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

3

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14

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

17

18 **Abstract**

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

31

32

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 to at least 140,000 years ago (Sehassseh et al.,
37 2021). Body painting, tattooing, scarification, wearing of ornaments, mutilations, hairstyles,
38 and clothing are amongst the best-known practices for performing these functions in
39 traditional societies (Barth, 1969; Dubin, 1999; Hodder, 1991; Klumpp & Kratz, 1993;
40 Sanders, 2002). The ethnographic record shows that personal ornaments, in particular, play a
41 crucial role in communicating ethnic affiliation, reinforcing the sense of belonging to the
42 group and its cohesion, establishing boundaries with neighboring groups, and conveying
43 information on linguistic, ideological, and religious membership (Dubin, 1987; Hatton et al.,
44 2022; Kuhn & Stiner, 2007; Kuper, 1973; Nițu et al., 2019; Pitarch Martí et al., 2017; Sciamia
45 & Eicher, 1998; Vanhaeren & d’Errico, 2006; Wright et al., 2014). Ornaments can also
46 provide information about social status, gender, marital situation, and the number of children
47 the wearer has had (Meisch, 1998; O’Hear, 1998; Sciamia & Eicher, 1998; Wickler & Seibt,
48 1995). Special ornaments and body paints may be put on at rites of passage occurring at the
49 individual birth, during initiation ceremonies, marriage, healing, or death (Beckwith & Fisher,
50 1999; Carey, 1991; Carter & Helmer, 2015; Nowell & Cooke, 2021; Ogundiran, 2002; Twala,
51 1958). The earliest use of red ochre goes back to 500 ka in Africa (Brooks et al., 2018;
52 Dapschaskas et al., 2022; Rosso, 2022; Watts et al., 2016), 380 ka in Europe (de Lumley et
53 al., 2016; Roebroeks et al., 2012; Rosso, 2022), and 73 ka in Asia (d’Errico, 2021; Langley et
54 al., 2019; Rosso, 2022). The wearing of personal ornaments, many of which are deliberately
55 covered with ochre, is attested since at least 142 ka in North Africa, 80 ka in Southern Africa,
56 and 120 ka in the Near East (Bar-Yosef Mayer et al., 2009, 2020; Bouzouggar et al., 2007;
57 d’Errico et al., 2005; d’Errico, Vanhaeren, et al., 2009; Sehassseh et al., 2021; Shipton et al.,
58 2018; Steele et al., 2019; Vanhaeren et al., 2006). Because the understanding by others of the
59 meaning attached to ornaments and body paints presupposes the existence of shared codes,
60 archaeological objects which have fulfilled these functions are often considered reliable
61 evidence for the emergence of symbolic material cultures in our genus and possibly language
62 (Davidson & Noble, 1989; d’Errico et al., 2005; d’Errico, Henshilwood, et al., 2009; d’Errico,
63 Vanhaeren, et al., 2009; Marshack, 1976; Vanhaeren et al., 2013), although there is no
64 consensus on the ornament-language relationship (Botha, 2008, 2009). In this regard, wearing
65 body adornments can be considered an archaeological indicator of modern social cognition,

66 defined as the entire set of cognitive processes related to social perception, judgement and
67 decision making that shape human interactions (Dunbar, 2003; Fiske & Taylor, 2017).
68 Although body symbols played a key role in all human societies and appeared very early in
69 human history, the cerebral regions mobilized by their perception and interpretation remain
70 unknown. Numerous studies have focused on the brain substrates of the emotional aspects of
71 social cognition (Lewis et al., 2011; Rameson et al., 2012; Spreng & Mar, 2012; Yang et al.,
72 2015; Zaki & Ochsner, 2012). The role of the medial prefrontal cortex, the temporoparietal
73 junction, and the temporal poles has been highlighted in their contribution to social cognition
74 (Adolphs, 2009; Frith, 2007). However, the neural network of social status judgment may not
75 completely overlap with that of emotion processing in social cognition. For example, one
76 study showed that lesions to the ventromedial prefrontal region only marginally affected
77 social dominance judgment (Karafin et al., 2004). Neuroimaging studies have confirmed that
78 the perception of social hierarchies relies on the intraparietal sulcus, the dorsolateral and
79 orbital frontal cortex, and the lateral occipital and occipitotemporal cortex (Chiao, 2010;
80 Chiao et al., 2009; Marsh et al., 2009; Zink et al., 2008). However, the identification of social
81 markers does not necessarily imply a ranking. One can, for example, recognize the status of
82 married women or men on the basis of the way they dress, without implying a hierarchical
83 judgment.

84 Body ornaments and facial paintings may convey information on social roles disconnected
85 from an enduring social hierarchy and embodied by individuals only on special occasions,
86 such as carnivals, line crossing ceremonies and the like. Although body paintings and the
87 wearing of beads to express social roles are already attested in the earliest African *Homo*
88 *sapiens* and, more rarely, in Neanderthals (Jaubert et al., 2022; Vanhaeren et al., 2019; Zilhão
89 et al., 2010), very little is known about the brain networks involved in processing such
90 information, the possible processes that led to a complexification of these behaviors, as well
91 as their timeline. In the broader field of social cognition, fMRI studies have emphasized the
92 role of the orbitofrontal cortex in social cognition and social behavior (Koski et al., 2017;
93 Marsh et al., 2009, see Forbes & Grafman, 2010 for a review), and, more specifically, in
94 explicit processing (Cunningham & Zelazo, 2007). The orbitofrontal cortex is sensitive to
95 non-verbal social signals (Marsh et al., 2009). Recent results indicate that this area is critical
96 in representing social status (Koski et al., 2017). In the anterior part of the ventral visual
97 pathway, the temporal pole is another structure that plays a privileged role in processing
98 social information. Several studies have documented its involvement in social cognition, and

99 this region is considered part of the social brain network (Balgova et al., 2022; Bechara, 2002;
100 Frith & Frith, 2010; Olson et al., 2007; Ross & Olson, 2010).

101 In the present study, participants were asked to assign social roles or statuses to faces adorned
102 with paintings, beads, or both. At the same time, their brain activity was monitored using
103 functional magnetic resonance imaging (fMRI). Participants were given no guidance on the
104 meaning of the face decorations and had to create their arbitrary social code. The attribution of
105 a social status mobilizes implicit and explicit processes. Implicit processes are rapid, require
106 little cognitive effort, and can occur without awareness (for example perceiving an individual
107 as having a high social status by his body language). Explicit processes are cognitively
108 demanding, slow, and deliberative (inferring for example an army officer's career and
109 achievements from the distinctions he wears on the uniform, or identifying an individual's
110 preferred musical style based on the tattoos, piercings, haircut style and studded clothing he
111 wears). In this study, we focused on explicit processes because the behavior that enabled the
112 use of body adornments to express a status or social role is based on explicit mechanisms of
113 social cognition, that is, voluntarily and consciously linking types of ornaments to a social role.
114 To isolate explicit processes, we included, using the same stimuli, a perceptual task (1-back) of
115 adorned faces that does not explicitly require a social role attribution. Subtracting it from the
116 status-assignment task removes the activations linked to the perception of ornate faces and to
117 possible implicit social judgments ("first impressions") that would occur automatically without
118 explicitly requesting any social judgment.

