

1 Neural correlates of perceiving and
2 interpreting engraved prehistoric patterns
3 as human production: effect of
4 archaeological expertise

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6 Salagnon M^{1,2,3}, Cremona S^{1,2,3}, Joliot M^{1,2,3}, d'Errico F^{4,5} Mellet E^{1,2,3*},

7
8 ¹ Univ. Bordeaux, GIN, IMN UMR 5293, Bordeaux, France

9 ² CNRS, GIN, IMN UMR 5293, Bordeaux, France

10 ³ CEA, GIN, IMN UMR 5293, Bordeaux, France

11 ⁴ Univ. Bordeaux, PACEA UMR 5199, CNRS, Pessac, France

12 ⁵ SFF Centre for Early Sapiens Behaviour (SapienCE), University of Bergen, Bergen,
13 Norway.

14
15 * Corresponding author
16 E-mail: emmanuel.mellet@u-bordeaux.fr

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20 Expertise, fMRI

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22

23 **Abstract**

24

25 It has been suggested that engraved abstract patterns dating from the Middle and Lower
26 Palaeolithic served as means of representation and communication. Identifying the brain
27 regions involved in visual processing of these engravings can provide insights into their
28 function. In this study, brain activity was measured during perception of the earliest known
29 Palaeolithic engraved patterns and compared to natural patterns mimicking human-made
30 engravings. Participants were asked to categorise marks as being intentionally made by humans
31 or due to natural processes (e.g. erosion, root etching). To simulate the putative familiarity of
32 our ancestors with the marks, the responses of expert archaeologists and control participants
33 were compared, allowing characterisation of the effect of previous knowledge on both
34 behaviour and brain activity in perception of the marks. Besides a set of regions common to
35 both groups and involved in visual analysis and decision-making, the experts exhibited greater
36 activity in the inferior part of the lateral occipital cortex, ventral occipitotemporal cortex, and
37 medial thalamic regions. These results are consistent with those reported in visual expertise
38 studies, and confirm the importance of the integrative visual areas in the perception of the
39 earliest abstract engravings. The attribution of a natural rather than human origin to the marks
40 elicited greater activity in the salience network in both groups, reflecting the uncertainty and
41 ambiguity in the perception of, and decision-making for, natural patterns. The activation of the
42 salience network might also be related to the process at work in the attribution of an intention
43 to the marks. The primary visual area was not specifically involved in the visual processing of
44 engravings, which argued against its central role in the emergence of engraving production.

45

46 **Introduction**

47
48 The cognitive abilities of our prehistoric ancestors and how they evolved have become a crucial
49 area of research in archaeology and anthropology (1–4). Different research strategies are
50 followed to investigate this topic. Past cognition can be inferred by analysing the material
51 culture prehistoric populations have left behind, under the assumption that behavioural patterns
52 reflect cognitive processes. A wide range of past behaviours have been investigated in this
53 perspective, such as subsistence strategies (5,6), stone and bone tool-making (7–15), containers
54 (16), pigments (17–21), tool hafting (22,23), mortuary practices (24,25), ornamental objects
55 (26–28), engraving and painting of cave walls and objects (29,30). More recently, past
56 cognition has become the subject of interdisciplinary research combining archaeological data
57 with methods and concepts from neuroscience (31–33).

58 Neuroarchaeology, as it has been termed, aims to create conceptual frameworks for modelling
59 the evolution of human cognition in light of advances in the neurosciences, and to test such
60 models experimentally based on data collected from modern participants. Research in this
61 domain has investigated the potential co-evolution of tool-making and language by studying
62 the overlap of the brain networks mobilised by these two skills (34–38). The implication of
63 executive functions and working memory in the production of knapped stone tools, involving
64 different levels of cognitive control and neural substrates depending on the complexity of the
65 practised stone tool technology, has also been the subject of studies (34,35,39,40).

66 The emergence of symbolic behaviour has also been investigated recently by neuroarchaeology.
67 Some archaeologists have argued that the earliest graphic manifestations, dating from the
68 Lower and Middle Palaeolithic in Eurasia and the African Middle Stone Age, were conceived
69 and used as signs or symbols, and thus demonstrate abstraction and communication capacities
70 that were not previously attributed to the human populations of those times (41–49). Others
71 contend that early abstract engraving production resulted from low-level visual perceptual

72 phenomena (50–52) and should be interpreted as a “proto-aesthetic” behaviour devoid of
73 semiotic intent. Still others see the production of abstract engravings as resulting from
74 kinaesthetic dynamics of a non-representational sort that allowed hominins to engage and
75 discover the semiotic affordances of mark-making (53), or as decorative, cultural transmitted
76 patterns with no apparent symbolic meaning (54). In a previous study (55), we characterised
77 the neural basis of the visual processing of prehistoric abstract engravings dated between
78 540,000 and 30,000 years before the present, and showed that despite their relatively simple
79 structure, engraving perception engaged the visual cortices of the ventral visual pathway that
80 are involved in the recognition and identification of objects.

81 Consistent with the view of their being representational in nature, our first results showed that
82 the primary visual area was not sensitive to the global organisation of the engravings, and thus
83 did not support the previously suggested hypothesis that this region played a specific and
84 exclusive role in the emergence and perception of the production of early engravings (50,56).
85 The debate stimulated by these findings (57,58) and, in particular, the criticism that inferences
86 drawn from experiences with present-day humans could be inadequate for understanding
87 perceptual processes specific to our prehistoric ancestors, makes it necessary to develop
88 strategies to overcome this potential drawback to the extent possible.

