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## Assigning a social status from face adornments: an fMRI study

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1 Assigning a social status from face  
2 adornments: an fMRI study

3

4

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14

15 **KEYWORDS:** Human evolution, symbols, social cognition, face perception,  
16 Neuroarchaelogy, fMRI

17

18 **Abstract**

19 The human face has been culturally modified for at least 150,000 years using practices like  
20 painting, tattooing and scarification to convey symbolic meanings and individual identity. The  
21 present study used functional magnetic resonance imaging to explore the brain networks  
22 involved in attributing social status from face decorations. Results showed the fusiform gyrus,  
23 orbitofrontal cortex, and salience network were involved in social encoding, categorization,  
24 and evaluation. The hippocampus and parahippocampus were activated due to the memory  
25 and associative skills required for the task, while the inferior frontal gyrus likely interpreted  
26 face ornaments as symbols. Resting-state functional connectivity analysis clarified the  
27 interaction between these regions. The study highlights the importance of these neural  
28 interactions in the symbolic interpretation of social markers on the human face, which were  
29 likely active in early Homo species and intensified with Homo sapiens populations as more  
30 complex technologies were developed to culturalize the human face.

31

32

33

## 34 **1. Introduction**

35 The use of technologies to change the appearance of our bodies to communicate information  
36 about our identity and social role dates back hundreds of thousands of years. Body painting,  
37 tattooing, scarification, wearing of ornaments, mutilations, hairstyles, and clothing are  
38 amongst the best-known practices for performing these functions in traditional societies <sup>1-5</sup>.  
39 Personal ornaments, in particular, play a crucial role in communicating ethnic affiliation,  
40 reinforcing the sense of belonging to the group and its cohesion, establishing boundaries with  
41 neighboring groups, and conveying information on linguistic, ideological, and religious  
42 membership <sup>6-14</sup>. Ornaments can also provide information about social status, gender, marital  
43 situation, and the number of children the wearer has had. Special ornaments and body paints  
44 may be put on at rites of passage occurring at the individual birth, during initiation  
45 ceremonies, marriage, healing, or death <sup>15-19</sup>.

46 The earliest use of red ochre goes back to 500 ka in Africa <sup>20-23</sup>, 380 ka in Europe  
47 <sup>22,24,25</sup>, and 73 ka in Asia <sup>22,26,27</sup>. Dapschaskas and colleagues (2022) identified three phases  
48 of ochre use in the African Middle Stone Age: an initial phase from 500 ka to 330 ka, an  
49 "emergent" phase from 330 ka to 160 ka, and a "habitual" phase from 160 ka to 40 ka. The  
50 latter phase, when a third of archaeological sites contain ochre, is interpreted by these authors  
51 as the manifestation of intensifying ritual activity in early populations of *Homo sapiens*. This  
52 view is consistent with the results of studies indicating that in this last and the previous phase,  
53 certain types of mineral pigments were transported over long distances <sup>20,28,29</sup>, that certain  
54 shades of red were particularly sought after <sup>30-32</sup>, that ochre was modified by heating to  
55 change its color <sup>33,34</sup> but see <sup>35</sup>, and that in some cases very small quantities of pigments were  
56 produced <sup>36</sup>, a behavior more consistent with a symbolic than a utilitarian function.

57 The wearing of personal ornaments, many of which are deliberately covered with  
58 ochre, is attested since at least 142 ka in North Africa, 80 ka in Southern Africa, and 120 ka in  
59 the Near East <sup>37-45</sup>. Because the understanding by others of the meaning attached to ornaments  
60 and body paints presupposes the existence of shared codes, archaeological objects which have  
61 fulfilled these functions are often considered reliable evidence for the emergence of language  
62 and symbolic material cultures in our genus <sup>40,41,46-49</sup>. In this regard, wearing body  
63 adornments can be considered an archaeological indicator of modern social cognition.

64 Although body symbols played a key role in all human societies and appeared very  
65 early in human history, the cerebral regions mobilized by their perception and interpretation

66 remain unknown. Numerous studies have focused on the brain substrates of the emotional  
67 aspects of social cognition and perspective-taking (Theory of Mind). They have emphasized  
68 the role of the medial prefrontal cortex, the temporoparietal junction, and the temporal poles  
69 <sup>50,51</sup>. However, one study showed that social status recognition was minimally disrupted  
70 following ventromedial lesions, suggesting that the network involved in this function would  
71 be distinct from that dealing with the emotional aspects of social cognition <sup>52</sup>. Neuroimaging  
72 studies have confirmed that the perception of social hierarchies relies on the intraparietal  
73 sulcus, the dorsolateral and orbital frontal cortex, and the lateral occipital and  
74 occipitotemporal cortex <sup>53-56</sup>. However, the identification of social markers does not  
75 necessarily imply a ranking.

76       Body ornaments and facial paintings may convey information on social roles disconnected  
77 from a social hierarchy. Although body paintings and the wearing of beads to express social  
78 roles are attested in the earliest *Homo sapiens* and probably in Neanderthals <sup>57-59</sup>, very little is  
79 known about the brain networks involved in processing such information, the possible  
80 processes that led to a complexification of these behaviors, as well as their timeline. In the  
81 present study, participants were asked to assign social roles or statuses to faces adorned with  
82 paintings, beads, or both. At the same time, their brain activity was monitored using  
83 functional magnetic resonance imaging (fMRI). Participants were given no guidance on the  
84 meaning of the face decorations and had to create their arbitrary social code. The attribution  
85 of a social status mobilizes implicit and explicit processes. Implicit processes are rapid,  
86 require little cognitive effort, and can occur without awareness. Explicit processes are  
87 cognitively demanding, slow, and deliberative <sup>60</sup>. To isolate explicit processes, we included,  
88 using the same stimuli, a perceptual task (1-back) that does not explicitly require a social role  
89 attribution. Brain activity during this task was compared to that performed during explicit  
90 social status attributions. In addition, at rest, the functional connectivity of the brain regions  
91 involved was analyzed to provide information on the interaction of the brain areas implicated  
92 in the social status attribution task. Our results identify, for the first time, the brain networks  
93 engaged in attributing social status from different arrangements of paintings and ornaments on  
94 the human face, the way they work in synergy, and provide sound bases on which build an  
95 evolutionary scenario for the gradual integration of these brain areas during the evolution of  
96 our genus.

97

98 **2. Materials and methods**

99 **2.1. Ethics statements**

100 The 'Nord-Ouest III' local Ethics Committee approved the study on 10/14/2021 (N° IDRCB:  
101 2021-A01817-34). All the participants signed informed consent before the MRI acquisition.

102

103 **2.2. Participants**

104 Thirty-five healthy adults (age range 18–29 years, mean age  $22 \pm 2$  years (SD), 18 women,  
105 four left-handed) with no neurological history were included. One participant was excluded  
106 from the analysis because of a brain abnormality discovered during MRI acquisition.

107

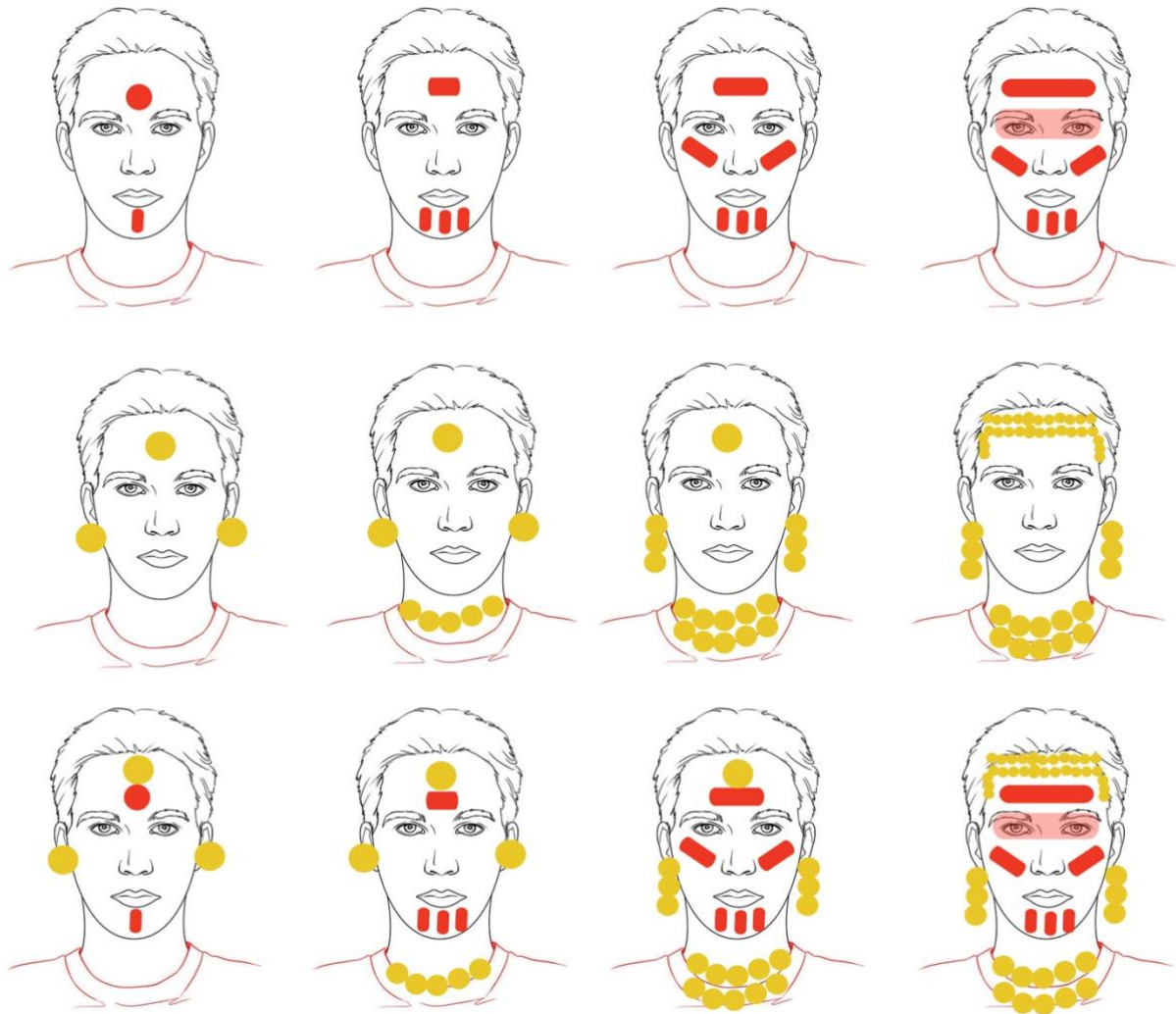
108 **2.3. Experimental design**

109 The functional acquisition was organized in a single session consisting of six runs during  
110 which participants had to perform a selection task (first three runs), then a 1-back task (last  
111 three runs). After receiving instructions for these tasks, participants completed a short training  
112 run outside the MRI.

113

114 **2.3.1. Stimuli**

115 The set of stimuli included pictures of faces (up to below the shoulders) of 34 unknown  
116 people in the same range of age (17 women, 17 men, around 30 years old) wearing ornaments  
117 and adopting a neutral expression. Each face was ornamented with either spherical wooden  
118 beads, red paintings, or a combination of both (Figure 1). Ornaments included earrings with  
119 one or three beads, necklaces with one or two chains of beads, a diadem consisting of a chain  
120 of beads, and a single large spherical bead in the middle of the forehead. Red paintings  
121 included one or three vertical lines on the chin; a dot or a horizontal line on the forehead;  
122 oblique lines on the cheeks; and a large horizontal band including the eyes. Associations of  
123 paintings and beads were designed to make both types of ornamentation gradually more  
124 invasive on the face. In all, twelve types of facial ornamentation have been designed and  
125 implemented.