119 In addition, at rest, the functional connectivity of the brain regions involved was analyzed to
120 provide information on the interaction of the brain areas implicated in the social status
121 attribution task. Our results identify, for the first time, the brain networks engaged in attributing
122 social status from different arrangements of paintings and ornaments on the human face, the
123 way they work in synergy, and provide sound bases on which build an evolutionary scenario
124 for the gradual integration of these brain areas during the evolution of our genus.

125

126 **2. Materials and methods**

127 **2.1. Ethics statements**

128 The 'Nord-Ouest III' local Ethics Committee approved the study on 10/14/2021 (N° IDRCB:
129 2021-A01817-34). All the participants signed informed consent before the MRI acquisition.

130

131 **2.2. Participants**

132 Thirty-five healthy adults (age range 18–29 years, mean age 22 ± 2 years (SD), 18 women, four
133 left-handed) with no neurological history were included. One participant was excluded from
134 the analysis because of a brain abnormality discovered during MRI acquisition. Of the 34
135 participants included, 31 were French and had grown up in France, two were of Malagasy origin
136 and one was Syrian. All participants were fluent in French. The vast majority of participants
137 were students from the Bordeaux university campus in various fields (psychology, medicine,
138 engineering, law, finance). Only four of them had a full-time professional activity.

139

140 **2.3. Experimental design**

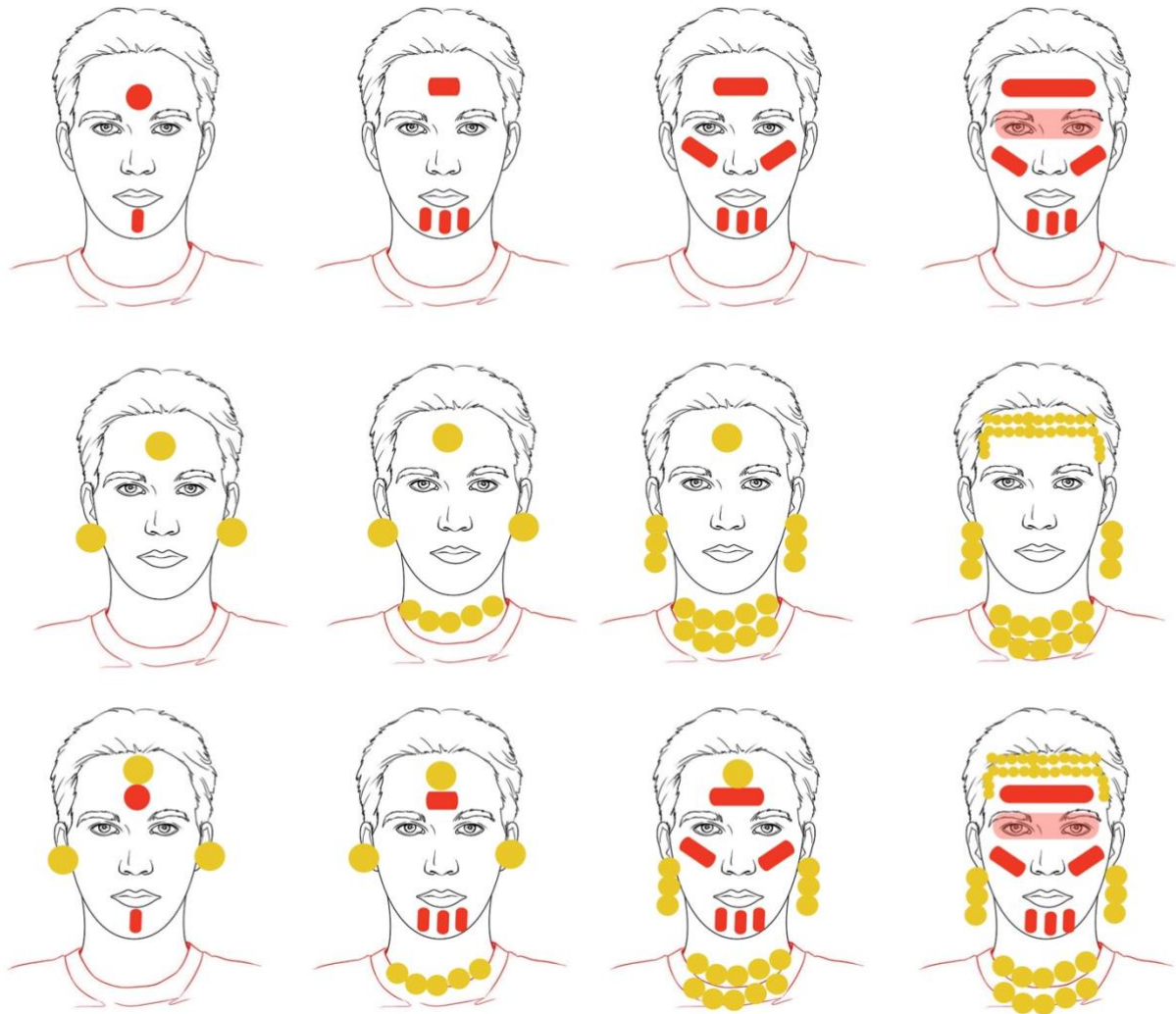
141 The functional acquisition was organized in a single session consisting of six runs during
142 which participants had to perform a selection task (first three runs), then a 1-back task (last
143 three runs). After receiving instructions for these tasks, participants completed a short training
144 run outside the MRI. Participants were familiarized with the tasks in the half hour before the
145 MRI session. In particular, it was ensured that all proposed social roles (see below) were
146 known to the participants. Clarifications were made if necessary.

147

148 **2.3.1. Stimuli**

149 The set of stimuli included pictures of faces (up to below the shoulders) of 34 unknown people,
150 who have given their written consent for their face to be published, in the same range of age
151 (17 women, 17 men, around 30 years old) wearing ornaments and adopting a neutral expression.
152 Each face was ornamented with either spherical wooden beads, red paintings, or a combination
153 of both (Figure 1). Ornaments included earrings with one or three beads, necklaces with one or
154 two chains of beads, a diadem consisting of a chain of beads, and a single large spherical bead
155 in the middle of the forehead. Red paintings included one or three vertical lines on the chin; a
156 dot or a horizontal line on the forehead; oblique lines on the cheeks; and a large horizontal band
157 including the eyes. Associations of paintings and beads were designed to make both types of
158 ornamentation gradually more invasive on the face. The choice of the types of adornment and
159 paint applied to the participants' faces responded to two requirements. They should be visually
160 perceived as mutually exclusive and establish no obvious link with existing codes used in
161 known human societies to culturalize the human face. In all, twelve types of facial
162 ornamentation have been designed and implemented.