89 Attributing intentional human agency to abstract marks is a prerequisite for using them as a
90 medium for culturally-mediated indexical communication. Our ancestors needed to distinguish
91 purposely made engravings from other accidental or natural marks in order to recognise their
92 communicative potential and use them as means to store, transmit and retrieve meaning. It is
93 reasonable to assume that if abstract engravings were used as signs or symbols by our ancestors,
94 the latter must have shared a knowledge that allowed them to recognise the engravings as the
95 result of a conscious, deliberate, technical action intended to embody meaning in a tangible
96 medium. To simulate this knowledge, we included archaeologist participants who are familiar

97 with or experts in prehistoric engravings. We compared them at both behavioural and brain
98 functional levels to a control group with no such expertise, paired for age, gender, and level of
99 education. The first aim of the present work was to estimate the effect of familiarity and prior
100 knowledge, hereafter referred to as *Expertise*, on the brain regions involved in the perception
101 of abstract engravings and their attribution to human agency. The present study investigated
102 this effect in a “Judgment” task where participants had to assess whether past humans had
103 produced the marks on objects intentionally, or whether the marks resulted from natural
104 processes such as erosion, carnivore gnawing or root etching. Therefore, this study explored
105 whether familiarity modifies the regions involved in the visual processing of engravings,
106 particularly in the primary visual area. The second aim of the study was to assess whether the
107 attribution of the marks to human *versus* non-human agency could be differentiated at the
108 functional brain level, and to what extent such difference could be conditioned by the observer's
109 expertise.

110 **Materials and Methods**

111

112 **Participants**

113 Thirty-one healthy adults with no neurological history were included after providing written
114 informed consent to participate in the study. They were divided into two groups according to
115 their expertise in Palaeolithic archaeology: Controls, without any prior background in the
116 discipline (n = 15, mean age \pm SD: 44 \pm 10 years, range: 30-63 years, six women, none left-
117 handed) and Experts, i.e. scholars actively working in the discipline with knowledge in
118 Palaeolithic art and bone modifications (n = 16, mean age \pm SD: 44.6 \pm 10 years, range: 32-61
119 years, six women, one left-handed). The two groups of participants were matched for age,
120 gender, and education level (PhD, 20 years of schooling after first grade).

121 **Ethics statements**

122 The 'Sud-Ouest outremer III' local Ethics Committee approved the study (N°=2016-A01007-
123 44).

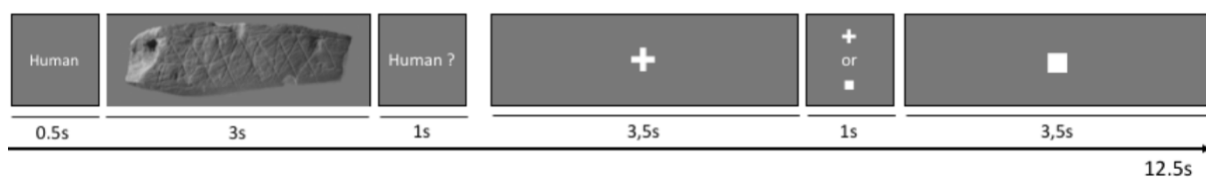
124 **MRI Acquisition**

125 The blood oxygen level-dependent (BOLD) signal was mapped in the 31 volunteers using
126 functional magnetic resonance imaging (fMRI) with a Siemens Prisma 3 Tesla MRI scanner.
127 The structural images were acquired with a high-resolution 3D T1-weighted sequence (TR =
128 2000 ms, TE = 2.03 ms; flip angle = 8°; 192 slices and 1 mm isotropic voxel size). The
129 functional images were acquired with a whole-brain T2*-weighted echo-planar image
130 acquisition (T2*-EPI Multiband x6, sequence parameters: TR = 850 ms; TE = 35 ms; flip angle
131 = 56°; 66 axial slices and 2.4 x 2.4 x 2.4 mm isotropic voxel size). The functional images were
132 acquired in three runs during a single session. The experimental design was programmed using
133 E-prime software (Psychology Software Tools, Pittsburgh, PA, USA). The stimuli were
134 displayed on a 27" screen. The participants viewed the stimuli through the magnet bore's rear
135 via a mirror mounted on the head coil.

136 **Description of the task**

137 Participants performed a judgment task based on the visual presentation of pictures of
138 intentionally human-made and natural marks. The judgment task included two conditions:
139 Attribution ("is the mark intentionally made by a human being?") or Orientation ("is the longest
140 axis of the medium on which the marks are present vertical?"). The Orientation task was a
141 control condition during which participants perceived the same stimuli as in the Attribution
142 condition. The contrast [Attribution minus Orientation] allowed activations that were not
143 specific to human/non-human judgment to be cancelled out. For each stimulus, the type of
144 judgment to be made (i.e. Attribution or Orientation) was displayed during 0.5s, before the
145 stimulus was presented. Then the stimulus was presented for 3s (Fig 1). Participants had to
146 answer "yes" or "no" by clicking on a response box as soon as the stimulus was replaced by the

147 one-second reminder of the instruction ("human?" or "vertical?"). During the baseline, a
148 fixation cross was displayed and a square appeared after a variable delay (3.5s \pm 1s).
149 Participants had to click on the response box as soon as the square appeared (Fig 1). The
150 participants saw a total of 21 different human-made marks and 21 different natural marks
151 divided into three runs lasting 5 min and 57 sec each, presented in a randomized order.
152 Participants thus saw the item twice, once in the Attribution judgement and once in the
153 Orientation judgement.