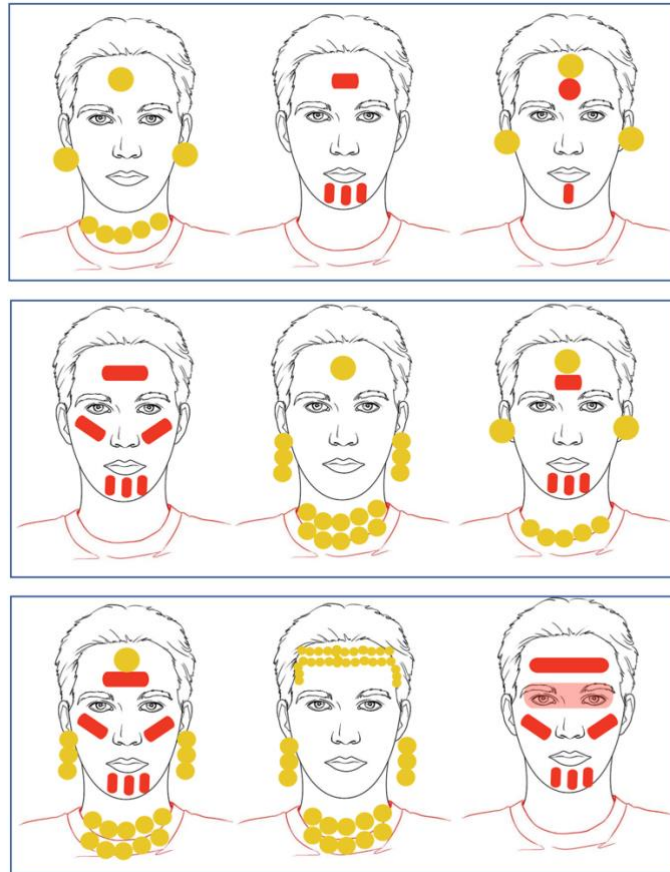
126  
127

128 Figure 1. Face ornamentations used in the tasks. Top row: paint only. The middle row: beadworks only. Bottom  
129 row: a combination of paint and beadworks.

### 130 **2.3.2. Selection task (event-related paradigm)**

131 These three runs followed a slow event-related design, i.e., the change in the BOLD signal  
132 was collected for each stimulus presentation, and the time between each presentation allowed  
133 the signal to return to its baseline level. The order of presentation was randomized. The  
134 stimuli corresponded to a triplet of photos of three different persons of the same gender (male  
135 or female), one wearing ornaments, one with paintings, and one with both (Figure 2). Within  
136 a triplet, the richness of the ornaments was comparable between the pictures to avoid biases in  
137 the choice. There were three levels of richness between the triplets (Figure 2).

138



139  
 140 Figure 2. Drawn version of some triplets of stimuli used in the selection task. Each triplet was composed of  
 141 individuals of the same sex (male or female). The three ranks correspond to three levels of richness. Note that in  
 142 the study, photographs of real people with adorned face were presented but could not be displayed here because  
 143 of their identifying nature.

144

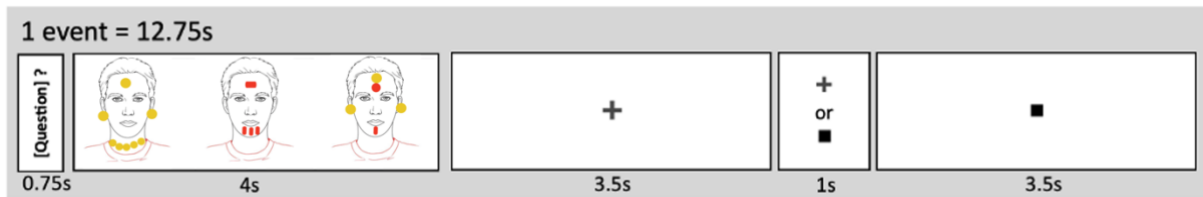
145 The selection task was implemented as follows (Figure 3): a question was displayed  
 146 during 0.75 s. The question could concern either the displayed persons' social role (Social  
 147 status condition) or the type of ornamentation they displayed (Ornament check condition).  
 148 Then, a new triplet of pictures was shown for 4 s. The participant had to choose, by pressing  
 149 the corresponding button of a response box as soon as they made their decision, the person  
 150 who best fitted the proposed social status, e.g., "Shaman" (Social status condition) or the  
 151 person who corresponded to the ornament type proposition, e.g., "Painted cheeks" (Ornament  
 152 check condition). Each question was asked twice for each gender. The list of questions is  
 153 displayed in Table 1.

154 The Ornament check condition was designed as a control condition, bearing the same  
 155 pictures as the social status condition. It required attention to the ornaments without  
 156 implementing social cognition processes. Then, a fixation cross was displayed, and a square  
 157 appeared after a variable delay ( $3.5 \text{ s} \pm 1 \text{ s}$ ). Participants had to click the "1" button on the



158 response box when the square appeared. This constituted the baseline, allowing the BOLD  
 159 signal to return to its baseline level between events. Each event lasted 12.75 s.

160



161

162 Figure 3. Organization of one event of the selection task.

163 Table 1. Questions in the social status and ornament check conditions. The wording of the questions was  
 164 gendered according to the stimulus.

Questions	Social status attribution	Ornament (control)
1	Chief?	Painted eyes?
2	Healer?	Double necklace?
3	Warrior?	Diadem?
4	Hunter / Huntress?	Painted cheeks?
5	Shaman?	Painted circle?
6	Musician?	No beads?
7	Storyteller?	No necklace?
8	Married?	No earrings?
9	Mother / Father?	No paint?
10	Scout?	No lines?

165 Over the three runs, participants saw 80 stimuli, 40 in the social status condition and 40 in the  
 166 ornament check condition. Each run lasted 5 min and 51 s each and included 27 events  
 167 (except run C, which included one less event) for a total duration of 5 min 38 s). Stimuli were  
 168 presented in random order within each run. Immediately after the MRI acquisition, the  
 169 experimenter asked the participant the criteria on which they based their social role attribution  
 170 in the status condition.

171

### 172 2.3.3. 1-back task (block design)

173 In the 1-back task, participants viewed a succession of ornamented faces (displayed for 1 s  
 174 each, with an interstimulus interval of 983 ms). The participants had to report the repetition of  
 175 two faces (Face condition) or two types of ornamentation (Ornament condition, including  
 176 three modalities: paintings, beads, or both simultaneously) by pressing the "1" button on the  
 177 response box. This repetition criterion was displayed during 750 ms at the beginning of each  
 178 block. Fifteen stimuli belonging to the same category of ornamentation were presented within  
 179 the same block (i.e., within a block, there were no images belonging to different categories).

180 There were three repetitions per block. Each of the three runs lasted 4 min and 15 s and  
181 included six experimental blocks of 30.6 s interspersed with seven fixation blocks of 10.2 s.  
182 Each run had four blocks of ornament condition and two blocks of face condition. The  
183 presentation order of the 1-back runs was randomized.

184

## 185 **2.4. MRI acquisition**

186 Neuroimaging data acquisition was performed using a Siemens Prisma 3 Tesla MRI scanner.  
187 Structural images were acquired using a high-resolution T1-weighted 3D sequence (TR =  
188 2000 ms, TE = 2.03 ms; flip angle = 8°; 192 slices and isotropic voxel volume of 1 mm<sup>3</sup>).  
189 Functional images were obtained using a whole-brain T2\*-weighted echo planar image  
190 acquisition (T2\*-EPI Multiband x6, sequence parameters: TR = 850 ms; TE = 35 ms; flip  
191 angle = 56°; 66 axial slices and isotropic voxel size of 2.4 mm<sup>3</sup>). The first sequence lasted 8  
192 min and recorded participants' brain activity during resting state (i.e., when they let their  
193 thoughts flow freely, without having a task to perform or falling asleep). This acquisition was  
194 used to perform a resting-state functional connectivity analysis. Then, functional images were  
195 acquired when the participants performed tasks based on stimuli perception. This was done  
196 during six runs (three for each task: selection and 1-back). The presentation of the experiment  
197 was programmed in E-prime software 3.0 (Psychology Software Tools, Pittsburgh, PA, USA).  
198 The stimuli were displayed on a 27" screen. Participants saw the stimuli through the back of  
199 the magnet tunnel via a mirror mounted on the head antenna.

200

## 201 **2.5. Data analysis**

### 202 **2.5.1. Behavioral analysis**

203 For the selection task, we evaluated the effects of condition (Social status or Ornament  
204 check), participant gender, and stimulus gender on reaction time using a linear mixed-effects  
205 model, adjusting for random effects at the participant level. A three-factor interaction term  
206 between condition, participant gender, and stimulus gender (and their lower-order terms) was  
207 defined as fixed-effect predictors and reaction time as the dependent variable. The  
208 significance of fixed effects was assessed through ANOVA components.

209

### 210 **2.5.2. Functional neuroimaging analysis**

211 T1-weighted scans were normalized via a specific template (T1-80TVS) corresponding to the  
212 MNI space using SPM12. The 192 EPI-BOLD scans were realigned in each run using a rigid

213 transformation to correct the participant's motion during the fMRI sessions. Then, the EPI-  
214 BOLD scans were rigidly registered structurally to the T1-weighted scan. All registration  
215 matrices were combined to warp the EPI-BOLD functional scans to standard space with  
216 trilinear interpolation. Once in standard space, a 5-mm-wavelength Gaussian filter was  
217 applied.

218 In the first level analysis, a generalized linear model (GLM, statistical parametric  
219 mapping (SPM 12), <http://www.fil.ion.ucl.ac.uk/spm/>) was performed for each participant to  
220 process the task-related fMRI data, with the effects of interest (tasks) modeled by boxcar  
221 functions corresponding to events or blocks, convolved with the standard hemodynamic SPM  
222 temporal response function. We then calculated the effect of individual contrast maps  
223 corresponding to each experimental condition. Note that eight non-interest regressors were  
224 included in the GLM analysis: time series for white matter, CSF (average time series of  
225 voxels belonging to each tissue class), the six motion parameters, and linear temporal drift.

226 Group analysis (second-level analysis) of fMRI data was conducted using JMP®  
227 software, version 15. SAS Institute Inc, Cary, NC, 1989-2019. The first step was to select the  
228 brain regions activated in the contrasts of interest, namely [Social status minus Ornament  
229 check] in the selection task and [Ornament minus Face] in the 1-back task. We extracted  
230 signal values from the [Social status minus Ornament check] contrast from each brain region  
231 of each participant (hROI, homotopic region of interest) in the AICHA atlas <sup>61</sup>. The MNI  
232 coordinates of the center of mass of each activated hROIs are given in the supplementary  
233 material section. The hROIs included in the analysis fulfilled the following criteria:  
234 significantly activated in the [Social status minus Ornament check] contrast (univariate t-test  
235  $p < 0.05$  FDR corrected); and significantly activated in the [Social status minus baseline]  
236 contrast (univariate t-test,  $p < 0.1$  uncorrected) to eliminate deactivated hROIs. 32 regions  
237 whose BOLD signal occupancy was less than 80% (susceptibility artifacts) were excluded  
238 from the analysis. The hROIs excluded are listed in the supplementary material.