163

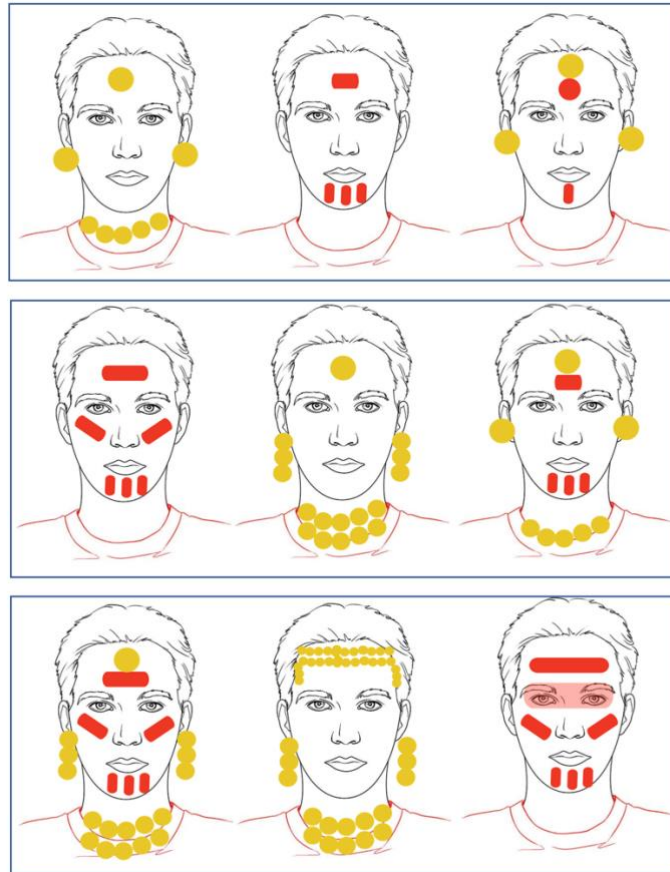


164
 165 Figure 1. Face ornamentations used in the tasks. Top row: paint only. Middle row: beadworks only. Bottom row:
 166 a combination of paint and beadworks.

167 **2.3.2. Selection task.**

168 In this task, the stimuli corresponded to a triplet of photos of three different persons of the
 169 same gender (male or female), one wearing ornaments, one with paintings, and one with both
 170 (Figure 2). The order of presentation of each stimulus was randomized. Within a triplet, the
 171 richness of the ornaments was comparable between the pictures to avoid biases in the choice.
 172 There were three levels of richness between the triplets (Figure 2).

173

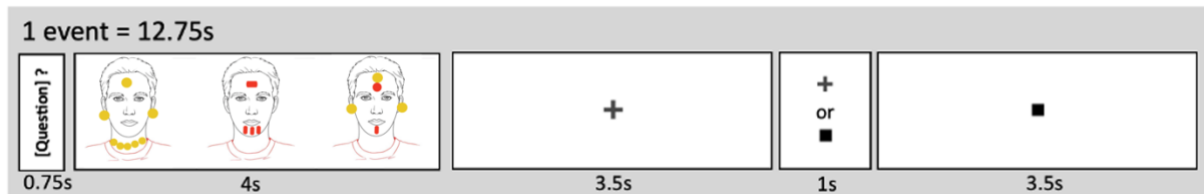


174
 175 Figure 2. Examples of triplet of photographs used in the selection task. The three columns correspond to three
 176 levels of richness. For each triplet, participants had to choose the ornaments that best matched the social status
 177 (social status condition: e.g., who is the shaman?) or that required an ornament check (ornament check
 178 condition: e.g., who has painted eyes). Note that in the study, photographs of real people with adorned face were
 179 presented but could not be displayed here because of their identifying nature

180 The selection task was implemented as follows (Figure 3): a short question (one or two words)
 181 was displayed during 0.75 s. The question could concern either the displayed persons' social
 182 role (Social status condition) or the type of ornamentation they displayed (Ornament check
 183 condition). Then, a new triplet of pictures was shown for 4 s. The participant had to choose, by
 184 pressing the corresponding button of a response box as soon as they made their decision, the
 185 person who best fitted the proposed social status, e.g., "Shaman" (Social status condition) or
 186 the person who corresponded to the ornament type proposition, e.g., "Painted cheeks"
 187 (Ornament check condition). Each question was asked twice for each gender. The list of
 188 questions is displayed in Table 1. During the familiarization phase, the participants have been
 189 explicitly instructed to use the ornaments as the basis for their social judgment.

190 The Ornament check condition was designed as a control condition, bearing the same pictures
 191 as the social status condition. It required attention to the ornaments without implementing
 192 social cognition processes.

193 Between each stimulus, a fixation cross was displayed, and a square appeared after a variable
 194 delay (3.5 s ± 1 s). Participants had to click the "1" button on the response box when the square
 195 appeared. This allowed the BOLD signal to return to its baseline level between stimuli while
 196 maintaining the attentional level. Each event lasted 12.75 s.
 197



198
 199 Figure 3. Organization of one event of the selection task.

200 Table 1. Questions in the social status and ornament check conditions. The wording of the questions was
 201 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?

202 Over the three runs, participants saw 80 stimuli, 40 in the social status condition (Figure S1 in
 203 supplementary material) and 40 in the ornament check condition. Each run lasted 5 min and
 204 51 s each and included 27 events (except run C, which included one less event) for a total
 205 duration of 5 min 38 s). Stimuli were presented in random order within each run. Immediately
 206 after the MRI acquisition, the experimenter asked the participant the criteria on which they
 207 based their social role attribution in the status condition.

208

209 2.3.3. 1-back task.

210 In the 1-back task, participants viewed a succession of ornamented faces (displayed for 1 s
 211 each, with an interstimulus interval of 983 ms). The participants had to report the repetition of
 212 two faces (Face condition) or two types of ornamentation (Ornament condition, including
 213 three modalities: paintings, beads, or both simultaneously) by pressing the "1" button on the
 214 response box. This repetition criterion was displayed during 750 ms at the beginning of each

215 block. Fifteen stimuli belonging to the same category of ornamentation were presented within
216 the same block (i.e., within a block, there were no images belonging to different categories).
217 There were three repetitions per block. Each of the three runs lasted 4 min and 15 s and
218 included six experimental blocks of 30.6 s interspersed with seven fixation blocks of 10.2 s.
219 Each run had four blocks of ornament condition and two blocks of face condition. The
220 presentation order of the 1-back runs was randomized.

