



HAL
open science

Assigning a social status from face adornments: an fMRI study

M Salagnon, F D'errico, S Rigaud, E Mellet

► **To cite this version:**

M Salagnon, F D'errico, S Rigaud, E Mellet. Assigning a social status from face adornments: an fMRI study. 2023. hal-04234997v1

HAL Id: hal-04234997

<https://hal.science/hal-04234997v1>

Preprint submitted on 10 Oct 2023 (v1), last revised 26 May 2024 (v2)

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

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

3

4

5 Salagnon M^{1,2}, d'Errico F^{2,3}, Rigaud S², Mellet E^{1*},

6

7 ¹ CNRS, CEA, IMN, GIN, UMR 5293, Université Bordeaux, Bordeaux, France

8 ² Univ. Bordeaux, PACEA UMR 5199, CNRS, Pessac, France

9 ³ SFF Centre for Early Sapiens Behaviour (SapienCE), University of Bergen, Bergen,
10 Norway.

11

12 * Corresponding author

13 E-mail: emmanuel.mellet@u-bordeaux.fr

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

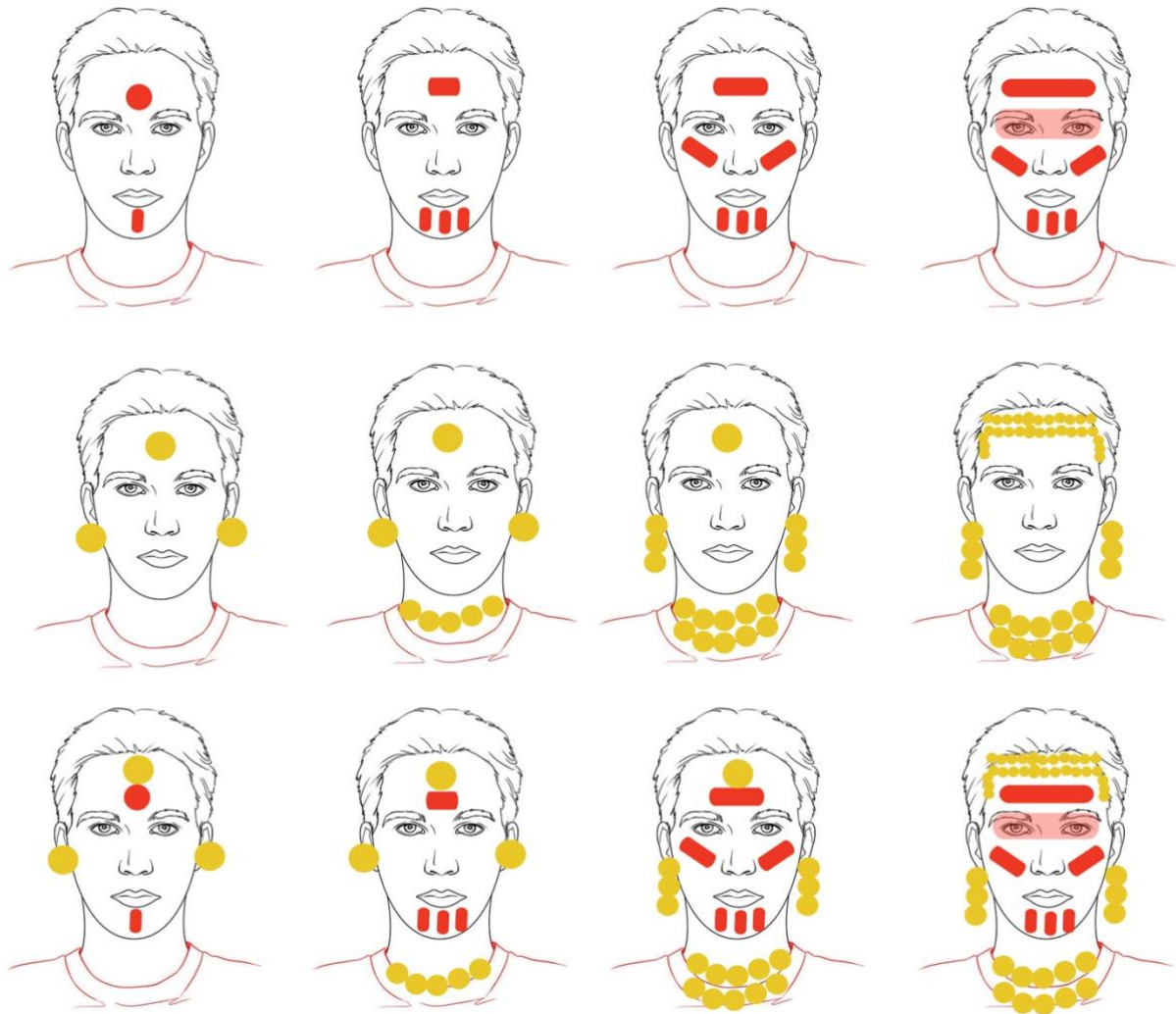
108 **2.3. Experimental design**

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.