239 This procedure led to 95 hROIs being more activated in the social status condition than  
240 in the ornament check condition. The same method was applied to the [Ornament minus Face]  
241 contrast and [Ornament minus baseline] contrast leading to 81 activated hROIS for the 1-back  
242 task. In addition, we applied a univariate t-test (FDR corrected,  $p < 0.05$ ) to compare the  
243 BOLD values in the 95 hROIs activated in the [Social status minus Ornament check] contrast  
244 to those 81 hROIs elicited by the [Ornament minus Face] contrast of the 1-back task. This  
245 allowed for refining the specificity of the regions involved in the social status attribution and

246 its explicit components. Thirty-seven hROIs were more activated in the [Social status minus  
247 Ornament check] contrast than in the [Ornament minus Face] contrast.

248

### 249 **2.5.3. Resting-state analysis**

250 The task-based functional analysis was complemented with a resting-state functional  
251 connectivity analysis using the CONN v 20.b toolbox software <sup>62</sup>, which runs under  
252 MATLAB 2021a.

253 Functional imaging data were pre-processed using the CONN default pre-processing  
254 pipeline for volume-based analyses. The steps for functional data comprise realignment and  
255 unwarping for subject motion estimation and correction (12 parameters). Next, centering to  
256 (0,0,0) coordinates and ART-based outlier detection identification was applied. Segmentation  
257 and normalization to MNI space were applied next. Structural data were translated to (0,0,0)  
258 center coordinates, segmented (gray/white/CSF), and normalized to MNI space. In the  
259 denoising step, we applied band-pass filtering (0.01–0.1 Hz) after regression of realignment  
260 parameters (12), white and gray matter, and CSF confounds. Then, we applied linear  
261 detrending and despiking after regression. For the ROI to ROI functional connectivity  
262 analyses, we used AICHA atlas <sup>61</sup>. We considered the 95 hROIs activated in the [Status minus  
263 Ornament] contrast. For group-level results, we calculated ROI-to-ROI connectivity  
264 correlations, threshold with a unilateral t-test, and FDR-corrected  $p < 0.05$ .

265

## 266 **3. Results**

### 267 **3.1. Behavioral results**

268 Participants responded faster in the ornament check condition (mean response time  $\pm$  SD: 1.3s  
269  $\pm$  0.5s) than in the social status condition (mean response time  $\pm$  SD: 2s  $\pm$  0.8s):  $F_{(1,32)} = 227.8$   
270  $p < 0.0001$ . Participant gender and stimulus gender had no significant effects (either main or  
271 interactions).

272

### 273 **3.2. Post-MRI debriefing of the selection task**

274 Twenty-two participants reported that they considered ornamentation a more important  
275 criterion than phenotype in assigning a social role/status. A few reported they sometimes paid  
276 attention to facial features, for example, in cases of indecision or for specific roles such as  
277 father/mother. Eleven participants reported paying more attention to facial characteristics than  
278 to ornamentation. Two participants stated that the most important criterion for them (facial

279 features or ornamentation) varied according to the questions. All participants reported that  
280 they never answered randomly, except in rare exceptions. Participants generally reported  
281 having an attribution strategy in place that they maintained throughout the experiment. For  
282 example, some participants associated the absence of beads with a mobile role, such as scout  
283 or hunter. For the same role, there was not necessarily a consensus among participants. For  
284 example, some participants attributed warrior status to faces wearing only beads, while others  
285 attributed this status to faces bearing only paintings.

286

### 287 **3.3. Neuroimaging results**

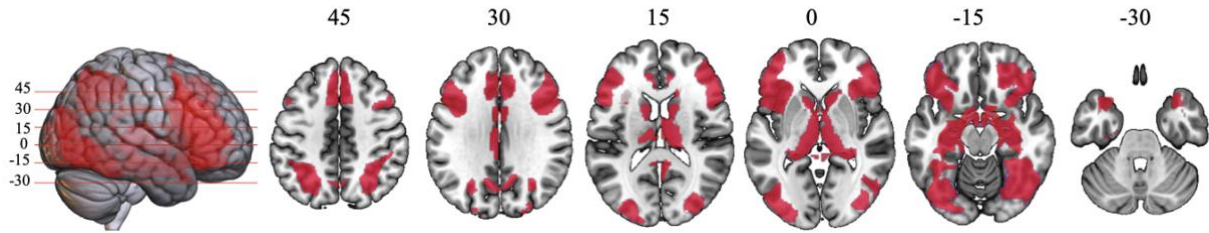
#### 288 **3.3.1. Social status minus Ornament check (event-related paradigm)**

289 The [Social status minus Ornament check] contrast revealed a set of 95 cortical and  
290 subcortical regions that were more activated when participants assigned social status to  
291 adorned faces than when they assessed the type of ornamentation (  
292 Table 2, Figure 4).

293 In the occipital lobe, these regions included the lateral occipital cortex and the fusiform gyrus  
294 (including the Fusiform Face Area, FFA). We used the Neurosynth platform<sup>63</sup> to synthesize  
295 the activations reported in the literature during face perception and ensure their consistency  
296 with our results. We conducted a meta-analysis including 125 studies that contained the term  
297 "neutral face" in their abstracts, i.e., pictures of faces adopting a neutral expression. It  
298 evidenced the involvement of a right fusiform region (MNI coordinates of the activation peak:  
299 38, -42, -16). This matched the location of the G\_Fusiform-4-R in our AICHA atlas (MNI  
300 coordinates of the center of mass: 44, -46, -18). The FFA occupied a large portion of this  
301 functional region of the AICHA atlas.

302 The activations extended to the parahippocampal gyrus on the medial side of the  
303 temporal lobe. In the parietal lobe, the intraparietal sulcus was activated bilaterally. In the  
304 frontal lobe, activations included the middle and inferior frontal gyri on the lateral side and  
305 the anterior part of the supplementary motor area medially. Activations also concerned  
306 several paralimbic and limbic cortex regions, such as the anterior insula, the anterior  
307 cingulate, the posterior cingulate and adjacent precuneus, the orbitofrontal cortex, the  
308 temporal poles, and the hippocampus. The subcortical structures, the head of the caudate  
309 nucleus, and the thalamus, especially in its mediodorsal part, were also involved.

310



311  
 312 Figure 4. Activated regions in [Social status minus Ornament check] contrast superimposed on an MRI template.  
 313 Numbers indicate the z value of the axial slice in MNI space.

### 314 3.3.2. Ornament minus Face (1-back paradigm)

315 The [Ornament minus Face] contrast revealed a set of 81 cortical and subcortical regions,  
 316 which were more activated when participants checked the repetition of ornamentation than  
 317 when they looked for the repetition of faces. These regions were mostly located in the lateral  
 318 and inferior occipital cortices and the fusiform gyrus, extending to the inferior temporal  
 319 gyrus. Participants also activated the intraparietal sulcus, the anterior insula, and some frontal  
 320 regions, such as the superior frontal sulcus, inferior frontal sulcus, the supplementary area,  
 321 and the middle frontal gyrus.

322 Among these regions, 37 hROIs were significantly less activated in the [Ornament  
 323 minus Face] contrast than in the [Social status minus Ornament check] contrast (Table 2).  
 324

325 Table 2. Mean, standard deviation, and p-value of the activated regions in the [Social status minus Ornament  
 326 check] contrast.

hROI Social status - Ornament check (* Specific to Social status – Ornament check, i.e., more or not activated in Ornament block – faces)	MNI coordinates of the center of mass	Mean (BOLD)	Standard deviation (BOLD)	p (FDR corrected)
<b>G_Cingulum_Ant-2-L*</b>	-7 34 22	0.12	0.16	0.0005
G_Cingulum_Ant-2-R	7 33 23	0.08	0.16	0.0173
G_Cingulum_Mid-2-L	-4 3 30	0.15	0.16	<.0001
G_Cingulum_Mid-2-R	4 4 30	0.11	0.18	0.0045
<b>S_Cingulate-1-L*</b>	-7 27 30	0.23	0.20	<.0001
S_Cingulate-1-R	7 27 31	0.20	0.19	<.0001
S_Cingulate-2-L	-7 16 41	0.22	0.22	<.0001
S_Cingulate-2-R	8 14 46	0.14	0.20	0.0011
G_Cingulum_Post-1-L	-4 -26 29	0.12	0.22	0.0072
G_Cingulum_Post-2-L	-4 -39 27	0.11	0.23	0.0121
G_Cingulum_Post-3-L	-5 -43 10	0.13	0.24	0.0071
G_Cingulum_Post-3-R	6 -42 10	0.10	0.22	0.0253
<b>G_Frontal_Inf_Orb-1-L*</b>	-42 31 -17	0.21	0.22	<.0001
<b>G_Frontal_Inf_Orb-1-R*</b>	44 33 -14	0.13	0.16	0.0001
<b>G_Frontal_Mid_Orb-2-L*</b>	-41 49 -5	0.23	0.30	0.0005
S_Orbital-1-R	25 41 -15	0.07	0.11	0.0023
<b>S_Orbital-2-L*</b>	-31 34 -13	0.26	0.21	<.0001
<b>S_Orbital-2-R*</b>	29 34 -13	0.18	0.17	<.0001