221

222 **2.4. MRI acquisition**

223 Neuroimaging data acquisition was performed using a Siemens Prisma 3 Tesla MRI scanner.
224 Structural images were acquired using a high-resolution T1-weighted 3D sequence (TR =
225 2000 ms, TE = 2.03 ms; flip angle = 8°; 192 slices and isotropic voxel volume of 1 mm³).
226 Functional images were obtained using a whole-brain T2*-weighted echo planar image
227 acquisition (T2*-EPI Multiband x6, sequence parameters: TR = 850 ms; TE = 35 ms; flip
228 angle = 56°; 66 axial slices and isotropic voxel size of 2.4 mm³). The first sequence lasted 8
229 min and recorded participants' brain activity during resting state (i.e., when they let their
230 thoughts flow freely, without having a task to perform or falling asleep). This acquisition was
231 used to perform a resting-state functional connectivity analysis. Then, functional images were
232 acquired when the participants performed tasks based on stimuli perception. This was done
233 during six runs (three for each task: selection and 1-back). The presentation of the experiment
234 was programmed in E-prime software 3.0 (Psychology Software Tools, Pittsburgh, PA, USA).
235 The stimuli were displayed on a 27" screen. Participants saw the stimuli through the back of
236 the magnet tunnel via a mirror mounted on the head antenna.

237

238 **2.5. Data analysis**

239 **2.5.1. Behavioral analysis**

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

246

247 **2.5.2. Functional neuroimaging analysis**

248 T1-weighted scans were normalized via a specific template (T1-80TVS) corresponding to the
249 MNI space using SPM12. The 192 EPI-BOLD scans were realigned in each run using a rigid
250 transformation to correct the participant's motion during the fMRI sessions. Then, the EPI-
251 BOLD scans were rigidly registered structurally to the T1-weighted scan. All registration
252 matrices were combined to warp the EPI-BOLD functional scans to standard space with
253 trilinear interpolation. Once in standard space, a 5-mm-wavelength Gaussian filter was
254 applied.

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

263 Group analysis (second-level analysis) of fMRI data was conducted using JMP®
264 software, version 15. SAS Institute Inc, Cary, NC, 1989-2019. The first step was to select the
265 brain regions activated in the contrasts of interest, namely [Social status minus Ornament
266 check] in the selection task and [Ornament minus Face] in the 1-back task. We extracted
267 signal values from the [Social status minus Ornament check] contrast from each brain region
268 of each participant (hROI, homotopic region of interest) in the AICHA atlas (Joliot et al.,
269 2015). The MNI coordinates of the center of mass of each activated hROIs are given in Table
270 3. The hROIs included in the analysis fulfilled the following criteria: significantly activated in
271 the [Social status minus Ornament check] contrast (univariate t-test $p < 0.05$ FDR corrected);
272 and significantly activated in the [Social status minus baseline] contrast (univariate t-test, $p <$
273 0.1 uncorrected) to eliminate deactivated hROIs. 32 regions whose BOLD signal occupancy
274 was less than 80% (susceptibility artifacts) were excluded from the analysis. The hROIs
275 excluded are listed in the supplementary material (Table S1).

276 This procedure led to 95 hROIs being more activated in the social status condition than
277 in the ornament check condition. The same method was applied to the [Ornament minus Face]
278 contrast and [Ornament minus baseline] contrast leading to 81 activated hROIS for the 1-back
279 task. In addition, we applied a univariate t-test (FDR corrected, $p < 0.05$) to compare the
280 BOLD values in the 95 hROIs activated in the [Social status minus Ornament check] contrast

281 to those 81 hROIs elicited by the [Ornament minus Face] contrast of the 1-back task. This
282 allowed for refining the specificity of the regions involved in the social status attribution and
283 its explicit components. Thirty-seven hROIs were more activated in the [Social status minus
284 Ornament check] contrast than in the [Ornament minus Face] contrast.

285

286 **2.5.3. Resting-state analysis**

287 The task-based functional analysis was complemented with a resting-state functional
288 connectivity analysis using the CONN v 20.b toolbox software (Whitfield-Gabrieli & Nieto-
289 Castanon, 2012), which runs under MATLAB 2021a.

290 Functional imaging data were pre-processed using the CONN default pre-processing
291 pipeline for volume-based analyses. The steps for functional data comprise realignment and
292 unwarping for subject motion estimation and correction (12 parameters). Next, centering to
293 (0,0,0) coordinates and ART-based outlier detection identification was applied. Segmentation
294 and normalization to MNI space were applied next. Structural data were translated to (0,0,0)
295 center coordinates, segmented (gray/white/CSF), and normalized to MNI space. In the
296 denoising step, we applied band-pass filtering (0.01–0.1 Hz) after regression of realignment
297 parameters (12), white and gray matter, and CSF confounds. Then, we applied linear
298 detrending and despiking after regression. For the ROI to ROI functional connectivity
299 analyses, we used AICHA atlas (Joliot et al., 2015). We considered the 95 hROIs activated in
300 the [Status minus Ornament] contrast. For group-level results, we calculated ROI-to-ROI
301 connectivity correlations, threshold with a unilateral t-test, and FDR-corrected $p < 0.05$.

302

303 **3. Results**

304 **3.1. Behavioral results**

305 Participants responded faster in the ornament check condition (mean response time \pm SD: 1.3s
306 \pm 0.5s) than in the social status condition (mean response time \pm SD: 2s \pm 0.8s): $F_{(1,32)} = 227.8$
307 $p < 0.0001$. Participant gender and stimulus gender had no significant effects (either main or
308 interactions). To ensure that participants used ornaments rather than face phenotypes to assign
309 social status, we have focused on some models who have been presented twice for the same
310 role with different categories of ornaments (paints, beads, or both). Model W adorned with
311 beads was chosen at 26% as a Healer but only at 6% when adorned with paintings. This was
312 also the case for model I, chosen at 56% as a Healer when wearing beads but at 3% when
313 wearing paintings only. Model F, adorned with beads, was chosen at 73% as married but only

314 at 6% when wearing paintings (see Figure S1 in supplementary material). These results
 315 demonstrate that ornamentation was more critical than facial characteristics, as identical
 316 phenotypes adorned differently led to different social status attributions.

317 Regarding the one-back task, the average of correct hits was $76.2\% \pm 18.8\%$ ($81.1 \pm 16.7\%$,
 318 $79.2 \pm 18.4\%$, $68.4 \pm 19.0\%$ for paints, beads, and, beads + paints respectively).

319

320 **3.2. Post-MRI debriefing of the selection task and analysis of status attribution**

321 Twenty-two participants reported that they considered ornamentation a more important
 322 criterion than phenotype in assigning a social role/status. A few reported they sometimes paid
 323 attention to facial features, for example, in cases of indecision or for specific roles such as
 324 father/mother. Ten participants reported paying more attention to facial characteristics than to
 325 ornamentation. Two participants stated that the most important criterion for them (facial
 326 features or ornamentation) varied according to the questions. All participants reported that they
 327 never answered randomly, except in rare exceptions. Participants generally reported having an
 328 attribution strategy in place that they maintained throughout the experiment. Table 2 shows that
 329 across all trials, "Hunter/Huntress" and "Warrior" demonstrate a predominant association with
 330 paintings (79.8% and 81.1%, respectively) compared to other adornments, while "Married" and
 331 "Musician" exhibited a preference for beads (62.6% and 61.6%, respectively) over other
 332 adornments. "Shaman" and "Healer" were preferentially attributed to models adorned with both
 333 paintings and bead 60.5% and 61.1%, respectively). Low standard deviations show a relative
 334 consistency between identical social status trials. However, there was not necessarily a consensus
 335 among participants for the same role. For example, some participants attributed chief status to
 336 faces wearing only beads, while others attributed this status to faces bearing paintings and beads
 337 (see Table 2).