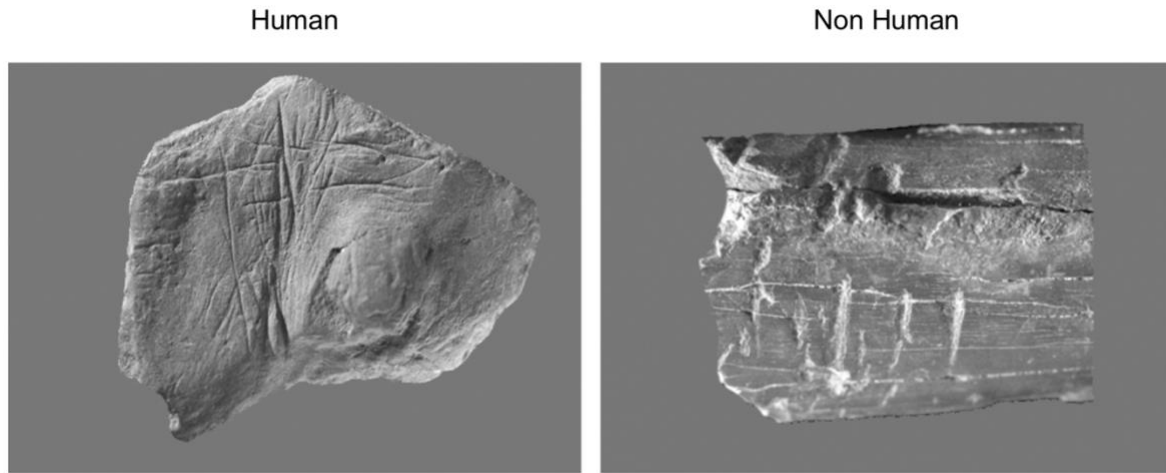


154

155 **Fig1. Organization of a trial in the judgment task.** Participants were presented each item twice (once during
156 the Attribution and once during the Orientation task). The participants were shown 21 different human-made and
157 21 natural marks.

158 **Stimuli**

159 The pictures consisted of photographs of 21 archaeological objects that previous studies had
160 shown to carry engravings of human origin (29,59,60). The engravings are dated between 540
161 ka and 30 ka, come from African and Eurasian sites, and are attributed to *Homo erectus*,
162 Neanderthals and Early Modern Humans. The original pictures were converted into greyscale
163 and put on a grey background (Fig 2, left). The natural marks category included 21 objects in
164 different materials bearing modifications produced by natural modelling of the bone surface
165 (e.g. imprints of nerves and vascular canals), gnawing by carnivores, root etching, erosion, and
166 fossilisation of plants (61). Pictures were converted into greyscale and displayed on a grey
167 background (Fig 2, right).



168

169 **Fig 2. Examples of stimuli used in the judgment task.** Left: human stimulus (engraving from Blombos Cave,
170 Southern Africa, c. 77,000 years old). Right: non-human marks due to carnivore gnawing.

171 **Post fMRI session debriefing**

172 After the fMRI session, the participants were asked to indicate the criteria on which they had
173 based their decision. The criteria were: shape of the marks, criss-cross patterns, presence of
174 parallel marks, repetition of identical marks, depth of the marks, number of marks and the
175 nature of medium of the marks.

176 In addition, the experts were asked whether they had ever seen any of the engravings.

177 **Data analysis**

178 **Preprocessing**

179 Functional volumes were processed using Nipype, which allows the different steps to be
180 chained together (62). The T1-weighted scans of the participants were normalised to a site-
181 specific template, matching the MNI space using the SPM12 'segment' procedure with the
182 default parameters. To correct for subject motion during the fMRI runs, the 192 EPI-BOLD
183 scans were realigned within each run using a rigid-body registration. Then, the EPI-BOLD
184 scans were rigidly registered structurally to the T1-weighted scan. The combination of all the
185 registration matrices allowed warping of the EPI-BOLD functional scans to the standard space

186 with trilinear interpolation. Once in the standard space, a 5 mm FWHM Gaussian filter was
187 applied.

188 **First level analysis**

189 For each subject, global linear modelling (GLM, statistical parametric mapping (SPM 12),
190 <http://www.fil.ion.ucl.ac.uk/spm/>) was used for processing the task-related fMRI data, with
191 effects of interest (tasks) being modelled by boxcar functions corresponding to paradigm
192 timing, convolved with the standard SPM hemodynamic temporal response function. We then
193 computed the effect of interest-related individual contrast maps, corresponding to each
194 experimental condition. Note that 8 regressors of no-interest were included in the GLM
195 analysis: time series for WM, CSF (average time series of voxels belonging to each tissue class),
196 the six motion parameters and the temporal linear trend.

197 **Analysis of behavioural response**

198 To assess whether the observed correct response rates were different from chance, we
199 calculated the 95% confidence interval of a random response rate for 42 trials. Rates outside
200 the 34-66% range were considered significantly different from chance.

201 To estimate the effect of Expertise on correct response rates, we analysed the behavioural
202 responses for Attribution and Orientation separately, since the distribution of the correct
203 response rate for the Orientation condition was not Gaussian. We used a non-parametric
204 Wilcoxon test to evaluate performance differences between Experts and Controls in the
205 Orientation condition.

206 To test whether the effect of Expertise depended on the type of judgment made in the
207 Attribution condition, we estimated the interaction effect between Expertise and Attribution on
208 the correct response rate, using a linear mixed-effect model fitting random effects at the
209 participant level. A two-way interaction term between Expertise and Attribution (and their
210 lower-order terms) was set as the fixed effect predictors, and correct response rate as the

211 dependent variable. The significance of fixed effects was assessed through ANOVA
212 components.

213 **Analysis of debriefing data**

214 To assess the effect of Expertise on the criteria used to discriminate intentional human marks
215 versus non-human ones, we computed a chi-squared test for each of the seven criteria.