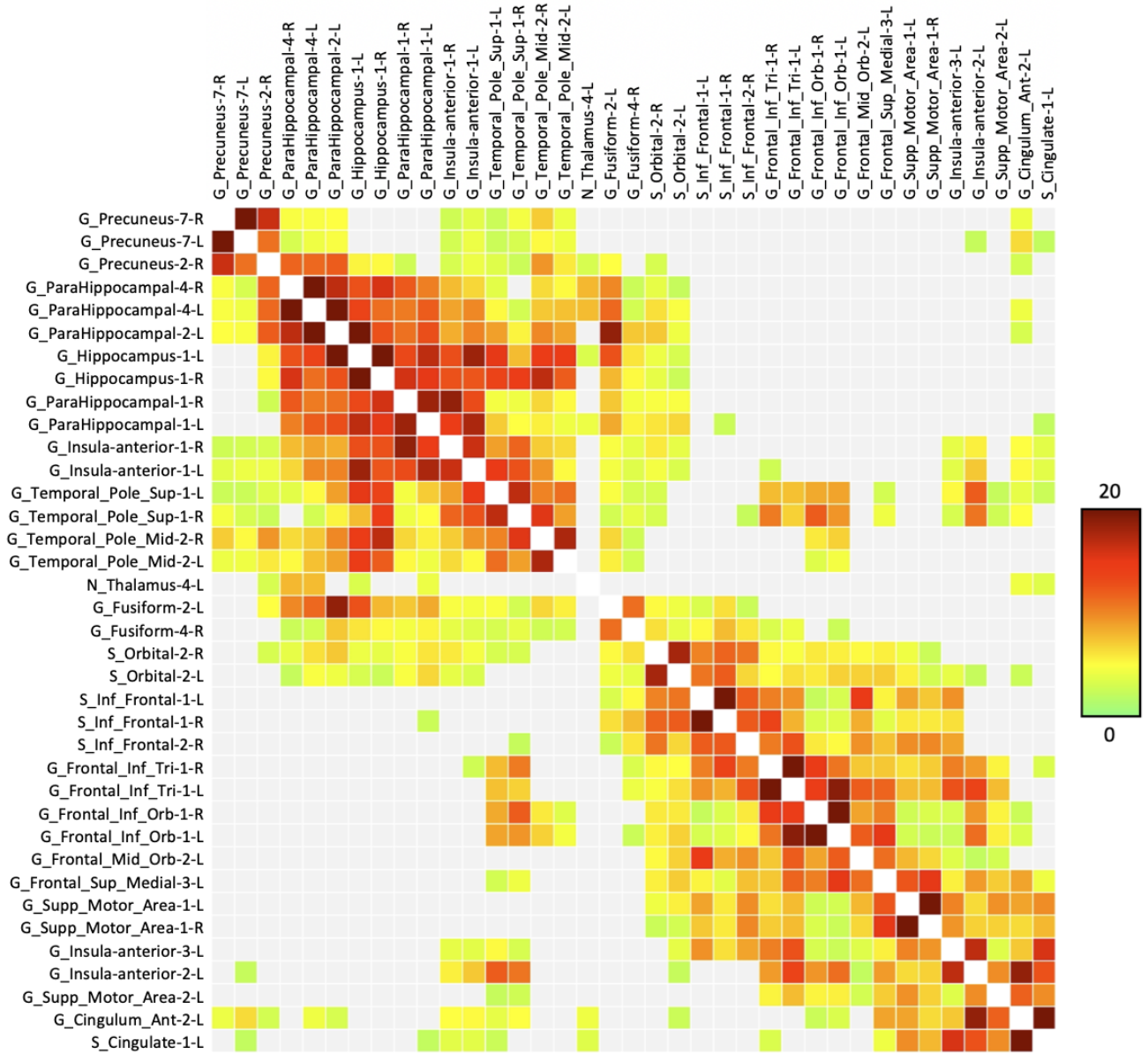
G_Frontal_Mid-1-R	41 44 13	0.09	0.16	0.0075
G_Frontal_Mid-5-L	-43 20 37	0.21	0.35	0.0038
G_Frontal_Mid-5-R	42 17 41	0.09	0.17	0.0132
<b>S_Inf_Frontal-1-L*</b>	-44 38 12	0.37	0.31	<.0001
<b>S_Inf_Frontal-1-R*</b>	46 40 10	0.24	0.21	<.0001
S_Inf_Frontal-2-L	-43 15 29	0.38	0.34	<.0001
<b>S_Inf_Frontal-2-R*</b>	44 19 28	0.28	0.21	<.0001
<b>G_Frontal_Inf_Tri-1-L*</b>	-49 26 5	0.15	0.22	0.0011
<b>G_Frontal_Inf_Tri-1-R*</b>	50 29 5	0.07	0.17	0.0434
S_Precentral-1-R	50 10 24	0.11	0.24	0.0178
<b>G_Frontal_Sup_Medial-3-L*</b>	-5 35 43	0.19	0.23	0.0002
G_Frontal_Sup_Medial-3-R	6 33 44	0.14	0.19	0.0006
<b>G_Supp_Motor_Area-1-L*</b>	-6 22 46	0.39	0.23	<.0001
<b>G_Supp_Motor_Area-1-R*</b>	6 21 48	0.37	0.26	<.0001
G_Supp_Motor_Area-2-L	-11 18 61	0.08	0.16	0.0134
<b>G_Insula-anterior-1-L*</b>	-20 5 -19	0.12	0.18	0.0013
<b>G_Insula-anterior-1-R*</b>	19 7 -19	0.07	0.17	0.0329
<b>G_Insula-anterior-2-L*</b>	-34 17 -13	0.17	0.24	0.0009
G_Insula-anterior-2-R	35 18 -13	0.10	0.18	0.0054
<b>G_Insula-anterior-3-L*</b>	-34 24 1	0.31	0.22	<.0001
G_Insula-anterior-3-R	37 24 0	0.20	0.15	<.0001
G_Insula-anterior-4-L	-41 15 3	0.08	0.21	0.0457
G_Occipital_Inf-1-R	50 -60 -9	0.22	0.19	<.0001
G_Occipital_Inf-2-L	-45 -71 -7	0.13	0.17	0.0003
G_Occipital_Inf-2-R	47 -65 -7	0.19	0.18	<.0001
G_Occipital_Lat-2-L	-26 -94 -1	0.06	0.15	0.0253
G_Occipital_Lat-3-L	-40 -84 -12	0.10	0.16	0.0041
G_Occipital_Lat-3-R	43 -81 -10	0.11	0.20	0.0078
G_Occipital_Lat-4-L	-31 -89 8	0.08	0.15	0.0078
G_Occipital_Lat-4-R	34 -85 9	0.09	0.15	0.0054
G_Occipital_Lat-5-L	-35 -79 -1	0.07	0.15	0.0132
G_Occipital_Lat-5-R	36 -76 2	0.07	0.14	0.0116
<b>G_Fusiform-2-L*</b>	-35 -26 -23	0.09	0.10	<.0001
G_Fusiform-4-L	-43 -50 -17	0.19	0.18	<.0001
<b>G_Fusiform-4-R*</b>	44 -46 -18	0.22	0.15	<.0001
G_Fusiform-5-L	-31 -50 -12	0.09	0.12	0.0006
G_Fusiform-5-R	32 -47 -41	0.09	0.12	0.0006
G_Fusiform-6-R	29 -62 -9	0.05	0.12	0.0489
S_Intraoccipital-1-L	-24 -72 32	0.09	0.23	0.0455
S_Intraoccipital-1-R	28 -69 33	0.15	0.21	0.0007
<b>G_Precuneus-2-R*</b>	5 -56 20	0.27	0.29	<.0001
<b>G_Precuneus-7-L*</b>	-6 -65 35	0.16	0.31	0.0097
<b>G_Precuneus-7-R*</b>	7 -63 36	0.21	0.29	0.0006
S_Intraparietal-2-L	-34 -58 45	0.22	0.29	0.0005
S_Intraparietal-2-R	37 -52 48	0.14	0.20	0.0010
S_Intraparietal-3-L	-27 -60 43	0.16	0.27	0.0051
S_Intraparietal-3-R	27 -61 46	0.13	0.19	0.0012
G_Temporal_Inf-4-R	54 -58 -11	0.10	0.19	0.0086
<b>G_Temporal_Pole_Sup-1-L*</b>	-35 11 -24	0.09	0.13	0.0019
<b>G_Temporal_Pole_Sup-1-R*</b>	36 16 -24	0.10	0.16	0.0044
<b>G_Temporal_Pole_Mid-2-L*</b>	-35 9 -33	0.05	0.10	0.0097
<b>G_Temporal_Pole_Mid-2-R*</b>	35 12 -34	0.04	0.09	0.0121
<b>G_Hippocampus-1-L*</b>	-30 -7 -19	0.06	0.11	0.0115
<b>G_Hippocampus-1-R*</b>	30 -5 -18	0.08	0.11	0.0005
G_Hippocampus-2-L	-25 -32 -3	0.04	0.09	0.0430
G_Hippocampus-2-R	25 -31 -2	0.06	0.09	0.0041
<b>G_ParaHippocampal-1-L*</b>	-16 -4 -18	0.24	0.23	<.0001

<b>G_ParaHippocampal-1-R*</b>	14 -4 -18	0.17	0.20	0.0001
<b>G_ParaHippocampal-2-L*</b>	-28 -27 -19	0.07	0.17	0.0253
G_ParaHippocampal-2-R	29 -25 -19	0.07	0.14	0.0169
<b>G_ParaHippocampal-4-L*</b>	-17 -27 -13	0.12	0.21	0.0071
<b>G_ParaHippocampal-4-R*</b>	17 -27 -10	0.15	0.18	0.0002
<hr/>				
N_Caudate-4-R	14 20 8	0.06	0.13	0.0237
N_Caudate-5-L	-13 10 8	0.17	0.21	0.0003
N_Caudate-5-R	12 10 9	0.16	0.22	0.0006
N_Thalamus-1-L	-4 0 1	0.18	0.29	0.0032
N_Thalamus-1-R	4 0 1	0.16	0.24	0.0012
N_Thalamus-2-R	9 -7 13	0.09	0.18	0.0120
N_Thalamus-3-L	-3 -7 -1	0.15	0.22	0.0017
<b>N_Thalamus-4-L*</b>	-3 -14 8	0.20	0.27	0.0005
N_Thalamus-4-R	3 -14 9	0.17	0.25	0.0017
N_Thalamus-5-L	-12 -19 7	0.09	0.14	0.0026
N_Thalamus-5-R	13 -17 6	0.07	0.14	0.0148
N_Thalamus-6-R	15 -27 13	0.05	0.12	0.0455
N_Thalamus-7-L	-9 -28 11	0.09	0.15	0.0054
N_Thalamus-9-L	-5 -11 -7	0.12	0.13	<.0001
N_Thalamus-9-R	5 -10 -6	0.11	0.16	0.0007

327



328 **3.3.3. Resting-state functional connectivity**



329  
 330 Figure 5. Resting-state connectivity matrix of 37 hROIs specific to the social status assignment (i.e., positive in  
 331 the contrast [Social status minus Ornament check] and positive in contrast [Ornament (1-back) minus Faces].  
 332 The color scale (green to red) reflects the t-value on each connection averaged across subjects.

333 The resting-state functional connectivity analysis revealed 348 positive connections  
 334 significant across subjects ( $p < 0.05$  FDR, univariate t-test) between the 37 hROIs. T-values  
 335 varied from 2 to 25 (Figure 5). These 37 hROIs can be divided into two groups based on their  
 336 resting-state functional connectivity. A network connected the precuneus and temporal lobe  
 337 regions, including the hippocampus, the parahippocampal cortex, the temporal pole, and a  
 338 part of the fusiform gyrus. A second network connected mainly frontal regions, including the

339 inferior frontal sulcus and gyrus, the orbitofrontal cortex, the dorsal anterior cingulate cortex,  
340 the supplementary motor area, and the anterior insula.

341 The G-Fusiform-4-R and the Temporal\_Pole\_Sup-1-R regions were connected to 22 and  
342 27 hROIS, respectively. The G-Fusiform-4-R and the Temporal\_Pole\_Sup-1-R regions were  
343 strongly connected to their group and many regions of the other group (see supplementary  
344 materials for detailed results). The S\_Orbital-2 was connected to 26 hROIs.

345

#### 346 **4. Discussion**

347 This study aimed to identify the brain regions involved in attributing social status from the  
348 visual analysis of adorned faces. Adorning one's body to transmit social information  
349 represents a symbolic behavior that appeared at least 150,000 years ago and probably much  
350 earlier. Therefore, we can assume that the networks revealed in the present study were, at  
351 least to a degree, functional in the earliest *Homo sapiens* and contemporary or earlier  
352 hominins displaying such behaviors.

353 These regions can be categorized into four groups: 1. occipitotemporal regions of the  
354 ventral visual pathway, including lateral occipital regions, fusiform gyrus, parahippocampal  
355 gyrus extending to the hippocampus, and the temporal poles; 2. regions belonging to the  
356 salience network such as the anterior insula and the anterior cingulate cortex; 3. the  
357 intraparietal sulcus; and 4. the ventral and dorsal regions of the lateral prefrontal cortex and  
358 the orbitofrontal cortex.

359 Some of these regions were also activated in the 1-back task, indicating that they are not  
360 specific to an explicit social attribution but may be involved in an implicit social appraisal.

