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

3

4

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6

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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 ¹⁻⁵.
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 ⁶⁻¹⁴. 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 ¹⁵⁻¹⁹.

46 The earliest use of red ochre goes back to 500 ka in Africa ²⁰⁻²³, 380 ka in Europe
47 ^{22,24,25}, and 73 ka in Asia ^{22,26,27}. 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 ^{20,28,29}, that certain
54 shades of red were particularly sought after ³⁰⁻³², that ochre was modified by heating to
55 change its color ^{33,34} but see ³⁵, and that in some cases very small quantities of pigments were
56 produced ³⁶, 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 ³⁷⁻⁴⁵. 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 ^{40,41,46-49}. 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 ^{50,51}. 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 ⁵². 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 ⁵³⁻⁵⁶. 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 ⁵⁷⁻⁵⁹, 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 ⁶⁰. 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 ± 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

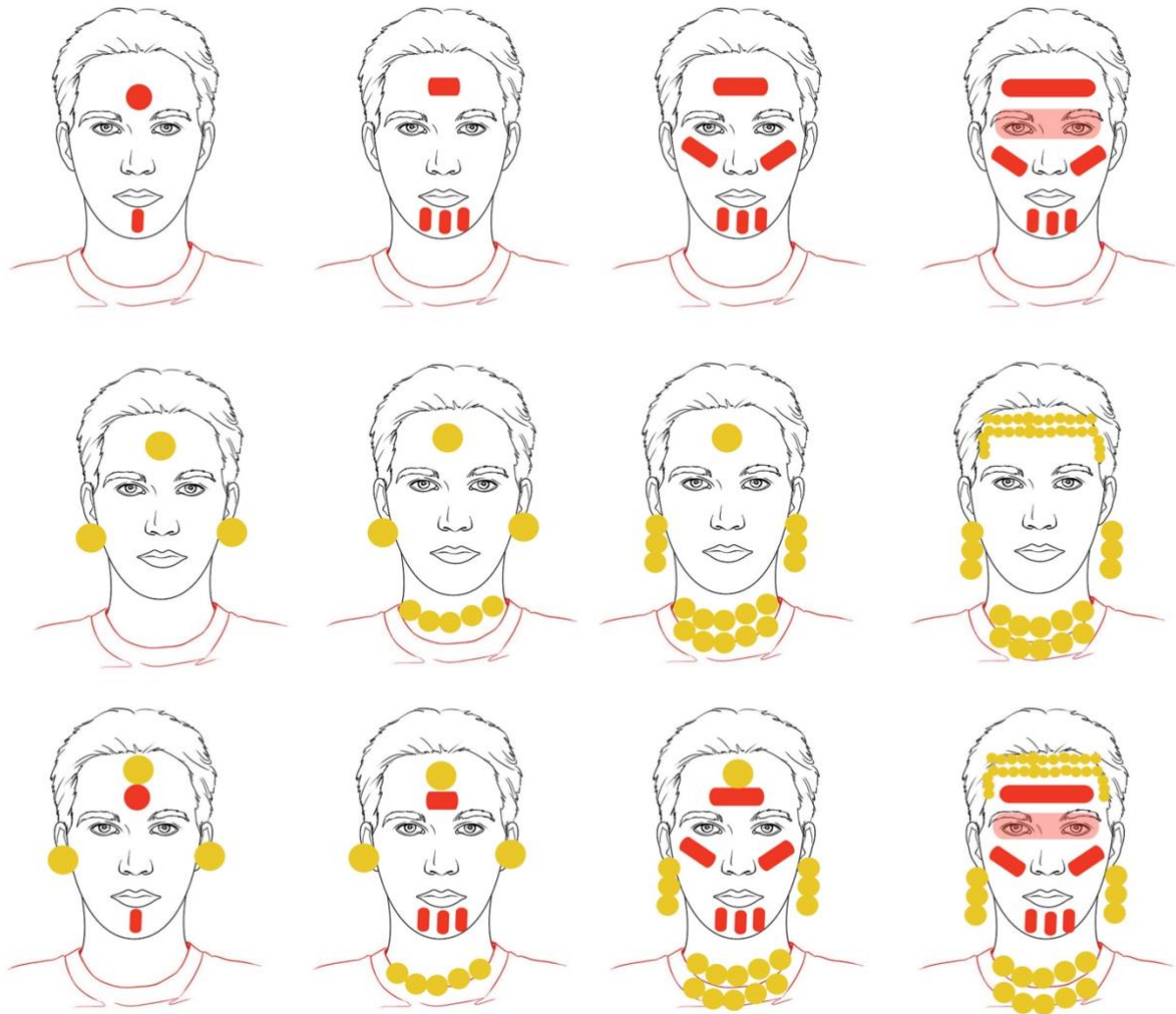
108 **2.3. Experimental design**

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.