216 **Analysis of fMRI data**

217 Group analysis of fMRI data was carried out using JMP®, Version 15. SAS Institute Inc., Cary,
218 NC, 1989-2019. A first step was to select the regions that were activated significantly in the
219 contrast of interest, namely [Attribution *minus* Orientation]. We extracted signal values from
220 the first-level analysis maps of each of the 192 homotopic regions of interest (hROI) of the
221 AICHA functional atlas (63) for each experimental condition. Two hROIs were excluded from
222 the analysis because of a lack of signal in at least 15% of their volume: gyrus parahippocampal-
223 4 (19% non-signal) and Thalamus-8 (46.66% non-signal). The hROIs included in the analysis
224 fulfilled two criteria in each group of participants: 1. Significantly more activated in the
225 [Attribution *minus* baseline (cross fixation)] contrast (univariate t-test $p < 0.05$ uncorrected) to
226 discard deactivated hROIs. 2. Significantly more activated in the [Attribution *minus*
227 Orientation] contrast (univariate t-test $p < 0.05$ FDR corrected) to discard activation not specific
228 to Attribution. hROIs selected for Experts and Controls were grouped to obtain the final list of
229 hROIs included in the subsequent analysis.

230 To assess the effect of Expertise on BOLD activations according to the Attribution response
231 (human or non-human marks), a mixed-effect linear regression model was implemented on the
232 BOLD values of the 64 hROIs activated in the [Attribution *minus* Orientation] contrast. A three-
233 way interaction term between hROIs (64) X Expertise (Experts, Controls) X Attribution
234 (Human, Non-human) and all lower order terms was set as the fixed effect predictors, BOLD

235 values as the dependent variable and random effects were fitted at the participant level. The
236 significance of fixed effects was assessed through ANOVA components.

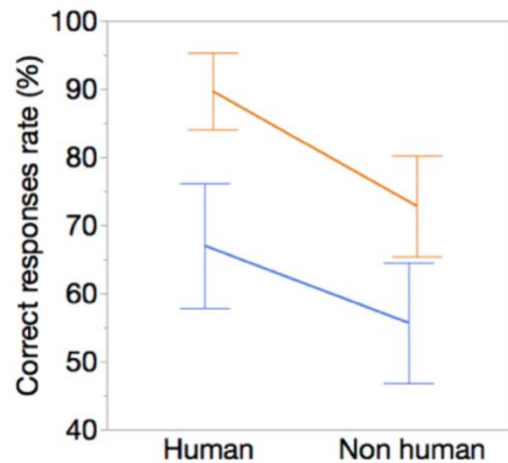
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238 **Results**

239 **Behavioural results**

240 In the Attribution condition, Experts gave 81.3% (mean) \pm 15% (SD) of correct responses (for
241 both human and non-human attribution) while Controls responded correctly to 61.3% (mean)
242 \pm 17% (SD) of the items. The number of correct responses in Orientation did not differ between
243 Experts and Controls (88.1% \pm 14% and 86.7% \pm 17% respectively, $p = 0.96$, Wilcoxon), thus
244 showing, as expected, that the expertise effect was present in Attribution but not in Orientation
245 condition.

246 We did not observe any significant interaction between Expertise and Attribution ($F_{(1,29)}=0.56$,
247 $p=.46$, Fig 3). However, the linear mixed-effect model revealed a main effect of Expertise, with
248 Experts exhibiting better performances than Controls ($F_{(1,29)}=31.3$, $p < 0.0001$), and a main
249 effect of Attribution, as the rate of correct responses was higher for human than non-human
250 judgments ($F_{(1,29)}=14.3$, $p < 0.0007$). Thus, whatever the type of judgment made, experts had a
251 better rate of correct response than controls on average and, whatever the level of expertise, the
252 correct response rate was higher on average for human than non-human judgment.



253

254 **Fig 3. Effects of Expertise and Attribution (human vs non-human marks) on the correct**
255 **response rate.** Orange: Expert, blue: Controls. Error bars represents the confidence interval
256 (95%).