361 This is the case for most visual regions (except Fusiform-4-R and Fusiform-2-L), the  
362 intraparietal sulcus, and most of the thalamus and retrosplenial regions. In contrast, activity in  
363 the inferior and orbital frontal areas, hippocampal and parahippocampal regions, the temporal  
364 poles, and the salience network, including the anterior cingulate and parts of the anterior  
365 insula, remained significant when activity in these regions during the 1-back task was  
366 subtracted.

367

##### 368 **4.1. Visual Ventral pathway and medial temporal regions**

369 Lateral and ventral occipital regions were more activated by the social status attribution than  
370 by the assessment of decoration type. This suggests that deeper visual processing is required  
371 to attribute a social status. Most of these occipitotemporal regions were also activated during

372 the 1-back task and were thus not specifically involved in assigning a social status to adorned  
373 faces. However, two hROIs were significantly more activated during social status attribution  
374 than in the 1-back task, namely G\_Fusiform-2-L and G\_Fusiform-4-R. The latter is  
375 particularly interesting since it includes the so-called fusiform face area (FFA), which is  
376 sensitive to face perception<sup>64-66</sup> and lateralized in the right hemisphere<sup>67</sup>. Thus, although all  
377 conditions included face perception and none required specific attention to faces, FFA  
378 appeared more solicited by social status assignment. It has been shown that FFA is sensitive  
379 to physical characteristics and their possible social correlates<sup>68,69</sup>. More recently, a study  
380 showed that FFA processes characteristics such as social traits, gender, and high-level visual  
381 features of faces<sup>70</sup> and might thus initiate the social processing of faces. The results of the  
382 present study suggest that, in the context of social role attribution, FFA can process non-  
383 physiognomic features. This is consistent with the fact that the FFA promotes holistic rather  
384 than local processing<sup>71-73</sup>. Ornamented faces may have been perceived as a whole in the  
385 social attribution task, while attention was focused on details during the assessment of  
386 decoration type and the 1-back task. In other words, attributing social status involves a more  
387 complex process relying on a set of components, such as the types of decoration, their  
388 association, their location on the face, and the face itself.

389 In summary, the activation of FFA in our social status assignment task could reflect  
390 the implementation of preliminary social categorization processes based on a holistic analysis  
391 of ornamented faces, which is further achieved in other regions of the brain, particularly the  
392 orbitofrontal cortex.

393 In the anterior extension of the ventral visual pathway, we found that the hippocampus  
394 and parahippocampal gyrus were more activated by the social status attribution than by the  
395 ornament type assignment and significantly more activated when compared to the 1-back  
396 task, reflecting their specificity to social status attribution. The hippocampus reflects episodic  
397 memorization processes strongly involved in social cognition<sup>74,75</sup>. The parahippocampus  
398 appears to play, among others, a pivotal role in contextual associative processing<sup>76,77</sup>, i.e., in  
399 binding elements composing stimuli. It provides a unified context for further processing (see  
400<sup>78</sup> for a review). In the framework of the present study, participants arbitrarily associated face  
401 decorations with social status. After the fMRI sessions, they reported that once they had  
402 established an ornament/status association strategy, they stuck to it throughout the sessions,  
403 with exceptional random responses. Contextual associations were thus an essential aspect of  
404 the processes involved in the status assignment task. The activation of the parahippocampal  
405 cortex reasonably reflects the implementation of these processes. It has been suggested that

406 the anterior part of the parahippocampus preferentially processes non-spatial contextual  
407 associations, and the posterior part, comprising the parahippocampal Place Area (PPA),  
408 spatial associations <sup>76,79</sup>. In the present study, the activation of the anterior parahippocampus  
409 is consistent with the non-spatial nature of the associations.

410 The activation of the medial temporal gyrus might be linked to one of the temporal poles.  
411 Several studies have documented the involvement of the temporal pole in social cognition,  
412 and this region is considered part of the social brain network <sup>80-84</sup>. Although its role is still  
413 under discussion, it has been proposed that this brain area is involved in encoding and  
414 retrieving social knowledge <sup>85</sup>. As was the case in this study, assigning social status mobilizes  
415 stereotypical social knowledge (e.g., the chief must have the most ornaments) and entails  
416 encoding: The participants associated a type of ornamentation with a social role and created  
417 an arbitrary social code that they reused throughout the task. Thus, we propose that the  
418 parahippocampus and the temporal pole, which are strongly functionally connected, work in  
419 synergy to facilitate the association of a type of ornamentation with a specific social status  
420 and then to encode and restore this association.

421

#### 422 **4.2. Inferior and orbitofrontal cortex**

423 Assigning a social status involved many frontal regions not solicited during the ornament type  
424 attribution condition. However, the specific areas for explicit processes, i.e., activated in the  
425 social attribution task compared to the 1-back task, were mainly in the lateral part of the  
426 inferior frontal gyrus and the orbitofrontal cortex as defined by Rudebeck and Rich <sup>86</sup>. The  
427 resting-state connectivity analysis showed that these regions were highly functionally linked.  
428 Previous studies have emphasized the role of the orbitofrontal cortex in social cognition in  
429 non-human primates and humans. It has been argued that this cortical area contains neurons  
430 sensitive to representing social categories <sup>87</sup> and evaluating social information <sup>88</sup> in non-  
431 human primates. In humans, a deficit in social perception after orbitofrontal cortex lesions <sup>89</sup>,  
432 an inability to judge social traits in a decision-making task <sup>90</sup>, or acquired sociopathy have  
433 been reported <sup>91</sup>.

434 In healthy participants, fMRI studies have emphasized the role of the orbitofrontal  
435 cortex in social cognition and social behavior (<sup>55,92</sup>; See <sup>60</sup> for a review) and, more  
436 specifically, in explicit processing <sup>93</sup>. The orbitofrontal cortex is sensitive to non-verbal social  
437 signals <sup>55</sup>. Recent results indicate that this area is critical in representing social status <sup>92</sup>. A  
438 recent fMRI study showed that the OFC represented the stereotypic social traits of others and  
439 that its pattern of activity was predictive of individual choices, highlighting its critical role in

440 social decision-making<sup>94</sup>. In these studies, participants had to behave according to the facial  
441 expression, attitude, or social category of the individuals presented in the experiment. Our  
442 results extend these findings. Unlike previous studies, participants based their decision on  
443 symbolic features (the type and arrangement of ornamentations), to which they arbitrarily  
444 attributed social meaning. This implies that the role of the orbitofrontal cortex in social  
445 decision-making is not restricted to processing stereotypical attitudes or social groups, a  
446 capacity shared with non-human primates. Social evaluation based on symbolic external  
447 attributes also involves this region in humans.

448         The social status attribution task heavily relies on high-order executive functions such  
449 as attentional control, selection, and flexibility. The activation of the pars triangularis of the  
450 inferior frontal gyrus extending to the inferior frontal sulcus reflects these aspects<sup>95</sup>.

451 Although the activation was bilateral, the right and left inferior frontal gyrus probably played  
452 a different role in the task. The right inferior frontal gyrus is explicitly associated with high-  
453 level social cognition<sup>96</sup>. The left inferior frontal gyrus is involved in selecting some aspects  
454 or subsets of available information among competing alternatives<sup>97,98</sup>. This region also plays  
455 a role in processing non-linguistic symbolic information<sup>99,100</sup>, consistent with the symbolic  
456 value attributed by the participants to face adornments.

457         Overall, the prefrontal cortex's involvement in the present study underlines its role in  
458 social decision-making. Our results extend their contribution to symbolic social  
459 communication, here materialized by face ornamentations.

460

### 461 **4.3. Salience network**

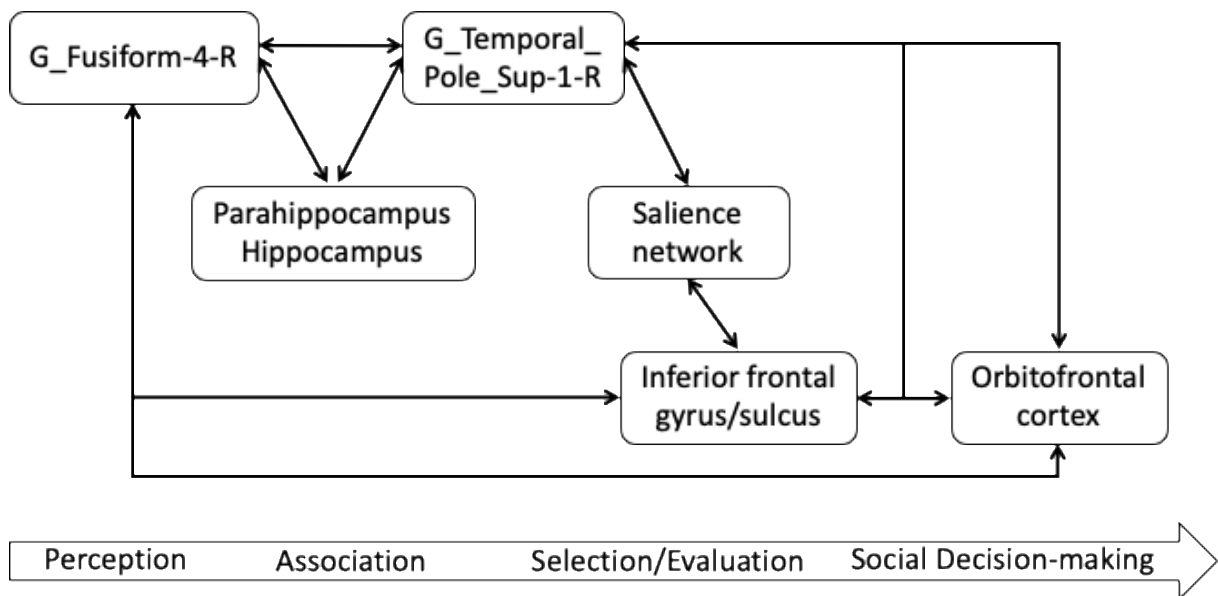
462 Social status attribution elicited activation in the anterior insula, the dorsal anterior cingulate  
463 cortex (dACC)/pre-SMA, and subcortical structures, such as the thalamus and the caudate  
464 nuclei. These regions constitute the so-called salience network, whose key components are the  
465 insula anterior and the dACC/pre-SMA<sup>101–103</sup>. This network is involved in selecting relevant  
466 elements of the environment for perceptual decision-making<sup>104–106</sup>. In our case, participants  
467 had to extract salient information from the ornamented faces to associate the proposed social  
468 status with one of the three faces presented to them. The salience network was also activated  
469 in the 1-back task by the need to detect the repetition of ornamental patterns. However, the  
470 greater uncertainty in decision-making during the attribution task can explain why activation  
471 of the salience network was more extensive during status attribution than the 1-back task<sup>107</sup>.  
472 To attribute a social status, participants had to make a forced choice among three possibilities,  
473 with several plausible answers and had to compare the different options and arbitrate to

474 choose only one. These aspects of the task have probably triggered the activation of the  
 475 dACC/pre-SMA, belonging to the salience network. The dACC/pre-SMA has been reported  
 476 as involved in conflict and performance monitoring <sup>108-110</sup>, and more recently in social  
 477 categorization domain <sup>111</sup>.