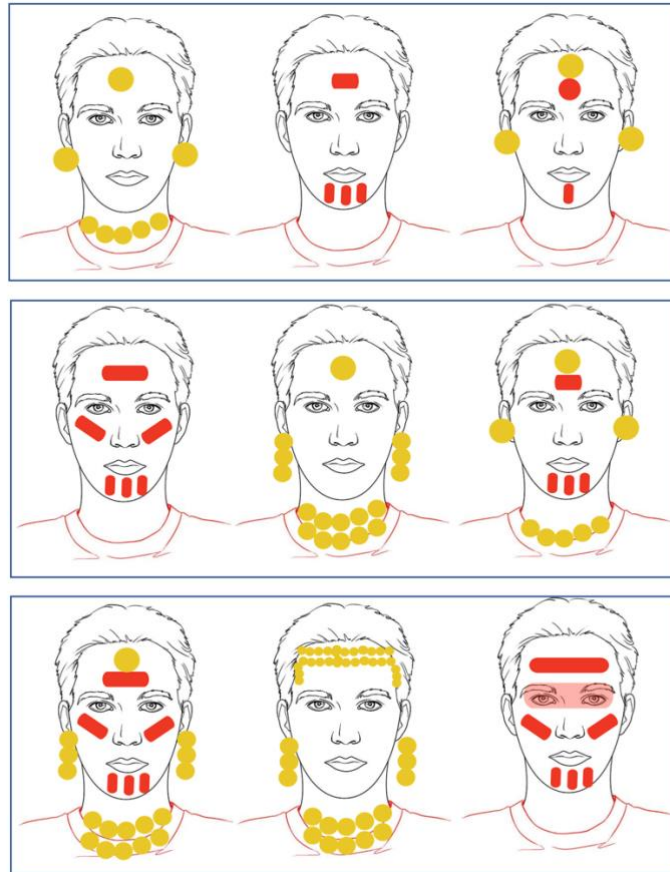
126
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128 Figure 1. Face ornamentations used in the tasks. Top row: paint only. The middle row: beadworks only. Bottom
129 row: a combination of paint and beadworks.

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.

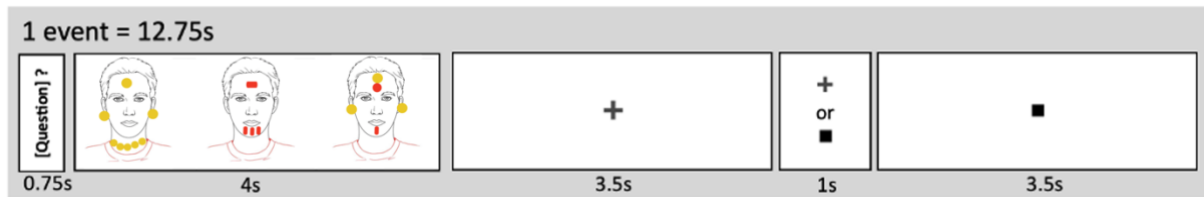
144

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 mm³).
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 mm³). 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 ⁶¹. 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 ⁶², 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 ⁶¹. 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**

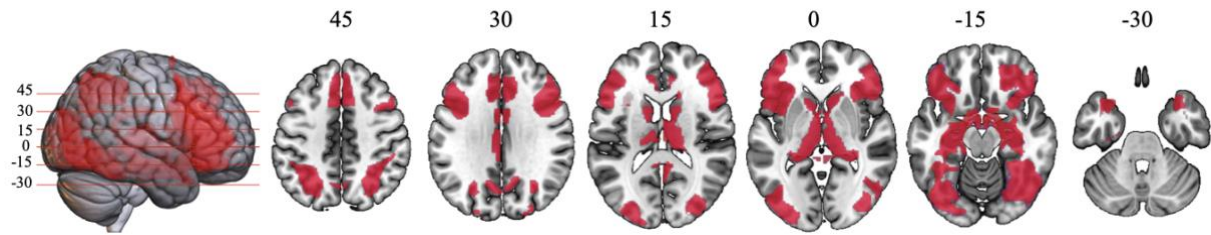
288 **3.3.1. Social status minus Ornament check (event-related paradigm)**

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 platform⁶³ 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.