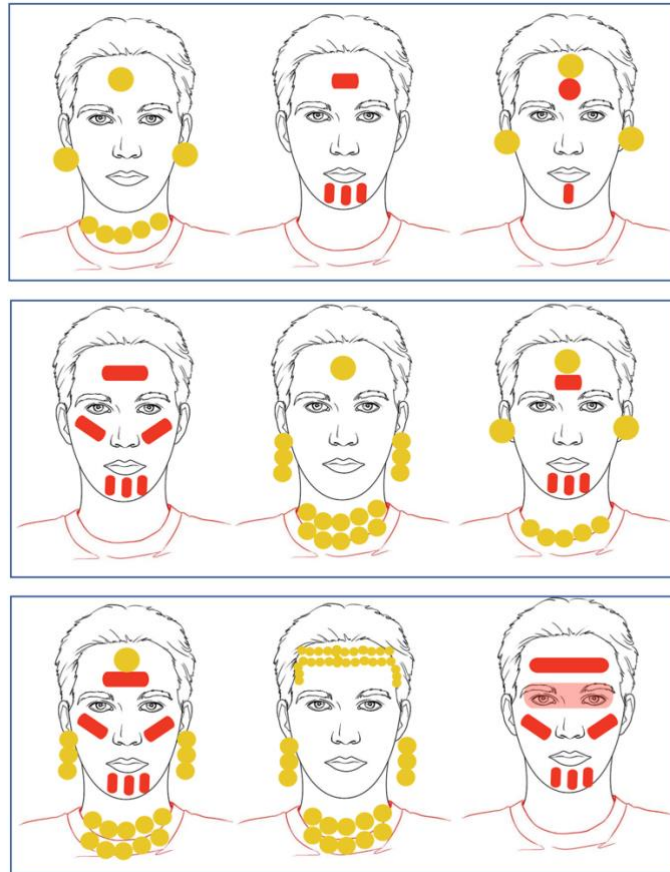
126
127

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

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

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

138



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

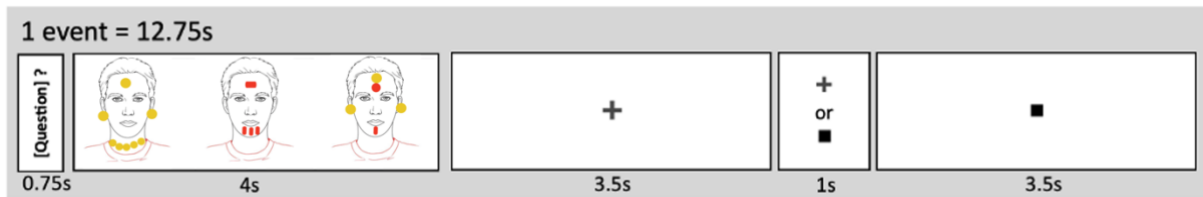
144

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

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

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

160



161

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

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

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

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

171

172 2.3.3. 1-back task (block design)

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

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

184

185 **2.4. MRI acquisition**

186 Neuroimaging data acquisition was performed using a Siemens Prisma 3 Tesla MRI scanner.
187 Structural images were acquired using a high-resolution T1-weighted 3D sequence (TR =
188 2000 ms, TE = 2.03 ms; flip angle = 8°; 192 slices and isotropic voxel volume of 1 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**

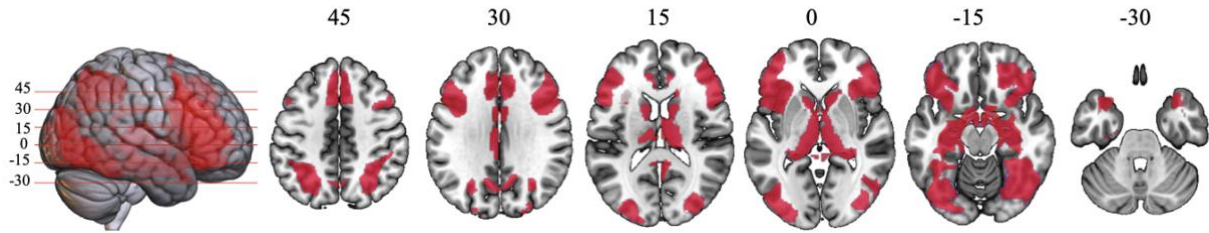
288 **3.3.1. Social status minus Ornament check (event-related paradigm)**

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 platform ⁶³ 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.