478

479 **4.4. Resting-state functional connectivity**

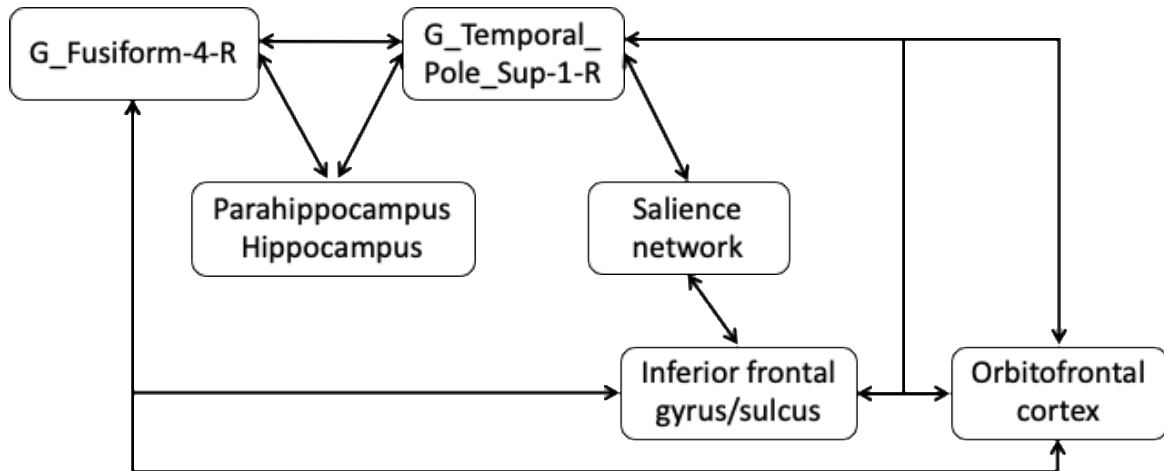
480 Resting-state functional connectivity provides insight into the potential interactions between  
 481 neural assemblies activated by the social status assignment task. The G\_Fusiform-4-R and the  
 482 G\_Temporal\_Pole\_Sup-1-R were characterized by many connections with other activated  
 483 regions (



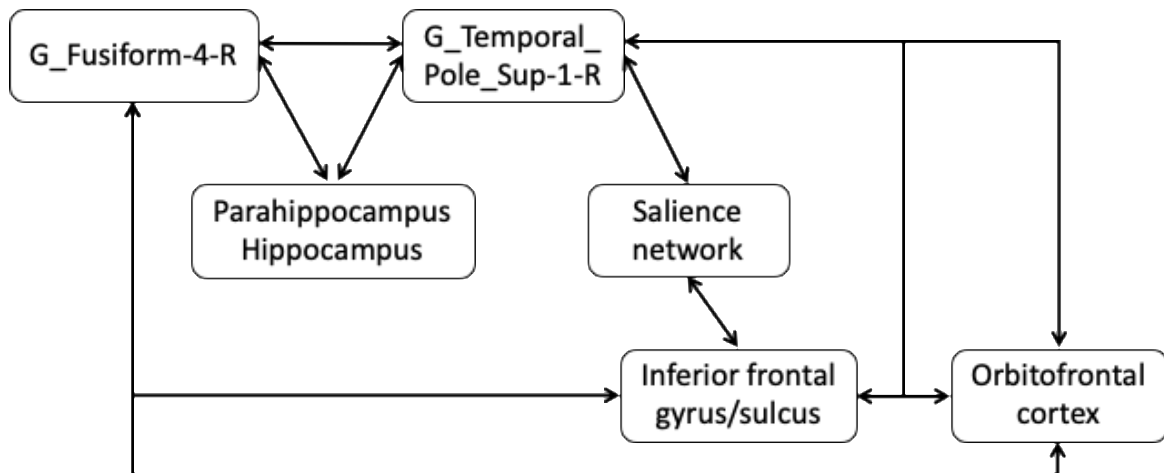
484

485 Figure 6). These two regions were connected with 22 and 27 hROIs, respectively. The  
 486 G\_Fusiform-4-R included the FFA (see results) and is likely involved in the initial processing  
 487 phase. The functional relationships between the medial temporal lobe, the fusiform gyrus, and  
 488 the temporal pole reflected the association of the perceptive, social, mnemonic, and associative  
 489 aspects of the task. In addition, the G\_Temporal\_Pole\_Sup-1-R was connected with frontal  
 490 regions and could act as a hub, allowing communication between visual areas and executive  
 491 frontal regions. The connection between the temporal pole and the salience network enables the  
 492 exchange of information necessary for evaluating and selecting inputs relevant to social  
 493 decision-making. The temporal pole and the salience network were related to the inferior frontal  
 494 gyrus, contributing to the evaluation of subjective confidence about a perceptual decision <sup>112</sup>.  
 495 The orbitofrontal cortex was functionally connected to the G\_Temporal\_Pole\_Sup-1-R and the  
 496 G\_Fusiform-4-R. These regions, whose essential role in social status evaluation has been

497 discussed above, could constitute the core network in the social attribution task (



498 Figure 6). They must have allowed the integration of information leading to the assignment of  
 499 social status based on the perception of symbolic cues.  
 500



501  
 502 Figure 6. Schematic resting-state functional connectivity network between regions activated during a  
 503 social status attribution task based on symbolic culturalized faces. Black arrows indicate the reciprocal  
 504 resting-state functional connectivity between brain regions (univariate t-test,  $p < 0.05$ , FDR corrected).

505 Notably, none of the regions involved in assigning social status exclusively dealt with  
 506 social information. Most of these regions are involved in many cognitive functions. The  
 507 functional connection of structures whose processing properties are beneficial for the  
 508 execution of the task allows the social judgment function to emerge. Human connections  
 509 exceed those of animals, including primates, at both the structural and functional levels <sup>113–115</sup>.

510 Thanks to creating functional connections (linking social cognition, memory, and executive  
511 functions), humans could use symbolic items and markings to signify social status.

512

## 513 **5. Conclusion**

514 This study delved into the neural mechanisms involved in the social interpretation of facial  
515 adornments and found that various brain regions, including the FFA, temporal poles, salience  
516 network, and orbitofrontal cortex, were involved in this process. Furthermore, assigning a  
517 social status from symbolic cues also activated the medial temporal regions and the inferior  
518 frontal gyrus, reflecting the role of episodic memory, contextual association, and executive  
519 functions. The complexity of this neural network raises questions about when it became fully  
520 functional in our ancestors and whether it resulted from a gradual process of integration and  
521 complexification or was already fully functional when the first archaeological evidence of  
522 culturalization of the human face was recorded.

523 The gradual complexification and patchy emergence of face adornment technologies over the  
524 last 500,000 years suggest a scenario of increasing but asynchronous integration of brain areas  
525 involved in social status recognition based on facial culturalization. This growing integration  
526 allowed the decoding of increasingly complex symbolic codes, supported by more demanding  
527 technologies for face adornment.

528 The interplay between cultural and biological mechanisms likely drove this process, with  
529 individuals gifted in acquiring, decoding, and creating these symbolic messages having  
530 selective advantages that favored the permanent inscription of a more integrated connectivity  
531 in the brain<sup>116–118</sup>. A progressive co-option of brain regions has also been suggested for the  
532 evolution of tool-making<sup>119–121</sup>. It would have enabled the development of increasingly  
533 complex tools.

534 The period between 140,000 and 70,000 years ago may have represented a key moment in  
535 this integration process, as this was when red pigments use became almost ubiquitous at  
536 African Middle Stone Age sites and marine shell beads were used for the first time in North  
537 Africa, the Near East, and Southern Africa. This diversification of colors, shapes, and  
538 technologies indicates a complexification of practices allowing wearers to use their faces to  
539 communicate information about their social role using more complex shared symbolic codes.  
540 It is reasonable to think that the human brain had largely equipped itself with the necessary  
541 connections to process and interpret these stimuli 70,000 years ago.

542



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549 **7. Authors' contributions**

550 MS, FE, SR, EM designed the study

551 MS, EM acquired the data

552 MS, EM analyzed the data

553 MS, FE, SR, EM wrote the article

554

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564 **9. Data Availability**

565 Raw BOLD values for all the hROIs and contrasts are available as supplementary material

566

567 **10. References**

- 568 1. Barth, F. *Ethnic Groups and Boundaries. The Social organization of culture difference.*  
569 (George Allen and Uwin, 1969).
- 570 2. Dubin, L. S. *North American Indian Jewelry and Adornment. From Prehistory to the*  
571 *Present.* (Harry N. Abrams Inc, 1999).
- 572 3. Hodder, I. *The Meanings of Things. Material Culture and Symbolic Expression.* (Harper

- 573 Collins, 1991).
- 574 4. Klumpp, D. & Kratz, C. Aesthetics, expertise, and ethnicity: Okiek and Maasai  
575 perspectives on personal ornament. in *Being Maasai: Ethnicity and Identity in East Africa* (eds.  
576 Speart, T. & Waller, R.) 195–221 (1993).
- 577 5. Sanders, J. M. Ethnic Boundaries and Identity in Plural Societies. *Annu. Rev. Sociol.* **28**,  
578 327–357 (2002).
- 579 6. Dubin, L. S. *The history of beads: from 30,000 B.C. to the present.* (Thames and  
580 Hudson, 1987).
- 581 7. Hatton, A., Collins, B., Schoville, B. J. & Wilkins, J. Ostrich eggshell beads from Ga-  
582 Mohana Hill North Rockshelter, southern Kalahari, and the implications for understanding  
583 social networks during Marine Isotope Stage 2. *PLOS ONE* **17**, e0268943 (2022).
- 584 8. Kuhn, S. L. & Stiner, M. C. Paleolithic Ornaments: Implications for Cognition,  
585 Demography and Identity. *Diogenes* **54**, 40–48 (2007).
- 586 9. Kuper, H. Costume and Identity. *Comp. Stud. Soc. Hist.* **15**, 348–367 (1973).
- 587 10. Nițu, E.-C. *et al.* Mobility and social identity in the Mid Upper Paleolithic: New  
588 personal ornaments from Poiana Cireșului (Piatra Neamț, Romania). *PLOS ONE* **14**, e0214932  
589 (2019).
- 590 11. Pitarch Martí, A., Wei, Y., Gao, X., Chen, F. & d’Errico, F. The earliest evidence of  
591 coloured ornaments in China: The ochred ostrich eggshell beads from Shuidonggou Locality 2.  
592 *J. Anthropol. Archaeol.* **48**, 102–113 (2017).
- 593 12. *Beads and bead makers: gender, material culture, and meaning.* (Berg, 1998).
- 594 13. Vanhaeren, M. & d’Errico, F. Aurignacian ethno-linguistic geography of Europe  
595 revealed by personal ornaments. *J. Archaeol. Sci.* **33**, 1105–1128 (2006).
- 596 14. Wright, D. *et al.* An Early Upper Palaeolithic decorated bone tubular rod from Pod  
597 Hradem Cave, Czech Republic. *Antiquity* **88**, 30–46 (2014).
- 598 15. Beckwith, C. & Fisher, A. *African ceremonies.* (Harry N. Abrams, 1999).
- 599 16. Carey, M. *Beads and Beadwork of West and Central Africa.* (Shrire, 1991).
- 600 17. Carter, B. & Helmer, M. Elite Dress and Regional Identity: Chimú-Inka Perforated  
601 Ornaments from Samanco, Nepeña Valley, Coastal Peru. *BEADS J. Soc. Bead Res.* **20**, 46–74  
602 (2015).
- 603 18. Ogundiran, A. Of Small Things Remembered: Beads, Cowries, and Cultural  
604 Translations of the Atlantic Experience in Yorubaland. *Int. J. Afr. Hist. Stud.* **35**, 427–457  
605 (2002).
- 606 19. Twala, R. G. Beads as regulating the social life of the Zulu and Swazi. *Afr. Stud.* **10**,