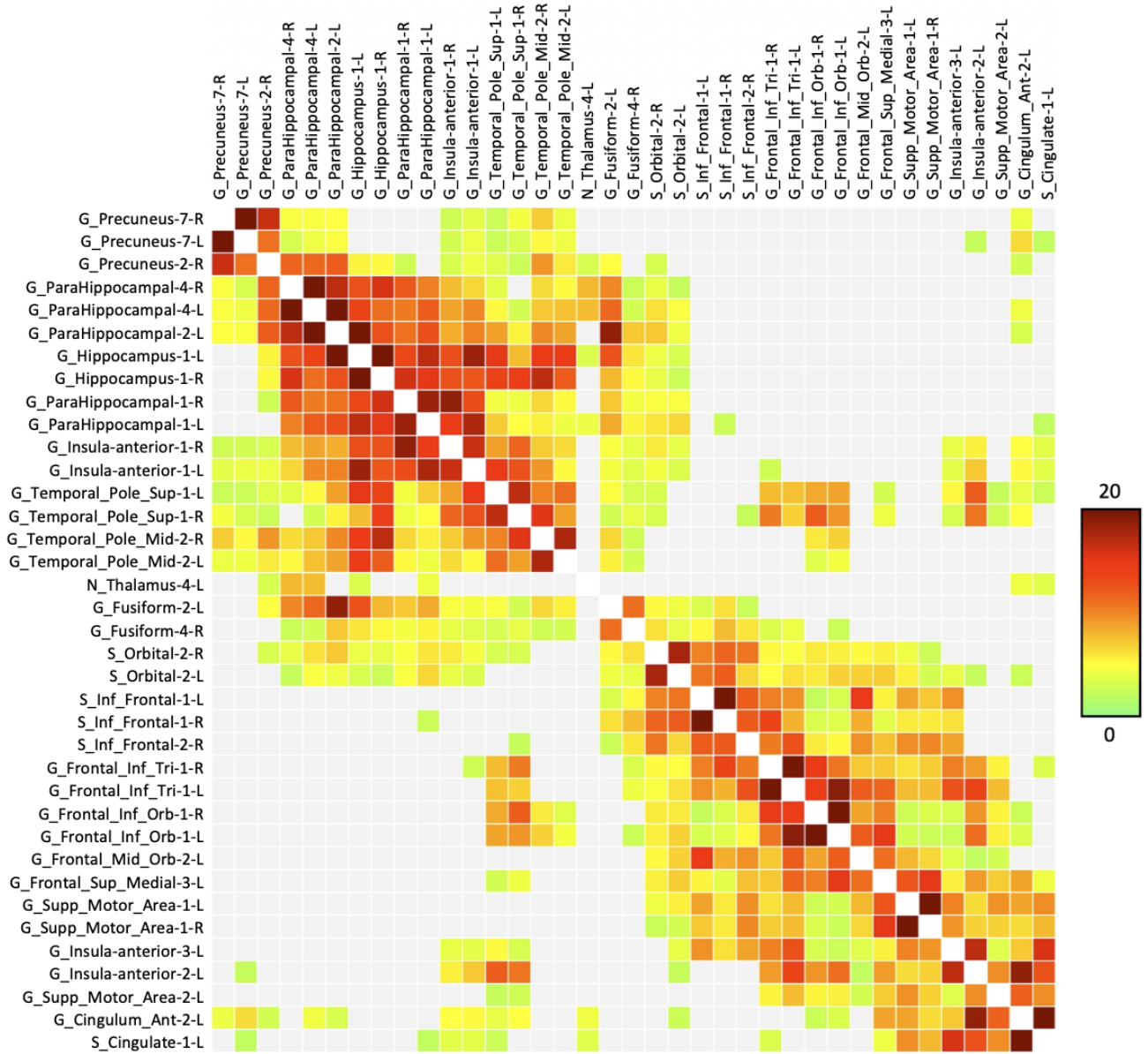
hROI Social status - Ornament check (* Specific to Social status – Ornament check, i.e., more or not activated in Ornament block – faces)	MNI coordinates of the center of mass	Mean (BOLD)	Standard deviation (BOLD)	p (FDR corrected)
G_Cingulum_Ant-2-L*	-7 34 22	0.12	0.16	0.0005
G_Cingulum_Ant-2-R	7 33 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
S_Cingulate-1-L*	-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
G_Frontal_Inf_Orb-1-L*	-42 31 -17	0.21	0.22	<.0001
G_Frontal_Inf_Orb-1-R*	44 33 -14	0.13	0.16	0.0001
G_Frontal_Mid_Orb-2-L*	-41 49 -5	0.23	0.30	0.0005
S_Orbital-1-R	25 41 -15	0.07	0.11	0.0023
S_Orbital-2-L*	-31 34 -13	0.26	0.21	<.0001
S_Orbital-2-R*	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
S_Inf_Frontal-1-L*	-44 38 12	0.37	0.31	<.0001
S_Inf_Frontal-1-R*	46 40 10	0.24	0.21	<.0001
S_Inf_Frontal-2-L	-43 15 29	0.38	0.34	<.0001
S_Inf_Frontal-2-R*	44 19 28	0.28	0.21	<.0001
G_Frontal_Inf_Tri-1-L*	-49 26 5	0.15	0.22	0.0011
G_Frontal_Inf_Tri-1-R*	50 29 5	0.07	0.17	0.0434
S_Precentral-1-R	50 10 24	0.11	0.24	0.0178
G_Frontal_Sup_Medial-3-L*	-5 35 43	0.19	0.23	0.0002
G_Frontal_Sup_Medial-3-R	6 33 44	0.14	0.19	0.0006
G_Supp_Motor_Area-1-L*	-6 22 46	0.39	0.23	<.0001
G_Supp_Motor_Area-1-R*	6 21 48	0.37	0.26	<.0001
G_Supp_Motor_Area-2-L	-11 18 61	0.08	0.16	0.0134
G_Insula-anterior-1-L*	-20 5 -19	0.12	0.18	0.0013
G_Insula-anterior-1-R*	19 7 -19	0.07	0.17	0.0329
G_Insula-anterior-2-L*	-34 17 -13	0.17	0.24	0.0009
G_Insula-anterior-2-R	35 18 -13	0.10	0.18	0.0054
G_Insula-anterior-3-L*	-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
G_Fusiform-2-L*	-35 -26 -23	0.09	0.10	<.0001
G_Fusiform-4-L	-43 -50 -17	0.19	0.18	<.0001
G_Fusiform-4-R*	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
G_Precuneus-2-R*	5 -56 20	0.27	0.29	<.0001
G_Precuneus-7-L*	-6 -65 35	0.16	0.31	0.0097
G_Precuneus-7-R*	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
G_Temporal_Pole_Sup-1-L*	-35 11 -24	0.09	0.13	0.0019
G_Temporal_Pole_Sup-1-R*	36 16 -24	0.10	0.16	0.0044
G_Temporal_Pole_Mid-2-L*	-35 9 -33	0.05	0.10	0.0097
G_Temporal_Pole_Mid-2-R*	35 12 -34	0.04	0.09	0.0121
G_Hippocampus-1-L*	-30 -7 -19	0.06	0.11	0.0115
G_Hippocampus-1-R*	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
G_ParaHippocampal-1-L*	-16 -4 -18	0.24	0.23	<.0001