338 Table 2 - Average percentage of attribution choices for each social status based on adornment (mean percentages
 339 of the total responses for the considered status, standard deviation in parentheses).

	Beads	Paintings	Both
Shaman	36.5% (6.6)	3.7% (2.0)	60.5% (6.5)
Hunter / Huntress	3.6% (1.0)	79.8% (7.9)	16.5% (6.9)
Chief	40.9% (2.8)	13.1% (6.3)	46.0% (5.7)
Storyteller	51.9% (6.9)	8.3% (7.5)	39.8% (10.1)
Scout	14.9% (1.8)	52.2% (3.2)	32.9% (5.0)
Warrior	4.3% (2.9)	81.1% (6.5)	16.7% (7.5)
Healer	34.3% (9.4)	4.5% (0.2)	61.1% (9.3)

Married	62.6% (11.2)	7.0% (3.7)	30.3% (7.5)
Musician	61.6% (5.0)	8.2% (1.9)	32.5% (2.8)
Mother / Father	49.5% (22.9)	12.2% (8.8)	38.3% (18.7)

340

341 **3.3. Neuroimaging results**

342 **3.3.1. Social status minus Ornament check (event-related paradigm)**

343 The [Social status minus Ornament check] contrast revealed a set of 95 cortical and subcortical
 344 regions that were more activated when participants assigned social status to adorned faces than
 345 when they assessed the type of ornamentation (

346 Table 3, Figure 4).

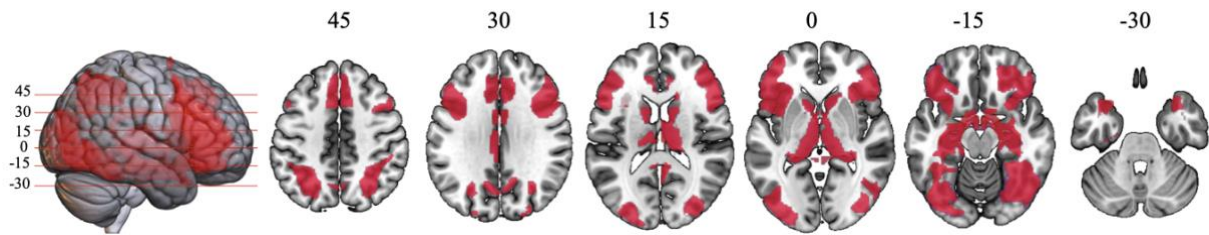
347 In the occipital lobe, these regions included the lateral occipital cortex and the fusiform gyrus
 348 (including the Fusiform Face Area, FFA). We used the Neurosynth platform (Yarkoni et al.,
 349 2011) to synthesize the activations reported in the literature during face perception and ensure
 350 their consistency with our results. We conducted a meta-analysis including 125 studies that
 351 contained the term "neutral face" in their abstracts, i.e., pictures of faces adopting a neutral
 352 expression. It evidenced the involvement of a right fusiform region (MNI coordinates of the
 353 activation peak: 38, -42, -16). This matched the location of the G_Fusiform-4-R in our
 354 AICHA atlas (MNI coordinates of the center of mass: 44, -46, -18). The FFA occupied a large
 355 portion of this functional region of the AICHA atlas.

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

364 We compared the activations of the 24 participants who primarily considered ornaments in
 365 their judgment to the 10 subjects who relied more on facial phenotype. No significant difference
 366 could be found in any of the 95 regions revealed by the contrast [status attribution-ornaments
 367 check]. That means that in the activated regions, the 10 subjects were indiscernible from the 24
 368 participants, probably because, as they reported, they also relied on the ornaments to assign a
 369 social role. For those subjects who occasionally paid attention to facial features, this involved

370 very few of the 40 stimuli they had to evaluate. It is, therefore, unlikely that this impacted the
 371 observed activations on average.

372



373

374

375

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

376 3.3.2. Ornament minus Face (1-back paradigm)

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

384 Among these regions, 37 hROIs were significantly less activated in the [Ornament
 385 minus Face] contrast than in the [Social status minus Ornament check] contrast (Table 3).
 386

387 Table 3. Coordinates, mean and standard deviation of BOLD variations, and p-value of the activated regions in
 388 the [Social status minus Ornament check] contrast.

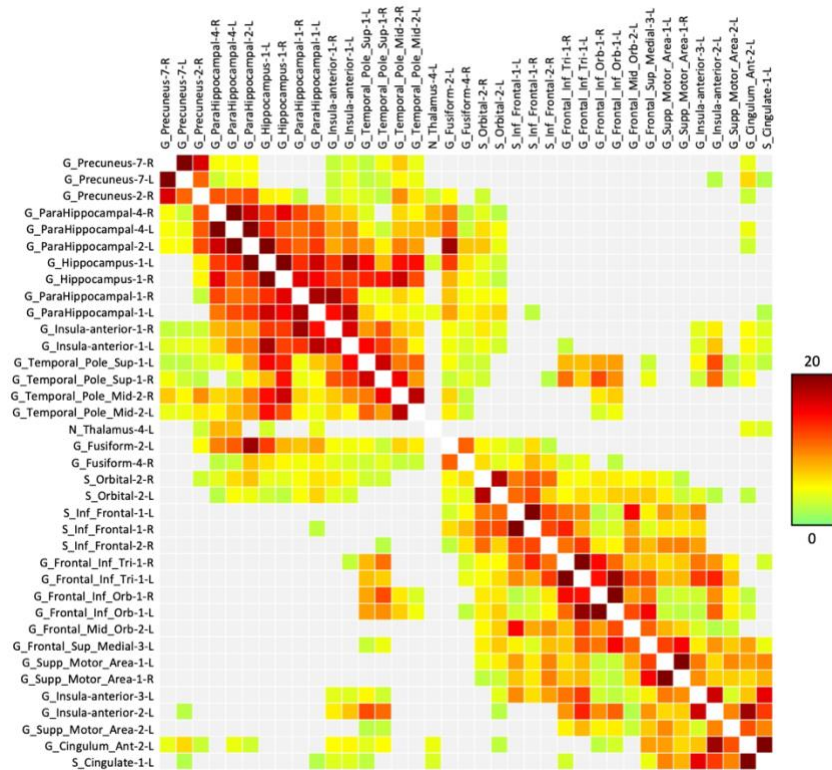
hROI Social status - Ornament check (* Specific to Social status – Ornament check, i.e., less or not activated in Ornament block – faces)	MNI coordinates of the center of mass	Mean (BOLD)	Standard deviation (BOLD)	p (FDR corrected)
G_Cingulum_Ant-2-L*	-7 34 22	0.12	0.16	0.0005
G_Cingulum_Ant-2-R	7 33 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

389

390 3.3.3. Resting-state functional connectivity



391

392 Figure 5. Resting-state connectivity matrix of 37 hROIs specific to the social status assignment (i.e., positive in
 393 the contrast [Social status minus Ornament check] and less or not activated in contrast [Ornament (1-back)
 394 minus Faces]. The color scale (green to red) reflects the t-value on each connection averaged across subjects.