- 607 113–123 (1958).
- 608 20. Brooks, A. S. *et al.* Long-distance stone transport and pigment use in the earliest Middle  
609 Stone Age. *Science* **360**, 90–94 (2018).
- 610 21. Dapschaskas, R., Göden, M. B., Sommer, C. & Kandel, A. W. The Emergence of  
611 Habitual Ochre Use in Africa and its Significance for The Development of Ritual Behavior  
612 During The Middle Stone Age. *J. World Prehistory* **35**, 233–319 (2022).
- 613 22. Rosso, D. E. The first uses of colour: what do we know? *J. Anthropol. Sci.* 45–69 (2022)  
614 doi:10.4436/JASS.10005.
- 615 23. Watts, I., Chazan, M. & Wilkins, J. Early Evidence for Brilliant Ritualized Display:  
616 Specularite Use in the Northern Cape (South Africa) between ~500 and ~300 Ka. *Curr.*  
617 *Anthropol.* **57**, 287–310 (2016).
- 618 24. de Lumley, H. *et al.* *Les crayons d'ocre du site acheuléen de Terra Amata.* (CNRS  
619 Editions, 2016).
- 620 25. Roebroeks, W. *et al.* Use of red ochre by early Neandertals. *Proc. Natl. Acad. Sci.* **109**,  
621 1889–1894 (2012).
- 622 26. d'Errico, F. L'émergence des comportements symboliques en Afrique et en Asie. in  
623 *Atas do Côa Symposium: novos olhares sobre a arte paleolítica: Museu do Côa: 4 a 6*  
624 *dezembro 2018* (eds. Aubry, T., Santos, A. T. & Martins, A.) 22–51 (Associação dos  
625 Arqueólogos Portugueses ; Fundação Côa Parque, 2021).
- 626 27. Langley, M. C., Clarkson, C. & Ulm, S. Symbolic expression in Pleistocene Sahul,  
627 Sunda, and Wallacea. *Quat. Sci. Rev.* **221**, 105883 (2019).
- 628 28. d'Errico, F., Salomon, H., Vignaud, C. & Stringer, C. Pigments from the Middle  
629 Palaeolithic levels of Es-Skhul (Mount Carmel, Israel). *J. Archaeol. Sci.* **37**, 3099–3110 (2010).
- 630 29. Dayet, L., Le Bourdonnec, F.-X., Daniel, F., Porraz, G. & Texier, P.-J. Ochre  
631 Provenance and Procurement Strategies During The Middle Stone Age at Diepkloof Rock  
632 Shelter, South Africa: Ochre during the MSA at Diepkloof rock shelter. *Archaeometry* **58**, 807–  
633 829 (2016).
- 634 30. Hovers, E., Ilani, S., Bar-Yosef, O. & Vandermeersch, B. An Early Case of Color  
635 Symbolism: Ochre Use by Modern Humans in Qafzeh Cave. *Curr. Anthropol.* **44**, 491–522  
636 (2003).
- 637 31. Watts, I. Red ochre, body painting, and language: interpreting the Blombos ochre. in  
638 *The cradle of language* (eds. Botha, R. & Knight, C.) vol. 2 93–129 (2009).
- 639 32. Watts, I. The pigments from Pinnacle Point Cave 13B, Western Cape, South Africa. *J.*  
640 *Hum. Evol.* **59**, 392–411 (2010).

- 641 33. Godfrey-Smith, D. I. & Ilani, S. Past thermal history of goethite and hematite fragments  
642 from Qafzeh Cave deduced from thermal activation characteristics of the 110°C TL peak of  
643 enclosed quartz grains. *Rev. Archéom.* **28**, 185–190 (2004).
- 644 34. Salomon, H. *et al.* Selection and heating of colouring materials in the Mousterian level  
645 of Es-Skhul (c. 100 000 years BP, Mount Carmel, Israel). *Archaeometry* **54**, 698–722 (2012).
- 646 35. Wadley, L. Post-depositional heating may cause over-representation of red-coloured  
647 ochre in stone age sites. *South Afr. Archaeol. Bull.* **64**, 166–171 (2009).
- 648 36. Rosso, D. E., d’Errico, F. & Queffelec, A. Patterns of change and continuity in ochre  
649 use during the late Middle Stone Age of the Horn of Africa: The Porc-Epic Cave record. *PLOS*  
650 *ONE* **12**, e0177298 (2017).
- 651 37. Bar-Yosef Mayer, D. E., Vandermeersch, B. & Bar-Yosef, O. Shells and ochre in  
652 Middle Paleolithic Qafzeh Cave, Israel: indications for modern behavior. *J. Hum. Evol.* **56**,  
653 307–314 (2009).
- 654 38. Bar-Yosef Mayer, D. E. *et al.* On holes and strings: Earliest displays of human  
655 adornment in the Middle Palaeolithic. *PLOS ONE* **15**, e0234924 (2020).
- 656 39. Bouzouggar, A. *et al.* 82,000-year-old shell beads from North Africa and implications  
657 for the origins of modern human behavior. *Proc. Natl. Acad. Sci.* **104**, 9964–9969 (2007).
- 658 40. d’Errico, F., Henshilwood, C., Vanhaeren, M. & van Niekerk, K. Nassarius kraussianus  
659 shell beads from Blombos Cave: evidence for symbolic behaviour in the Middle Stone Age. *J.*  
660 *Hum. Evol.* **48**, 3–24 (2005).
- 661 41. d’Errico, F. *et al.* Additional evidence on the use of personal ornaments in the Middle  
662 Paleolithic of North Africa. *Proc. Natl. Acad. Sci.* **106**, 16051–16056 (2009).
- 663 42. Sehassseh, E. M. *et al.* Early Middle Stone Age personal ornaments from Bizmoune  
664 Cave, Essaouira, Morocco. *Sci. Adv.* **7**, eabi8620 (2021).
- 665 43. Shipton, C. *et al.* 78,000-year-old record of Middle and Later Stone Age innovation in  
666 an East African tropical forest. *Nat. Commun.* **9**, 1832 (2018).
- 667 44. Steele, T. E., Álvarez-Fernández, E. & Hallet-Desguez, E. Personal ornaments in early  
668 prehistory a review of shells as personal ornamentation during the African Middle Stone Age.  
669 *PaleoAnthropology* 24–51 (2019).
- 670 45. Vanhaeren, M. *et al.* Middle Paleolithic Shell Beads in Israel and Algeria. *Science* **312**,  
671 1785–1788 (2006).
- 672 46. d’Errico, F., Henshilwood, M. C., Maureille, G. B., Gambier, D. & Tillier, A. M. From  
673 the origin of language to the diversification of languages. *Becom. Eloquent Adv. Emergence*  
674 *Lang. Hum. Cogn. Mod. Cult.* (2009).

- 675 47. Davidson, I. & Noble, W. The Archaeology of Perception : traces of depiction and  
676 language. *Curr. Anthropol.* **30**, 125–154 (1989).
- 677 48. Marshack, A. Some Implications of the Paleolithic Symbolic Evidence For the Origin  
678 of Language. *Curr. Anthropol.* **17**, 274–282 (1976).
- 679 49. Vanhaeren, M., d’Errico, F., van Niekerk, K. L., Henshilwood, C. S. & Erasmus, R. M.  
680 Thinking strings: Additional evidence for personal ornament use in the Middle Stone Age at  
681 Blombos Cave, South Africa. *J. Hum. Evol.* **64**, 500–517 (2013).
- 682 50. Adolphs, R. The Social Brain: Neural Basis of Social Knowledge. *Annu. Rev. Psychol.*  
683 **60**, 693–716 (2009).
- 684 51. Frith, C. D. The social brain? *Philos. Trans. R. Soc. B Biol. Sci.* **362**, 671–678 (2007).
- 685 52. Karafin, M. S., Tranel, D. & Adolphs, R. Dominance Attributions Following Damage  
686 to the Ventromedial Prefrontal Cortex. *J. Cogn. Neurosci.* **16**, 1796–1804 (2004).
- 687 53. Chiao, J. Y. Neural basis of social status hierarchy across species. *Curr. Opin.*  
688 *Neurobiol.* **20**, 803–809 (2010).
- 689 54. Chiao, J. Y. *et al.* Neural representations of social status hierarchy in human inferior  
690 parietal cortex. *Neuropsychologia* **47**, 354–363 (2009).
- 691 55. Marsh, A. A., Blair, K. S., Jones, M. M., Soliman, N. & Blair, R. J. R. Dominance and  
692 Submission: The Ventrolateral Prefrontal Cortex and Responses to Status Cues. *J. Cogn.*  
693 *Neurosci.* **21**, 713–724 (2009).
- 694 56. Zink, C. F. *et al.* Know Your Place: Neural Processing of Social Hierarchy in Humans.  
695 *Neuron* **58**, 273–283 (2008).
- 696 57. Jaubert, J., Maureille, B. & Peresani, M. Spiritual and symbolic activities of  
697 Neanderthals. in *Updating Neanderthals* 261–274 (Elsevier, 2022). doi:10.1016/B978-0-12-  
698 821428-2.00005-6.
- 699 58. Vanhaeren, M., Julien, M., d’Errico, F., Mourer-Chauviré, C. & Lozouet, P. Les objets  
700 de parure. in *Le Châtelperronien de la Grotte du Renne (Arcy-Sur-Cure)*. (ed. Julien, M.) 259–  
701 285 (2019).
- 702 59. Zilhão, J. *et al.* Symbolic use of marine shells and mineral pigments by Iberian  
703 Neandertals. *Proc. Natl. Acad. Sci.* **107**, 1023–1028 (2010).
- 704 60. Forbes, C. E. & Grafman, J. The Role of the Human Prefrontal Cortex in Social  
705 Cognition and Moral Judgment. *Annu. Rev. Neurosci.* **33**, 299–324 (2010).
- 706 61. Joliot, M. *et al.* AICHA: An atlas of intrinsic connectivity of homotopic areas. *J.*  
707 *Neurosci. Methods* **254**, 46–59 (2015).
- 708 62. Whitfield-Gabrieli, S. & Nieto-Castanon, A. *Conn* : A Functional Connectivity Toolbox