G_ParaHippocampal-1-R*	14 -4 -18	0.17	0.20	0.0001
G_ParaHippocampal-2-L*	-28 -27 -19	0.07	0.17	0.0253
G_ParaHippocampal-2-R	29 -25 -19	0.07	0.14	0.0169
G_ParaHippocampal-4-L*	-17 -27 -13	0.12	0.21	0.0071
G_ParaHippocampal-4-R*	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
N_Thalamus-4-L*	-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 perception⁶⁴⁻⁶⁶ and lateralized in the right hemisphere⁶⁷. 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^{68,69}. More recently, a study
380 showed that FFA processes characteristics such as social traits, gender, and high-level visual
381 features of faces⁷⁰ 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 processing⁷¹⁻⁷³. 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^{74,75}. The parahippocampus
398 appears to play, among others, a pivotal role in contextual associative processing^{76,77}, i.e., in
399 binding elements composing stimuli. It provides a unified context for further processing (see
400⁷⁸ 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 ^{76,79}. 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 ⁸⁰⁻⁸⁴. 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 ⁸⁵. 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 ⁸⁶. 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 ⁸⁷ and evaluating social information ⁸⁸ in non-
431 human primates. In humans, a deficit in social perception after orbitofrontal cortex lesions ⁸⁹,
432 an inability to judge social traits in a decision-making task ⁹⁰, or acquired sociopathy have
433 been reported ⁹¹.