395 The resting-state functional connectivity analysis revealed 348 positive connections
396 significant across subjects ($p < 0.05$ FDR, univariate t-test) between the 37 hROIs. T-values
397 varied from 2 to 25 (Figure 5). These 37 hROIs can be divided into two groups based on their
398 resting-state functional connectivity. A network connected the precuneus and temporal lobe
399 regions, including the hippocampus, the parahippocampal cortex, the temporal pole, and a
400 part of the fusiform gyrus. A second network connected mainly frontal regions, including the
401 inferior frontal sulcus and gyrus, the orbitofrontal cortex, the dorsal anterior cingulate cortex,
402 the supplementary motor area, and the anterior insula.

403 The G-Fusiform-4-R and the Temporal_Pole_Sup-1-R regions were connected to 22 and
404 27 hROIS, respectively. The G-Fusiform-4-R and the Temporal_Pole_Sup-1-R regions were
405 strongly connected to their group and many regions of the other group (see Table S2 in the
406 supplementary material for detailed results). The S_Orbital-2 was connected to 26 hROIs.

407

408 **4. Discussion**

409 This study aimed to identify the brain regions involved in attributing social status from
410 the visual analysis of adorned faces. These regions can be categorized into four groups: 1.
411 occipitotemporal regions of the ventral visual pathway, including lateral occipital regions,
412 fusiform gyrus, parahippocampal gyrus extending to the hippocampus, and the temporal
413 poles; 2. regions belonging to the salience network such as the anterior insula and the anterior
414 cingulate cortex; 3. the intraparietal sulcus; and 4. the ventral and dorsal regions of the lateral
415 prefrontal cortex and the orbitofrontal cortex. The act of adorning one's body has originated at
416 least 140,000 years ago, supported by the discovery of shell beads from this period (Sehasseh
417 et al., 2021) and a contemporary increased use of mineral pigments in Africa (Dapschaskas
418 et al., 2022). Around 45,000 BP, certain Paleolithic societies surpassed the number of
419 adornment objects produced by many ethnographically studied societies. Therefore, we can
420 assume that the networks revealed in the present study were fully functional 45,000 BP and,
421 at least to a degree, also functional in the earliest *Homo sapiens* and contemporary or earlier
422 hominins displaying such behaviors.

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

425 This is the case for most visual regions (except Fusiform-4-R and Fusiform-2-L), the
426 intraparietal sulcus, and most of the thalamus and retrosplenial regions. In contrast, activity in
427 the inferior and orbital frontal areas, hippocampal and parahippocampal regions, the temporal

428 poles, and the salience network, including the anterior cingulate and parts of the anterior
429 insula, remained significant when activity in these regions during the 1-back task was
430 subtracted.

431

432 **4.1. Visual Ventral pathway and medial temporal regions**

433 Lateral and ventral occipital regions were more activated by the social status attribution than
434 by the assessment of decoration type. This suggests that deeper visual processing is required
435 to attribute a social status. Most of these occipitotemporal regions were also activated during
436 the 1-back task and were thus not specifically involved in assigning a social status to adorned
437 faces. However, two hROIs were significantly more activated during social status attribution
438 than in the 1-back task, namely G_Fusiform-2-L and G_Fusiform-4-R. The latter is
439 particularly interesting since it includes the so-called fusiform face area (FFA), which is
440 sensitive to face perception (Kanwisher et al., 1997; Kanwisher & Yovel, 2006; McCarthy et
441 al., 1997) and lateralized in the right hemisphere (Rossion et al., 2012). Thus, although all
442 conditions included face perception and none required specific attention to faces, FFA
443 appeared more solicited by social status assignment. It has been shown that FFA is sensitive
444 to physical characteristics and their possible social correlates (Contreras et al., 2013; Freeman
445 et al., 2010). More recently, a study showed that FFA processes characteristics such as social
446 traits, gender, and high-level visual features of faces (Tsantani et al., 2021) and might thus
447 initiate the social processing of faces. The results of the present study suggest that, in the
448 context of social role attribution, FFA can process non-physiognomic features. This is
449 consistent with the fact that the FFA promotes holistic rather than local processing (Andrews
450 et al., 2010; Kok et al., 2021; Zhang et al., 2012). Ornamented faces may have been perceived
451 as a whole in the social attribution task, while attention was focused on details during the
452 assessment of decoration type and the 1-back task. In other words, attributing social status
453 involves a more complex process relying on a set of components, such as the types of
454 decoration, their association, their location on the face, and the face itself.

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

459 In the anterior extension of the ventral visual pathway, we found that the hippocampus
460 and parahippocampal gyrus were more activated by the social status attribution than by the
461 ornament type assignment and significantly more activated when compared to the 1-back

462 task, reflecting their specificity to social status attribution. The hippocampus reflects episodic
463 memorization processes strongly involved in social cognition (Laurita & Nathan Spreng,
464 2017; Montagrin et al., 2018). The parahippocampus appears to play, among others, a pivotal
465 role in contextual associative processing (Aminoff et al., 2007; Li et al., 2016), i.e., in binding
466 elements composing stimuli. It provides a unified context for further processing (see
467 (Aminoff et al., 2013) for a review). In the framework of the present study, participants
468 arbitrarily associated face decorations with social status. After the fMRI sessions, they
469 reported that once they had established an ornament/status association strategy, they stuck to
470 it throughout the sessions, with exceptional random responses. Contextual associations were
471 thus an essential aspect of the processes involved in the status assignment task. The activation
472 of the parahippocampal cortex reasonably reflects the implementation of these processes. It
473 has been suggested that the anterior part of the parahippocampus preferentially processes non-
474 spatial contextual associations, and the posterior part, comprising the parahippocampal Place
475 Area (PPA), spatial associations (Aminoff et al., 2007; Bar & Aminoff, 2003). In the present
476 study, the activation of the anterior parahippocampus is consistent with the non-spatial nature
477 of the associations.

478 The activation of the medial temporal gyrus might be linked to one of the temporal poles.
479 Although the role of temporal poles is still under discussion, it has been proposed that this
480 brain area is involved in encoding and retrieving social knowledge (Olson et al., 2013). As
481 was the case in this study, assigning social status mobilizes stereotypical social knowledge
482 (e.g., the chief must have the most ornaments) and entails encoding: The participants
483 associated a type of ornamentation with a social role and created an arbitrary social code that
484 they reused throughout the task. Thus, we propose that the parahippocampus and the temporal
485 pole, which are strongly functionally connected, work in synergy to facilitate the association
486 of a type of ornamentation with a specific social status and then to encode and restore this
487 association.