- 709 for Correlated and Anticorrelated Brain Networks. *Brain Connect.* **2**, 125–141 (2012).
- 710 63. Yarkoni, T., Poldrack, R. A., Nichols, T. E., Van Essen, D. C. & Wager, T. D. Large-  
711 scale automated synthesis of human functional neuroimaging data. *Nat. Methods* **8**, 665–670  
712 (2011).
- 713 64. Kanwisher, N., McDermott, J. & Chun, M. M. The fusiform face area: a module in  
714 human extrastriate cortex specialized for face perception. *J. Neurosci.* **17**, 4302–4311 (1997).
- 715 65. Kanwisher, N. & Yovel, G. The fusiform face area: a cortical region specialized for the  
716 perception of faces. *Philos. Trans. R. Soc. B Biol. Sci.* **361**, 2109–2128 (2006).
- 717 66. McCarthy, G., Puce, A., Gore, J. C. & Allison, T. Face-Specific Processing in the  
718 Human Fusiform Gyrus. *J. Cogn. Neurosci.* **9**, 605–610 (1997).
- 719 67. Rossion, B., Hanseeuw, B. & Dricot, L. Defining face perception areas in the human  
720 brain: A large-scale factorial fMRI face localizer analysis. *Brain Cogn.* **79**, 138–157 (2012).
- 721 68. Contreras, J. M., Banaji, M. R. & Mitchell, J. P. Multivoxel Patterns in Fusiform Face  
722 Area Differentiate Faces by Sex and Race. *PLoS ONE* **8**, e69684 (2013).
- 723 69. Freeman, J. B., Rule, N. O., Adams, R. B. & Ambady, N. The Neural Basis of  
724 Categorical Face Perception: Graded Representations of Face Gender in Fusiform and  
725 Orbitofrontal Cortices. *Cereb. Cortex* **20**, 1314–1322 (2010).
- 726 70. Tsantani, M. *et al.* FFA and OFA Encode Distinct Types of Face Identity Information.  
727 *J. Neurosci.* **41**, 1952–1969 (2021).
- 728 71. Andrews, T. J., Davies-Thompson, J., Kingstone, A. & Young, A. W. Internal and  
729 External Features of the Face Are Represented Holistically in Face-Selective Regions of Visual  
730 Cortex. *J. Neurosci.* **30**, 3544–3552 (2010).
- 731 72. Kok, E. M. *et al.* Holistic processing only? The role of the right fusiform face area in  
732 radiological expertise. *PLOS ONE* **16**, e0256849 (2021).
- 733 73. Zhang, J., Li, X., Song, Y. & Liu, J. The Fusiform Face Area Is Engaged in Holistic,  
734 Not Parts-Based, Representation of Faces. *PLoS ONE* **7**, e40390 (2012).
- 735 74. Laurita, A. C. & Nathan Spreng, R. The Hippocampus and Social Cognition. in *The*  
736 *Hippocampus from Cells to Systems* (eds. Hannula, D. E. & Duff, M. C.) 537–558 (Springer  
737 International Publishing, 2017). doi:10.1007/978-3-319-50406-3\_17.
- 738 75. Montagrin, A., Saiote, C. & Schiller, D. The social hippocampus: M ONTAGRIN ET AL .  
739 *Hippocampus* **28**, 672–679 (2018).
- 740 76. Aminoff, E., Gronau, N. & Bar, M. The Parahippocampal Cortex Mediates Spatial and  
741 Nonspatial Associations. *Cereb. Cortex* **17**, 1493–1503 (2007).
- 742 77. Li, M., Lu, S. & Zhong, N. The Parahippocampal Cortex Mediates Contextual

- 743 Associative Memory: Evidence from an fMRI Study. *BioMed Res. Int.* **2016**, 1–11 (2016).
- 744 78. Aminoff, E., Kveraga, K. & Bar, M. The role of the parahippocampal cortex in  
745 cognition. *Trends Cogn. Sci.* **17**, 379–390 (2013).
- 746 79. Bar, M. & Aminoff, E. Cortical analysis of visual context. *Neuron* **38**, 347–358 (2003).
- 747 80. Balgova, E., Diveica, V., Walbrin, J. & Binney, R. J. The role of the ventrolateral  
748 anterior temporal lobes in social cognition. *Hum. Brain Mapp.* **43**, 4589–4608 (2022).
- 749 81. Bechara, A. The neurology of social cognition. *Brain* **125**, 1673–1675 (2002).
- 750 82. Frith, U. & Frith, C. The social brain: allowing humans to boldly go where no other  
751 species has been. *Philos. Trans. R. Soc. B Biol. Sci.* **365**, 165–176 (2010).
- 752 83. Olson, I. R., Plotzker, A. & Ezzyat, Y. The Enigmatic temporal pole: a review of  
753 findings on social and emotional processing. *Brain* **130**, 1718–1731 (2007).
- 754 84. Ross, L. A. & Olson, I. R. Social cognition and the anterior temporal lobes. *NeuroImage*  
755 **49**, 3452–3462 (2010).
- 756 85. Olson, I. R., McCoy, D., Klobusicky, E. & Ross, L. A. Social cognition and the anterior  
757 temporal lobes: a review and theoretical framework. *Soc. Cogn. Affect. Neurosci.* **8**, 123–133  
758 (2013).
- 759 86. Rudebeck, P. H. & Rich, E. L. Orbitofrontal cortex. *Curr. Biol.* **28**, R1083–R1088  
760 (2018).
- 761 87. Barat, E., Wirth, S. & Duhamel, J.-R. Face cells in orbitofrontal cortex represent social  
762 categories. *Proc. Natl. Acad. Sci.* **115**, (2018).
- 763 88. Azzi, J. C. B., Sirigu, A. & Duhamel, J.-R. Modulation of value representation by social  
764 context in the primate orbitofrontal cortex. *Proc. Natl. Acad. Sci. U. S. A.* **109**, 2126–2131  
765 (2012).
- 766 89. Mah, L., Arnold, M. C. & Grafman, J. Impairment of Social Perception Associated With  
767 Lesions of the Prefrontal Cortex. *Am. J. Psychiatry* **161**, 1247–1255 (2004).
- 768 90. Xia, C., Stolle, D., Gidengil, E. & Fellows, L. K. Lateral Orbitofrontal Cortex Links  
769 Social Impressions to Political Choices. *J. Neurosci.* **35**, 8507–8514 (2015).
- 770 91. Blair, R. J. R. Impaired social response reversal: A case of 'acquired sociopathy'. *Brain*  
771 **123**, 1122–1141 (2000).
- 772 92. Koski, J. E., Collins, J. A. & Olson, I. R. The neural representation of social status in  
773 the extended face-processing network. *Eur. J. Neurosci.* **46**, 2795–2806 (2017).
- 774 93. Cunningham, W. A. & Zelazo, P. D. Attitudes and evaluations: a social cognitive  
775 neuroscience perspective. *Trends Cogn. Sci.* **11**, 97–104 (2007).
- 776 94. Kobayashi, K., Kable, J. W., Hsu, M. & Jenkins, A. C. Neural representations of others'

777 traits predict social decisions. *Proc. Natl. Acad. Sci.* **119**, e2116944119 (2022).

778 95. Koechlin, E. & Summerfield, C. An information theoretical approach to prefrontal  
779 executive function. *Trends Cogn. Sci.* **11**, 229–235 (2007).

780 96. Hartwigsen, G., Neef, N. E., Camilleri, J. A., Margulies, D. S. & Eickhoff, S. B.  
781 Functional Segregation of the Right Inferior Frontal Gyrus: Evidence From Coactivation-Based  
782 Parcellation. *Cereb. Cortex* **29**, 1532–1546 (2019).

783 97. Thompson-Schill, S. L., D’Esposito, M., Aguirre, G. K. & Farah, M. J. Role of left  
784 inferior prefrontal cortex in retrieval of semantic knowledge: A reevaluation. *Proc. Natl. Acad.*  
785 *Sci.* **94**, 14792–14797 (1997).

786 98. Zhang, J. X., Feng, C.-M., Fox, P. T., Gao, J.-H. & Tan, L. H. Is left inferior frontal  
787 gyrus a general mechanism for selection? *NeuroImage* **23**, 596–603 (2004).

788 99. Muayqil, T., Davies-Thompson, J. & Barton, J. J. S. Representation of visual symbols  
789 in the visual word processing network. *Neuropsychologia* **69**, 232–241 (2015).

790 100. Xu, J., Gannon, P. J., Emmorey, K., Smith, J. F. & Braun, A. R. Symbolic gestures and  
791 spoken language are processed by a common neural system. *Proc. Natl. Acad. Sci.* **106**, 20664–  
792 20669 (2009).

793 101. Menon, V. Salience Network. in *Brain Mapping* 597–611 (Elsevier, 2015).  
794 doi:10.1016/B978-0-12-397025-1.00052-X.

795 102. Seeley, W. W. *et al.* Dissociable Intrinsic Connectivity Networks for Salience  
796 Processing and Executive Control. *J. Neurosci.* **27**, 2349–2356 (2007).

797 103. Zhou, K. *et al.* The Contribution of Thalamic Nuclei in Salience Processing. *Front.*  
798 *Behav. Neurosci.* **15**, 634618 (2021).

799 104. Chand, G. B. & Dhamala, M. The salience network dynamics in perceptual decision-  
800 making. *NeuroImage* **134**, 85–93 (2016).

801 105. Lamichhane, B., Adhikari, B. M. & Dhamala, M. Salience Network Activity in  
802 Perceptual Decisions. *Brain Connect.* **6**, 558–571 (2016).

803 106. Uddin, L. Q. Salience processing and insular cortical function and dysfunction. *Nat.*  
804 *Rev. Neurosci.* **16**, 55–61 (2015).

805 107. White, T. P., Engen, N. H., Sørensen, S., Overgaard, M. & Shergill, S. S. Uncertainty  
806 and confidence from the triple-network perspective: Voxel-based meta-analyses. *Brain Cogn.*  
807 **85**, 191–200 (2014).

808 108. Botvinick, M. M., Cohen, J. D. & Carter, C. S. Conflict monitoring and anterior  
809 cingulate cortex: an update. *Trends Cogn. Sci.* **8**, 539–546 (2004).

810 109. Dosenbach, N. U. F. *et al.* A Core System for the Implementation of Task Sets. *Neuron*



811 **50**, 799–812 (2006).

812 110. Neta, M., Schlaggar, B. L. & Petersen, S. E. Separable responses to error, ambiguity,  
813 and reaction time in cingulo-opercular task control regions. *NeuroImage* **99**, 59–68 (2014).

814 111. Stolier, R. M. & Freeman, J. B. A Neural Mechanism of Social Categorization. *J.*  
815 *Neurosci.* **37**, 5711–5721 (2017).

816 112. Sherman, M. T., Seth, A. K. & Kanai, R. Predictions Shape Confidence in Right Inferior  
817 Frontal Gyrus. *J. Neurosci.* **36**, 10323–10336 (2016).

818 113. Mars, R. B. *et al.* Whole brain comparative anatomy using connectivity blueprints. *eLife*  
819 **7**, e35237 (2018).

820 114. Thiebaut de Schotten, M. & Forkel, S. J. The emergent properties of the connected brain.  
821 *Science* **378**, 505–510 (2022).

822 115. Xu, T. *et al.* Cross-species functional alignment reveals evolutionary hierarchy within  
823 the connectome. *NeuroImage* **223**, 117346 (2020).

824 116. Colagè, I. & d’Errico, F. Culture: The Driving Force of Human Cognition. *Top. Cogn.*  
825 *Sci.* (2018) doi:10.1111/tops.12372.

826 117. Colagè, I. & d’Errico, F. The Roots of Creativity: investing in Cultural Transmission.  
827 *Acta Philos.* **32**, 95–116 (2023).

828 118. d’Errico, F. & Colagè, I. Cultural Exaptation and Cultural Neural Reuse: A Mechanism  
829 for the Emergence of Modern Culture and Behavior. *Biol. Theory* **13**, 213–227 (2018).

830 119. Stout, D., Hecht, E., Khreisheh, N., Bradley, B. & Chaminade, T. Cognitive Demands  
831 of Lower Paleolithic Toolmaking. *PLOS ONE* **10**, e0121804 (2015).

832 120. Hecht, E. E. *et al.* Acquisition of Paleolithic toolmaking abilities involves structural  
833 remodeling to inferior frontoparietal regions. *Brain Struct. Funct.* **220**, 2315–2331 (2015).

834 121. Putt, S., Wijekumar, S. & Spencer, J. P. Prefrontal cortex activation supports the  
835 emergence of early stone age toolmaking skill. *NeuroImage* **199**, 57–69 (2019).

836