434 In healthy participants, fMRI studies have emphasized the role of the orbitofrontal
435 cortex in social cognition and social behavior (^{55,92}; See ⁶⁰ for a review) and, more
436 specifically, in explicit processing ⁹³. The orbitofrontal cortex is sensitive to non-verbal social
437 signals ⁵⁵. Recent results indicate that this area is critical in representing social status ⁹². 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-making⁹⁴. 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 aspects⁹⁵.

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 cognition⁹⁶. The left inferior frontal gyrus is involved in selecting some aspects
454 or subsets of available information among competing alternatives^{97,98}. This region also plays
455 a role in processing non-linguistic symbolic information^{99,100}, 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**

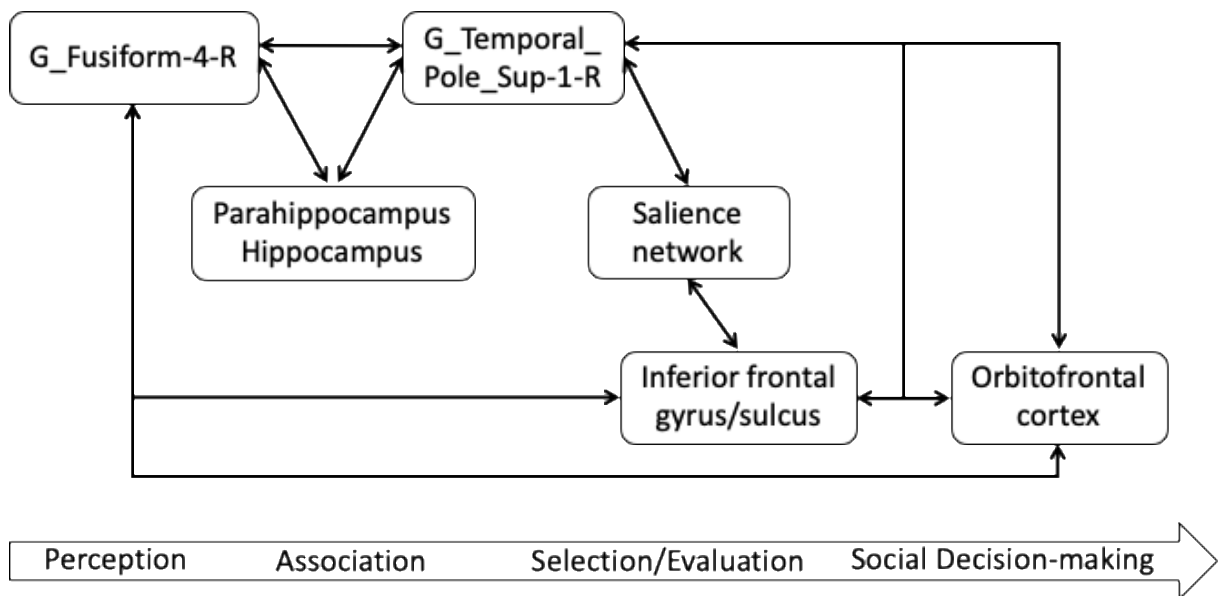
462 Social status attribution elicited activation in the anterior insula, the dorsal anterior cingulate
463 cortex (dACC)/pre-SMA, and subcortical structures, such as the thalamus and the caudate
464 nuclei. These regions constitute the so-called salience network, whose key components are the
465 insula anterior and the dACC/pre-SMA^{101–103}. This network is involved in selecting relevant
466 elements of the environment for perceptual decision-making^{104–106}. 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 task¹⁰⁷.
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 ¹⁰⁸⁻¹¹⁰, and more recently in social
 477 categorization domain ¹¹¹.