257

258 **Debriefing results**

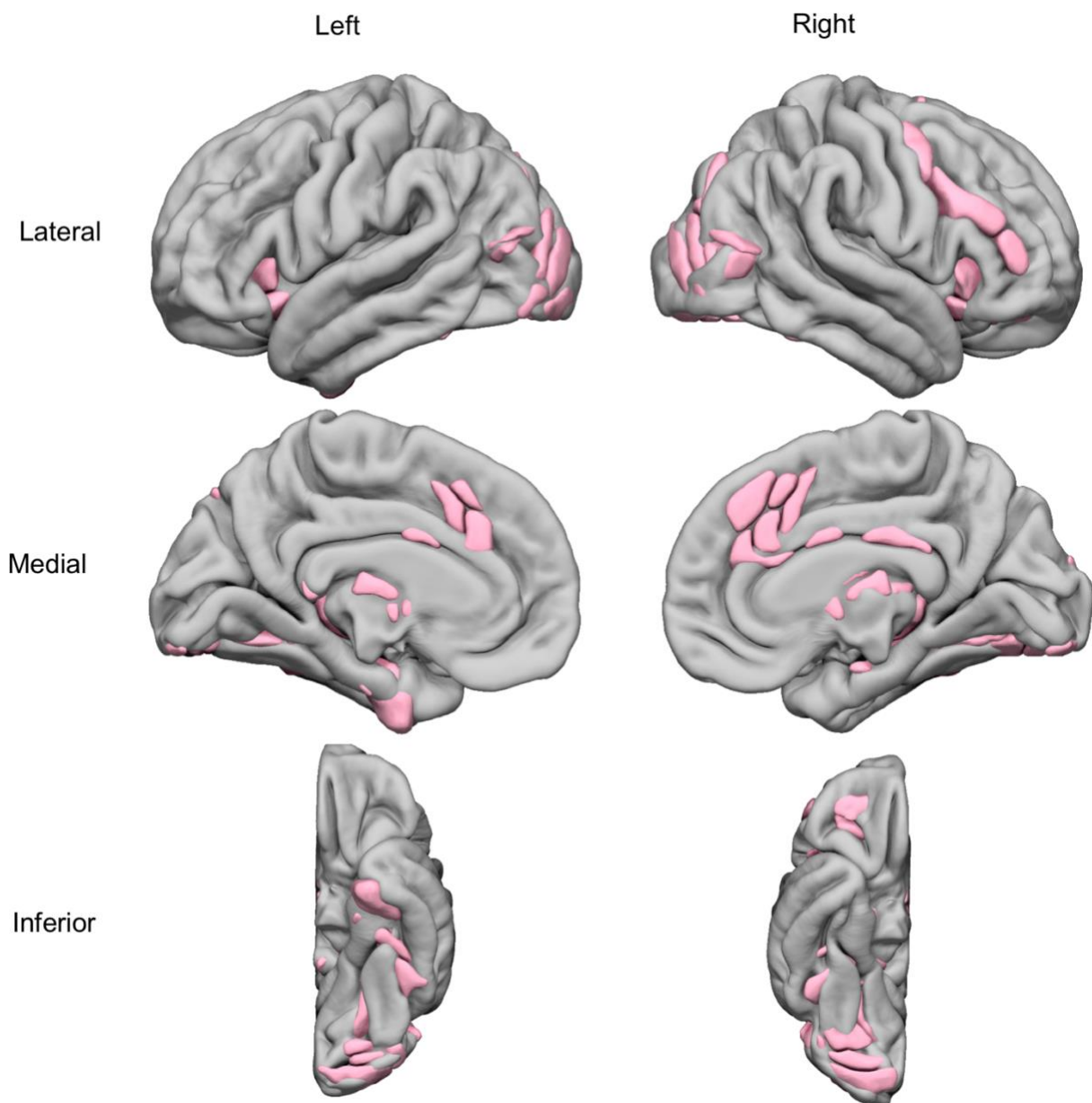
259 The decision criteria reported by the participants for attributing a human agency to abstract
260 marks were repetition of identical marks, shape of the marks, presence of parallel marks, and
261 presence of criss-cross patterns. Some participants also reported paying attention to the support
262 of the marks, the depth of the marks, and the number of marks. Despite a higher rate of correct
263 responses for Experts than Controls, Expertise had no effect on the decision criteria reported
264 by subjects in the debriefing ($p > .05$ for all chi-squared tests).

265 **Neuroimaging results**

266 **Selection of hROIs**

267 The comparison of the Attribution and Orientation conditions evidenced 64 hROIs that were
268 significantly more activated in Attribution than in Orientation (Fig 4, and see S1 Table and S2
269 Table in supporting information). They included the occipito-temporal regions, lateral occipital
270 cortex, anterior insula, parahippocampal cortex, hippocampus, medial frontal cortex, anterior

271 cingulate and at the subcortical level, thalamus and caudate nuclei . The effect of expertise and
272 the type of judgement (*i.e.* human or non-human) were explored within this set of hROIs.



273

274 **Fig 4. Superimposition on an MRI template of the 64 hROIs activated during the [Attribution minus**
275 **Baseline] condition and showing a significant BOLD signal increase in the Attribution minus Orientation**
276 **contrast ($p < 0.05$, FDR corrected).**

277

278 **Effect of Expertise and Attribution on BOLD activations in the 64 selected**
279 **hROIs**

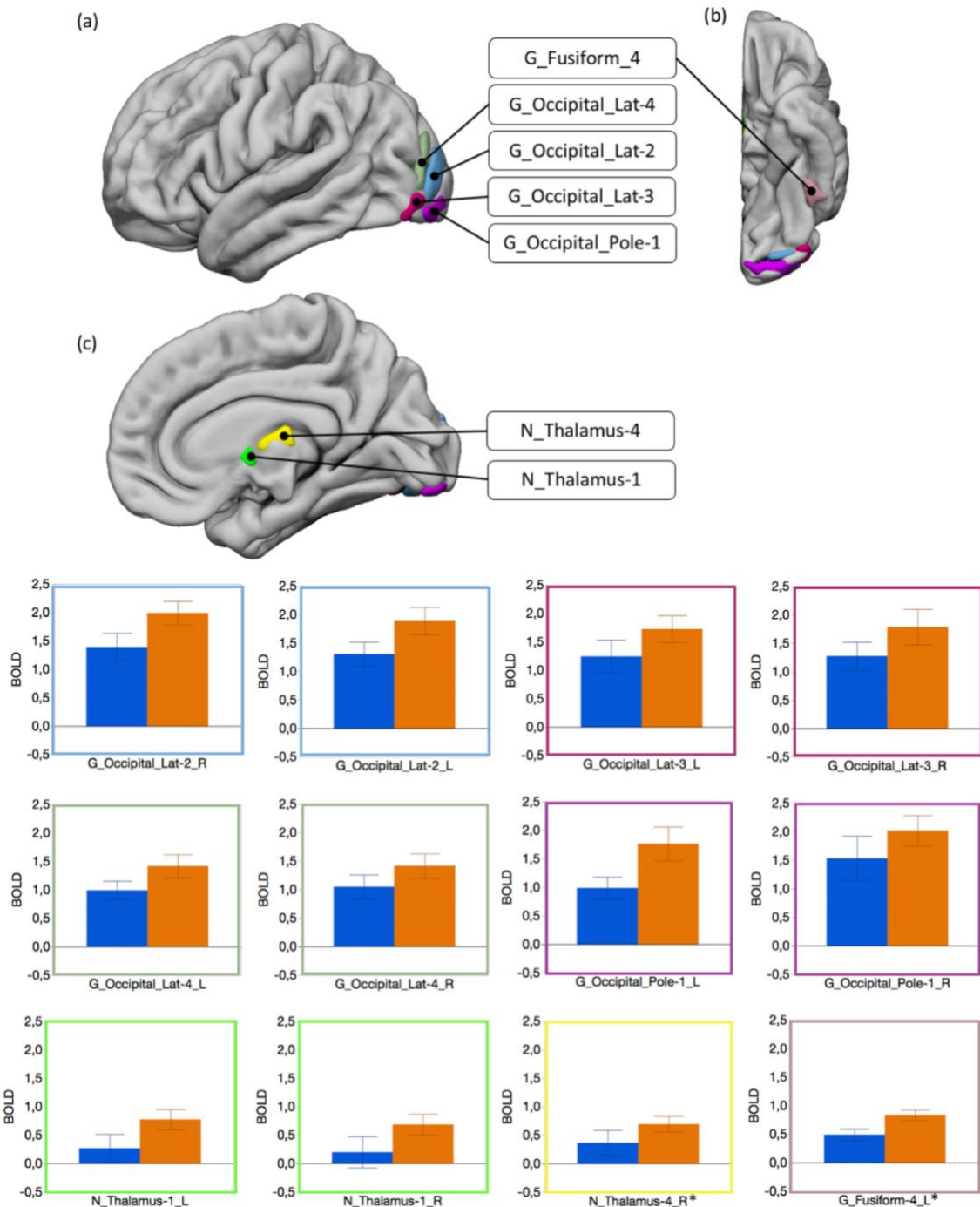
280 To assess whether Expertise interacts with Attribution and hROIs to modify BOLD levels, we