488

489 **4.2. Inferior and orbitofrontal cortex**

490 Assigning a social status involved many frontal regions not solicited during the ornament type
491 attribution condition. However, the specific areas for explicit processes, i.e., activated in the
492 social attribution task compared to the 1-back task, were mainly in the lateral part of the
493 inferior frontal gyrus and the orbitofrontal cortex as defined by Rudebeck and Rich
494 (Rudebeck & Rich, 2018). The resting-state connectivity analysis showed that these regions
495 were highly functionally linked. Previous studies have emphasized the role of the

496 orbitofrontal cortex in social cognition in non-human primates and humans. It has been
497 argued that this cortical area contains neurons sensitive to representing social categories
498 (Barat et al., 2018) and evaluating social information (Azzi et al., 2012) in non-human
499 primates. In humans, a deficit in social perception after orbitofrontal cortex lesions (Mah et
500 al., 2004), an inability to judge social traits in a decision-making task (Xia et al., 2015), or
501 acquired sociopathy have been reported (Blair, 2000).

502 fMRI studies have stressed the role of the orbitofrontal cortex in social cognition and
503 social behavior (see (Forbes & Grafman, 2010) for a review). A recent fMRI study showed
504 that the OFC represented the stereotypic social traits of others and that its pattern of activity
505 was predictive of individual choices, highlighting its critical role in social decision-making
506 (Kobayashi et al., 2022). In these studies, participants had to behave according to the facial
507 expression, attitude, or social category of the individuals presented in the experiment. Our
508 results extend these findings. Unlike previous studies, participants based their decision on
509 symbolic features (the type and arrangement of ornamentations), to which they arbitrarily
510 attributed social meaning. This implies that the role of the orbitofrontal cortex in social
511 decision-making is not restricted to processing stereotypical attitudes or social groups, a
512 capacity shared with non-human primates. Social evaluation based on symbolic external
513 attributes also involves this region in humans.

514 The social status attribution task heavily relies on high-order executive functions such
515 as attentional control, selection, and flexibility. The activation of the pars triangularis of the
516 inferior frontal gyrus extending to the inferior frontal sulcus reflects these aspects (Koechlin
517 & Summerfield, 2007). Although the activation was bilateral, the right and left inferior frontal
518 gyrus probably played a different role in the task. The right inferior frontal gyrus is explicitly
519 associated with high-level social cognition (Hartwigsen et al., 2019). The left inferior frontal
520 gyrus is involved in selecting some aspects or subsets of available information among
521 competing alternatives (Thompson-Schill et al., 1997; J. X. Zhang et al., 2004). This region
522 also plays a role in processing non-linguistic symbolic information (Muayqil et al., 2015; Xu
523 et al., 2009), consistent with the symbolic value attributed by the participants to face
524 adornments.

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

528

529 **4.3. Salience network**

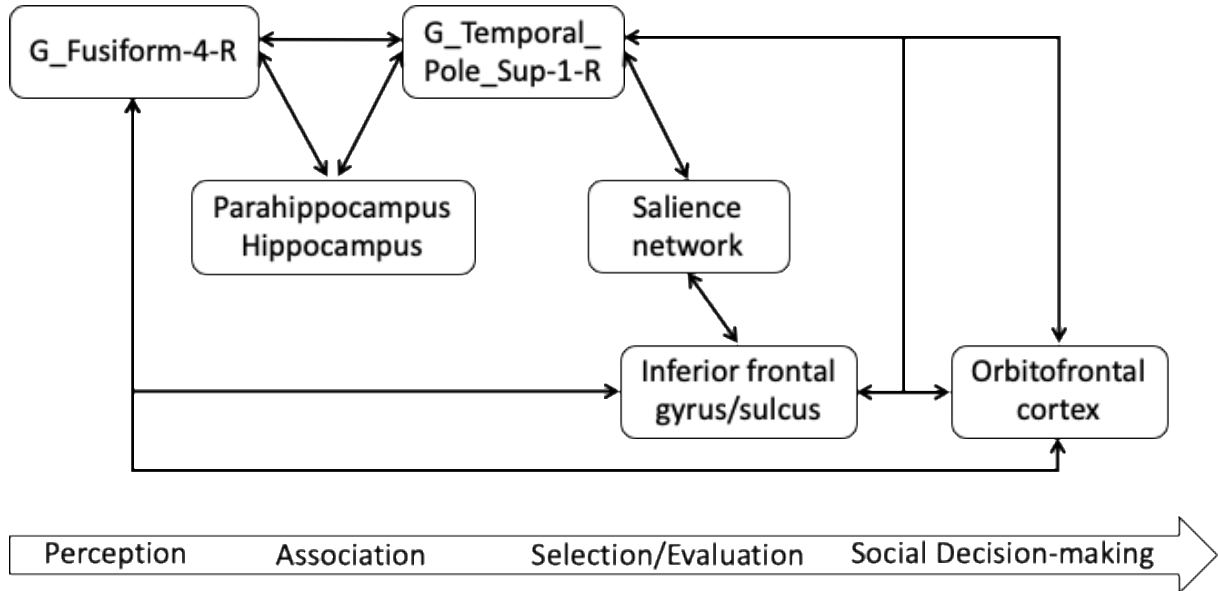
530 Social status attribution elicited activation in the anterior insula, the dorsal anterior cingulate
531 cortex (dACC)/pre-SMA, and subcortical structures, such as the thalamus and the caudate
532 nuclei. These regions constitute the so-called salience network, whose key components are the
533 insula anterior and the dACC/pre-SMA (Menon, 2015; Seeley et al., 2007; Zhou et al., 2021).
534 This network is involved in selecting relevant elements of the environment for perceptual
535 decision-making (Chand & Dhamala, 2016; Lamichhane et al., 2016; Uddin, 2015). In our
536 case, participants had to extract salient information from the ornamented faces to associate the
537 proposed social status with one of the three faces presented to them. The salience network
538 was also activated in the 1-back task by the need to detect the repetition of ornamental
539 patterns. However, the greater uncertainty in decision-making during the attribution task can
540 explain why activation of the salience network was more extensive during status attribution
541 than the 1-back task (White et al., 2014). To attribute a social status, participants had to make
542 a forced choice among three possibilities, with several plausible answers and had to compare
543 the different options and arbitrate to choose only one. These aspects of the task have probably
544 triggered the activation of the dACC/pre-SMA, belonging to the salience network. The
545 dACC/pre-SMA has been reported as involved in conflict and performance monitoring
546 (Botvinick et al., 2004; Dosenbach et al., 2006; Neta et al., 2014), and more recently in social
547 categorization domain (Stolier & Freeman, 2017).

