Chloé Bryche: Writing – original draft, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Mathieu Lesourd:** Writing – original draft, Software, Formal analysis, Data curation. **Arthur Seye:** Writing – review & editing, Investigation, Conceptualization. **Alexandre Bluet:** Writing – review & editing, Conceptualization. **Natalie Uomini:** Writing – review & editing, Conceptualization. **Yves Rossetti:** Writing – review & editing, Funding acquisition. **Emmanuelle Reynaud:** Writing – review & editing, Supervision, Methodology, Data curation, Conceptualization. **Giovanni Federico:** Writing – review & editing, Conceptualization. **François Osiurak:** Writing – original draft, Supervision, Project administration, Methodology, Funding acquisition, Formal analysis, Conceptualization.

Declaration of competing interest

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

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at [doi:10.1016/j.neuroimage.2025.121404](https://doi.org/10.1016/j.neuroimage.2025.121404).

Data availability

Data will be made available on request.

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