281 set their 3-way interaction as fixed effects in a mixed-effect linear regression model. We

282 observed no interaction between Expertise, Attribution, and hROIs ($F_{(63,1827)} = 0.63$, $p = 0.99$)
283 nor between Expertise and Attribution ($F_{(1,29)} = 0.01$, $p = 0.90$). This suggests that differences in
284 brain region between attribution of human and non-human origin of the marks were the same
285 in Experts and Controls.

286 **Effect of Expertise**

287 We found that regional BOLD response differed between Experts and Controls (Expertise X
288 hROI interaction: $F_{(63,1827)} = 2.14$, $p < .0001$). *Posthoc* analysis revealed that visual areas were
289 more activated by Experts than by Controls (Fig 5). It included regions belonging to the lateral
290 occipital cortex, the occipital pole (all $p < .05$, FDR corrected) and a part of the left fusiform
291 gyrus that nearly reached significance after correction for multiple testing ($p = .02$,
292 uncorrected). In addition, Experts activated the anterior medial thalamus more strongly
293 ($p < .05$, corrected), while a more posterior part of the medial thalamus did not survive
294 correction ($p = .04$, uncorrected). No region was more activated in Controls than in Experts.



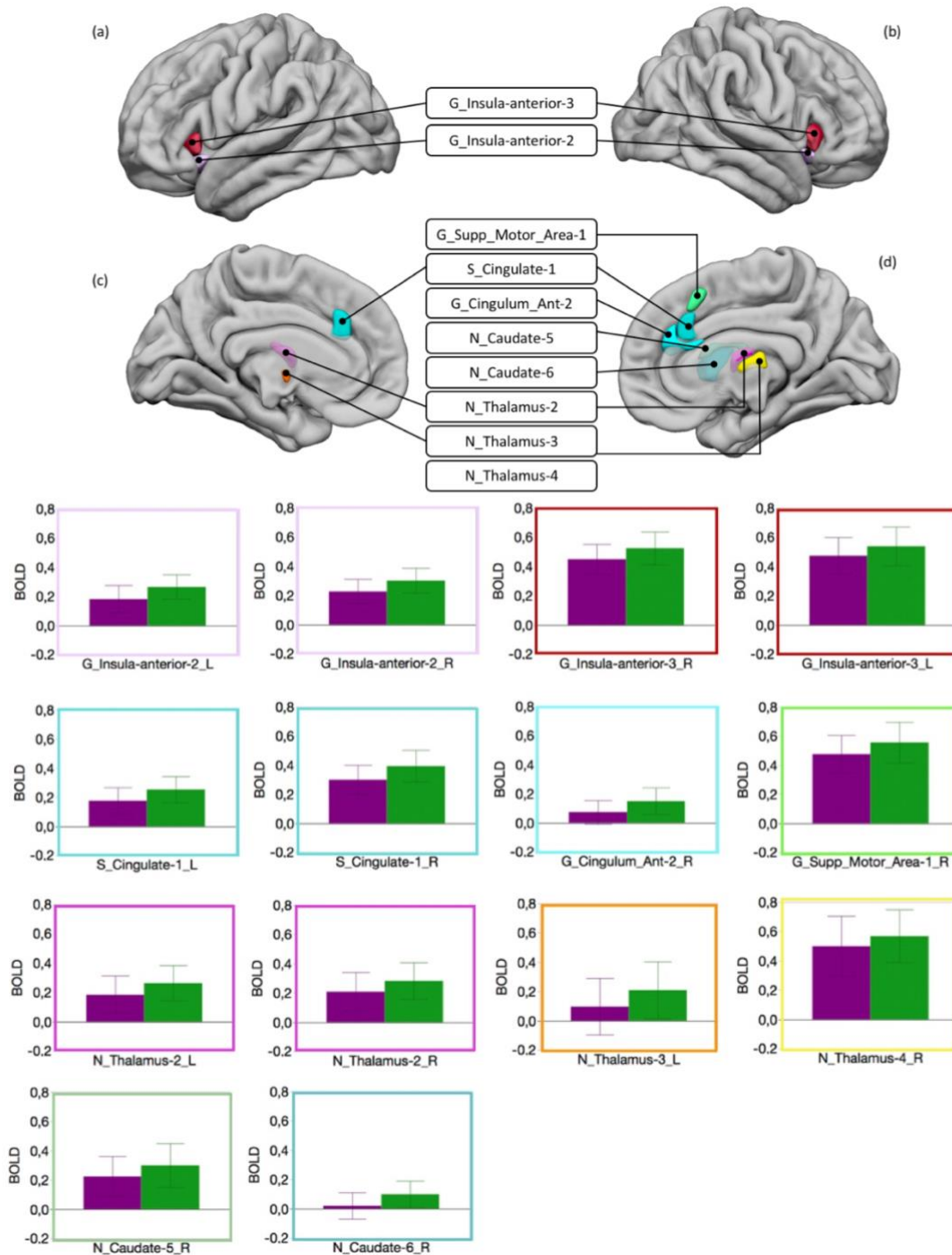
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296 **Fig 5. Experts compared to Controls in the Judgment task.** Top: hROIs that showed a greater activity in Experts
 297 than in Controls. *: G_Fusiform-4_L and N_Thalamus-4_R were significant at uncorrected threshold only ($p_{uncorr}=$
 298 0.015 and $p_{uncorr}= 0.019$, respectively). (a) Lateral view of the left hemisphere. (b) Inferior view of the left
 299 hemisphere. (c) Medial view of the left hemisphere. Bottom: plots of the BOLD values in these regions in Controls
 300 (blue) and Experts (orange). Error bars represents the confidence interval (95%).
 301