548

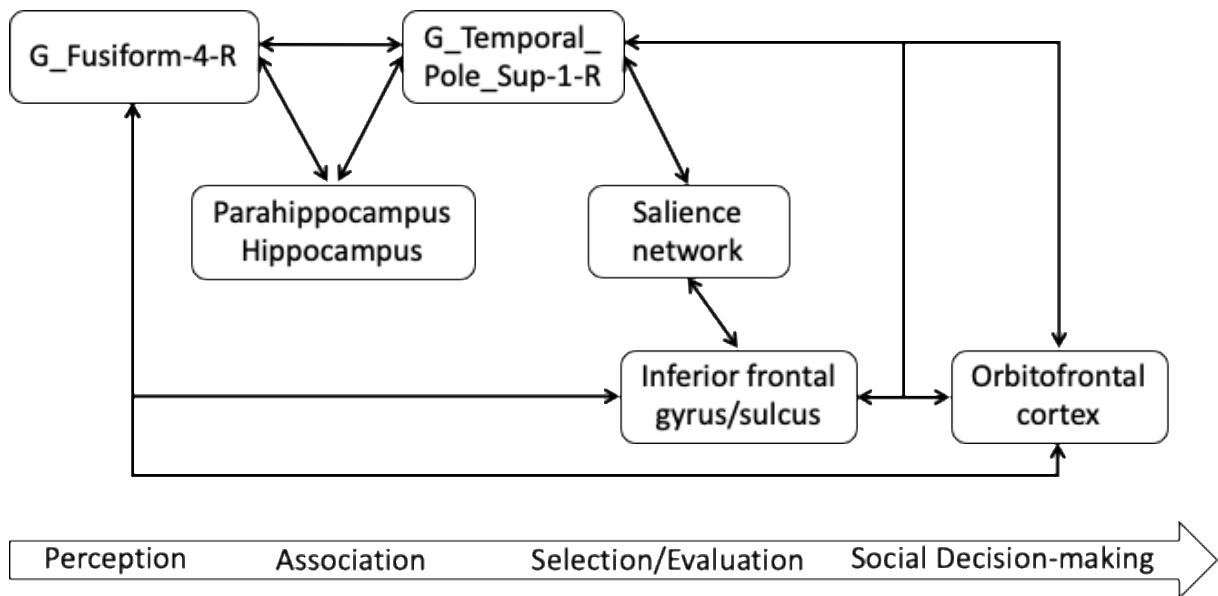
549 **4.4. Resting-state functional connectivity**

550 Resting-state functional connectivity provides insight into the potential interactions between
551 neural assemblies activated by the social status assignment task. The G_Fusiform-4-R and the
552 G_Temporal_Pole_Sup-1-R were characterized by many connections with other activated
553 regions (Figure 5). These two regions were connected with 22 and 27 hROIs, respectively.
554 The G_Fusiform-4-R included the FFA (see results) and is likely involved in the initial
555 processing phase. The functional relationships between the medial temporal lobe, the fusiform
556 gyrus, and the temporal pole reflected the association of the perceptive, social, mnemonic,
557 and associative aspects of the task. In addition, the G_Temporal_Pole_Sup-1-R was
558 connected with frontal regions and could act as a hub, allowing communication between
559 visual areas and executive frontal regions. The connection between the temporal pole and the
560 salience network enables the exchange of information necessary for evaluating and selecting
561 inputs relevant to social decision-making. The temporal pole and the salience network were
562 related to the inferior frontal gyrus, contributing to the evaluation of subjective confidence

563 about a perceptual decision (Sherman et al., 2016). The orbitofrontal cortex was functionally
 564 connected to the G_Temporal_Pole_Sup-1-R and the G_Fusiform-4-R. These regions, whose
 565 essential role in social status evaluation has been discussed above, could constitute the core
 566 network in the social attribution task (



567 Figure 6). They must have allowed the integration of information leading to the assignment of
 568 social status based on the perception of symbolic cues.
 569



570 Figure 6. Schematic resting-state functional connectivity network between regions activated during a social
 571 status attribution task based on symbolic culturalized faces. Black arrows indicate the reciprocal resting-state
 572 functional connectivity between brain regions (univariate t-test, $p < 0.05$, FDR corrected).
 573

574 Notably, none of the regions involved in assigning social status exclusively dealt with social
 575 information. Most of these regions are involved in many cognitive functions. The functional

576 connection of structures whose processing properties are beneficial for the execution of the
577 task allows the social judgment function to emerge. Human connections exceed those of
578 animals, including primates, at both the structural and functional levels (Mars et al., 2018;
579 Thiebaut de Schotten & Forkel, 2022; Xu et al., 2020). Thanks to creating functional
580 connections (linking social cognition, memory, and executive functions), humans could use
581 symbolic items and markings to signify social status.

582 The complexity of this neural network raises questions about when it became fully functional
583 in our ancestors and whether it resulted from a gradual process of integration and
584 complexification or was already fully functional when the first archaeological evidence of
585 culturalization of the human face was recorded.

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

591 The interplay between cultural and biological mechanisms likely drove this process, with
592 individuals gifted in acquiring, decoding, and creating these symbolic messages having
593 selective advantages that favored the permanent inscription of a more integrated connectivity
594 in the brain (Colagè & d'Errico, 2018, 2023; d'Errico & Colagè, 2018). A progressive co-
595 option of brain regions has also been suggested for the evolution of tool-making (Hecht et al.,
596 2015; Putt et al., 2019; Stout et al., 2015). It would have enabled the development of
597 increasingly complex tools.

598 The period between 140,000 and 70,000 years ago may have represented a key moment in
599 this integration process, as this was when red pigments use became almost ubiquitous at
600 African Middle Stone Age sites and marine shell beads were used for the first time in North
601 Africa, the Near East, and Southern Africa. This diversification of colors, shapes, and
602 technologies indicates a complexification of practices allowing wearers to use their faces to
603 communicate information about their social role using more complex shared symbolic codes.
604 It is reasonable to think that the human brain had largely equipped itself with the necessary
605 connections to process and interpret these stimuli 120,000-70,000 years ago.

606

607 **5. Conclusion**

608 This study delved into the neural mechanisms involved in the social interpretation of facial
609 adornments and found that various brain regions, including the FFA, temporal poles, salience
610 network, and orbitofrontal cortex, were involved in this process. Furthermore, assigning a
611 social status from symbolic cues also activated the medial temporal regions and the inferior
612 frontal gyrus, reflecting the role of episodic memory, contextual association, and executive
613 functions. Reconciling these results with archaeological data suggests a gradual organization
614 of the connectivity of these networks, leading to the possibility of social processing of
615 symbolic information.

616

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623

624 **7. Authors' contributions**

625 MS, FdE, SR, EM designed the study

626 MS, EM acquired the data

627 MS, EM analyzed the data

628 MS, FdE, SR, EM wrote the article

629

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639 **9. Data Availability**

640 BOLD values for each participant, hROI, and contrast are available as supplementary material.

641

642 **10. References**

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