478

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

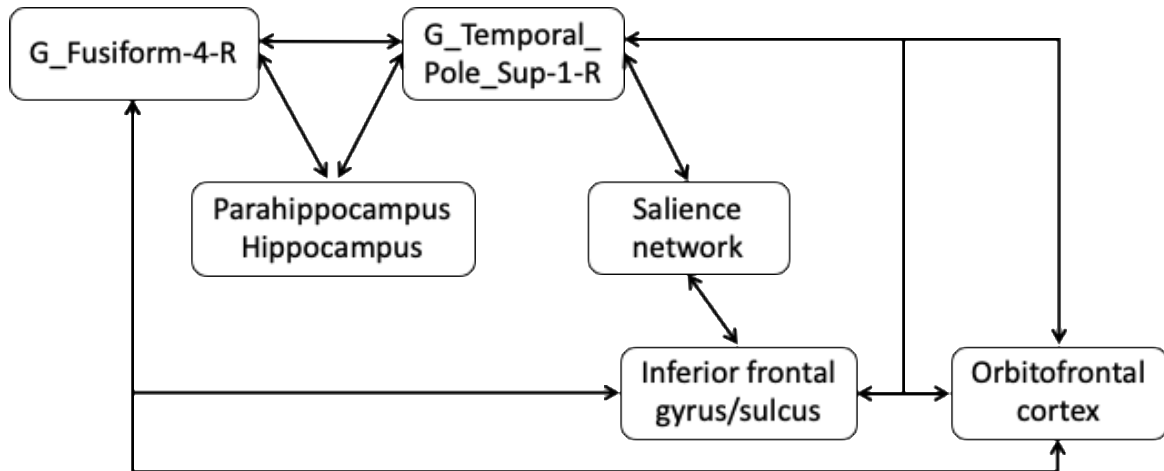
480 Resting-state functional connectivity provides insight into the potential interactions between
 481 neural assemblies activated by the social status assignment task. The G_Fusiform-4-R and the
 482 G_Temporal_Pole_Sup-1-R were characterized by many connections with other activated
 483 regions (



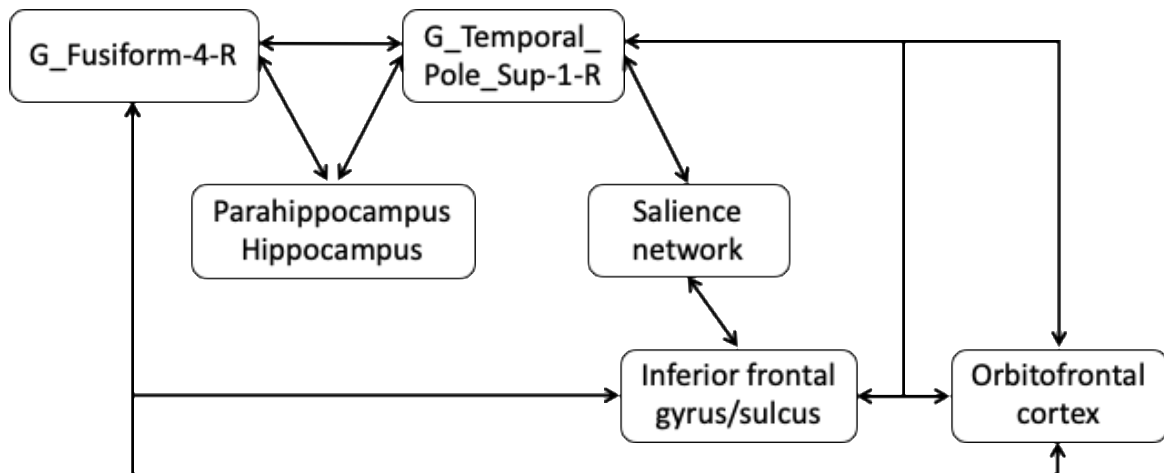
484

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 ¹¹².
 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 ^{113–115}.

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^{116–118}. A progressive co-option of brain regions has also been suggested for the
532 evolution of tool-making^{119–121}. 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

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