302 Effect of Attribution

303 We found that regional BOLD response differed according to the type of judgment expressed
 304 during the Attribution condition (Attribution X hROI interaction: $F_{(63,1827)} = 2.87$, $p < .0001$).

305 Post-hoc analysis revealed that regions belonging to the anterior insula, the anterior cingulate,
 306 the medial thalamus, and the right caudate nucleus were significantly more activated when a
 307 non-human origin was attributed to the marks (Fig 6, all $p < .05$, FDR corrected). No regions
 308 were more activated for the “Human” attribution.



309

310 **Fig 6. Human vs Non-human attribution** Top: hROIs that showed a greater activity for non-human than for
 311 human attribution. (a) Lateral view of the left hemisphere. (b) Lateral view of the right hemisphere. (c)
 312 Medial view of the left hemisphere. (d) Medial view of the right hemisphere. Bottom: plots of the BOLD values in these

313 regions for human attribution (purple) and non-human attribution (green). Error bars represents the confidence
314 interval (95%).

315

316 **Discussion**

317 This study aimed to characterise the effect of expertise in the perception of the earliest
318 Palaeolithic abstract engravings at the behavioural and brain levels, using a judgment task
319 between human-made engravings and surface modifications resulting from natural phenomena.

320 **Effect of expertise**

321 During the Attribution condition of the judgement task, the participants had to decide whether
322 the marks were intentionally human-made or the result of natural processes. This task was
323 contrasted with an Orientation condition in which the same stimuli were used without
324 participants paying attention to the marks on the supports. Although the distinction criteria did
325 not differ between experts and controls, the performances were significantly better for the
326 experts. Note that archaeologists usually rely on much more refined analysis, not limited to a
327 short visual analysis, to discern the human or natural origin of the marks. Nonetheless, the
328 archaeologists confirmed their expertise in judging the natural or human origin of the
329 engravings better than Controls, while they did not differ from them in the Orientation
330 condition. As experts, the performances of archaeologists benefited from a greater ability to
331 focus on the most discriminating elements, thus reducing the complexity of perceptual analysis.
332 In addition, they could connect the perceptual analysis to knowledge stored in long-term
333 memory and gained over many years and even decades. One could argue that these better
334 performances reflected recognition of engravings previously encountered in the literature or
335 their own research rather than an actual process of visual analysis. However, although a
336 majority of experts recognised some of the engravings, only three recognised about ten, while
337 the others recognised less than five. In addition, the experts were also better at identifying traces
338 of natural origin, which supports the role of expertise in determining their higher performances.

339 During Attribution, Experts showed greater activation in the ventral part of the lateral occipital
340 cortex and a strong trend in the left fusiform gyrus (G_Fusiform-4 in the AICHA atlas) in the
341 occipito-temporal cortex (OTC). This result could reflect more discriminating visual analysis,
342 which allowed a correct diagnosis of the origin of the marks. It has already been shown that the
343 visual cortex and particularly OTC are involved in the visual processing of objects pertaining
344 to the domain of expertise of the observer (64,65). For example, in a field that involves long-
345 term acquired knowledge, as in the present study, it has been shown that experienced
346 radiologists exhibit greater activation in OTC than less experienced ones when they detect
347 lesions on chest radiographs (66,67). Most of the studies demonstrating the role of OTC in
348 expertise have reported activation of a part of the fusiform gyrus called FFA (68–72). It has
349 been suggested that this region, which is crucial in face recognition, is more generally
350 specialised in discriminating between stimuli that share common (prototypical) visual features
351 and differences that are essentially accessible to the expert. This region is included in
352 G_Fusiform-6 in the AICHA atlas and was not activated differently in Experts and Controls.
353 Most of the studies that reported more activated FFA in experts relied on tasks favouring
354 holistic processing (as in face recognition, (64)). In our study, participants based their decision
355 on visual details (number of crossings, depth of marks) and were therefore processing the marks
356 analytically rather than holistically. This could explain the lack of an expertise effect in this
357 region, while it was present in adjacent areas.

358 The involvement of the "low level" visual areas was limited to a small region of the occipital
359 pole (Fig 5, light purple blob), which was detected in both groups and more important in Experts
360 than in Controls. Activity in the calcarine sulcus, which includes the primary visual area, did
361 not increase during the attribution task compared to the Orientation task. This lack of activation
362 argues against the hypothesis that low-level perceptual processes in this area are at the origin
363 of the emergence of engravings production, as previously suggested (52,56), even in subjects

364 familiar with Palaeolithic marks. As a matter of fact, the vast majority of activations were in
365 the associative visual cortex, including the OTC. The involvement of the visual cortex in this
366 study illustrates its role in visual expertise. It does not fundamentally alter the conclusions of a
367 previous study that highlighted the role of these regions in the visual analysis of engravings
368 (55). In particular, it confirms that the visual analysis of the earliest abstract engravings engaged
369 integrative visual areas involved in identifying visual percepts.

370 In the present work, Experts showed a greater involvement of the medial thalamus than
371 Controls. The mediodorsal part of the thalamus is known to be involved in familiarity,
372 corresponding to the impression that a percept or percepts of the same category have been
373 experienced previously (73,74). In the present study, the archaeologists did not implement a
374 different strategy from the control participants. Both groups relied on similar criteria to decide
375 whether the engravings were of human or natural origin. The main difference is the long
376 experience of archaeologists with both types of marks. Activation of the mediodorsal thalamus
377 in the experts could reflect familiarity with these types of stimuli.

378 **Attributing a human or non-human origin to the marks**

379 Our results showed that attributing a human or non-human origin to the marks is not equivalent,
380 whether at the behavioural or the neural level. The lack of interaction between the Attribution,
381 Expertise and hROIs indicated that the type of judgment (i.e. human or not human) did not
382 affect BOLD differently in Experts and Controls. This is congruent with the absence of
383 interaction between the attributed origin of the marks and the level of expertise at the
384 behavioural level, indicating that both Experts and Controls made more errors for non-human
385 than human attribution (with the Experts being better than controls in both categories). At the
386 cerebral level, attributing a non-human origin to the marks resulted in greater activation in
387 subcortical regions such as the head of the caudate nucleus and the thalamus and cortical areas
388 including the anterior insula and the anterior cingulate, compared to assigning a human origin.

389 All these regions belong to the so-called salience network (75–77). This plays a fundamental
390 role in detecting and selecting behaviourally relevant stimuli and is thus crucial in the decision-
391 making process (78–80). It is therefore not surprising that it was activated in our attribution
392 task. The question is why it was activated more by the "non-human" choice than by the "human"
393 choice. A meta-analysis showed that the activity in this network increased with uncertainty
394 (81). The rate of correct responses indicated that deciding that a mark was non-human was more
395 uncertain than the opposite choice and might have triggered the greater activation of the
396 salience network. This hypothesis is further supported by the fact that the anterior insula and
397 anterior cingulate cortex would be particularly active during decision-making in a context of
398 strong perceptual ambiguity (82,83).

399 Interestingly, it has recently been shown that the cingulate and insular cortex in the salience
400 network were involved in attributing others' intentions (84). In addition, the anterior insula
401 region is also generally associated with the sense of agency, *i.e.*, the awareness of who performs
402 an action (85). In the present study, the participants discriminated between marks resulting from
403 human intention and those caused by fortuitous natural events. The processes associated with
404 this choice likely contributed to the mobilisation of the cingulate and insular regions, thus
405 suggesting that the salience network could be involved in attributing an origin to the outcome
406 of an action, in addition to its role in attributing an action or intention. Notably, the regions
407 concerned belong to the dorsal part of the salience network, mainly involved in cognition (86).
408 Interestingly, this subnetwork has not been found in the macaque, suggesting that it is engaged
409 in human-specific abilities (87). Distinguishing between human production and natural marks
410 could be part of these functions.

411

412 **Conclusion**

413 In a first study, we showed that the perception of schematic engravings engaged visual
414 associative areas similar to those involved in object recognition (55). This result was compatible
415 with a representational function of the engravings. The present study represents a further step.
416 Whereas the first study was based on a brief presentation of schematised engravings, the
417 experimental protocol of the present study involved a more careful inspection of actual pictures
418 to recognize intentionally-made engravings from non-human marks. In addition, this study
419 allowed the effect of expertise to be characterised, as well as the direct comparison of attributing
420 human or not human origin to abstract marks. The comparison of activations between
421 archaeologists and controls showed that the effect of familiarity mainly concerned visual
422 associative areas, confirming their central role in the visual processing of engravings. The
423 results showed that it was easier to correctly attribute a human than a non-human origin to the
424 marks, whichever the expertise level, but that the nature of the attribution did not bear on visual
425 regions. Since Palaeolithic abstract patterns resulted from human intention, the judgment
426 concerning their attribution involved the salience network, which plays a pivotal role in
427 perceptual decision-making and attribution of intention. The present study indicates that the
428 visual processing of the earliest known engravings involves two categories of brain regions: 1.
429 visual regions and, more specifically, associative visual areas for the processing of their global
430 visual organisation, some of which are sensitive to familiarity, and 2. the salience network,
431 which is necessary for deciding whether the marks result from a human intention. This result
432 confirms that mere and exclusive processing of abstract engravings by the primary visual cortex
433 is unlikely to explain their emergence and pristine perception, which required actions,
434 intentions and the brain areas to infer the communicative potential of visual patterns.

435

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