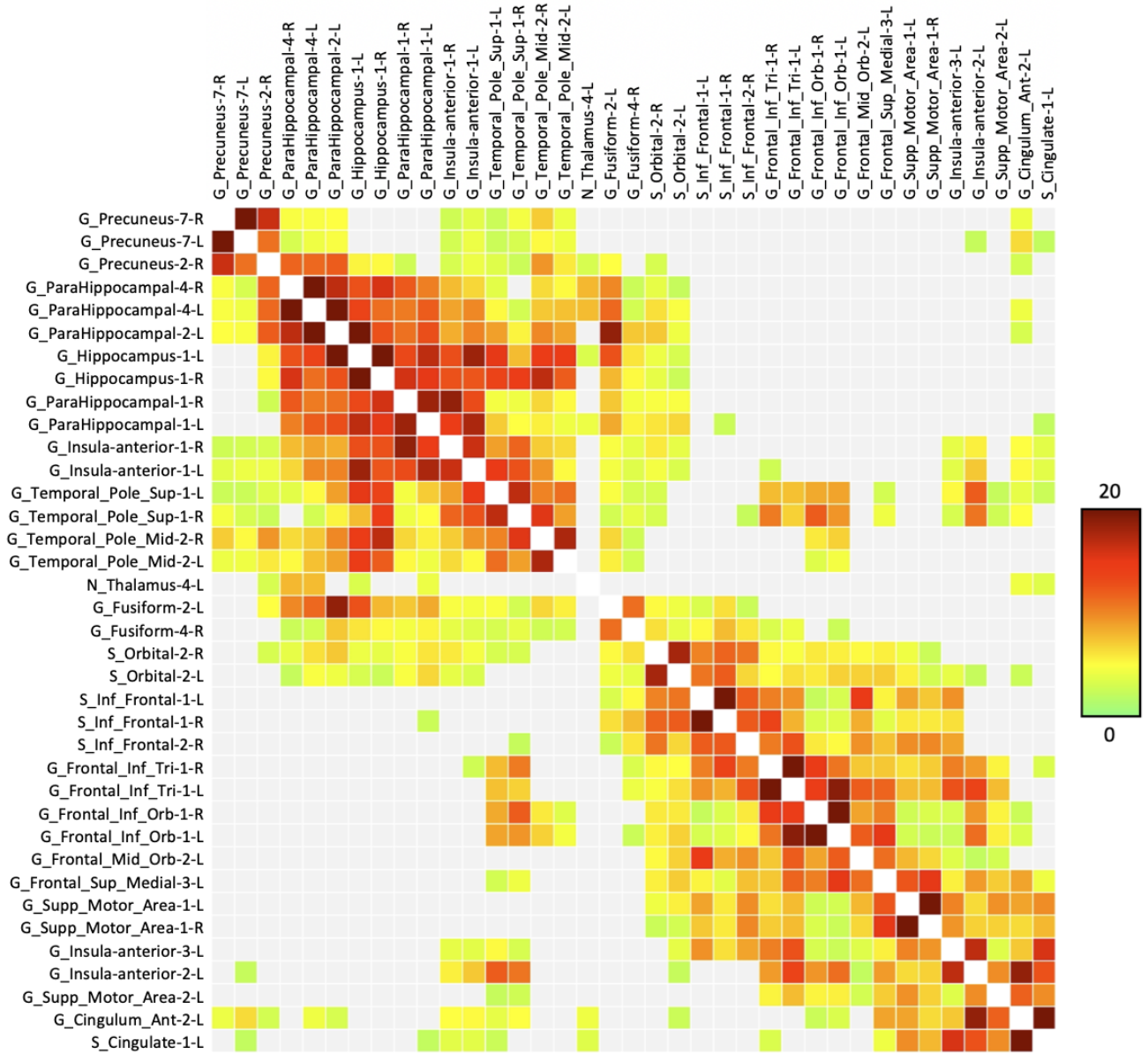
hROI Social status - Ornament check (* Specific to Social status – Ornament check, i.e., more or not activated in Ornament block – faces)	MNI coordinates of the center of mass	Mean (BOLD)	Standard deviation (BOLD)	p (FDR corrected)
G_Cingulum_Ant-2-L*	-7 34 22	0.12	0.16	0.0005
G_Cingulum_Ant-2-R	7 33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

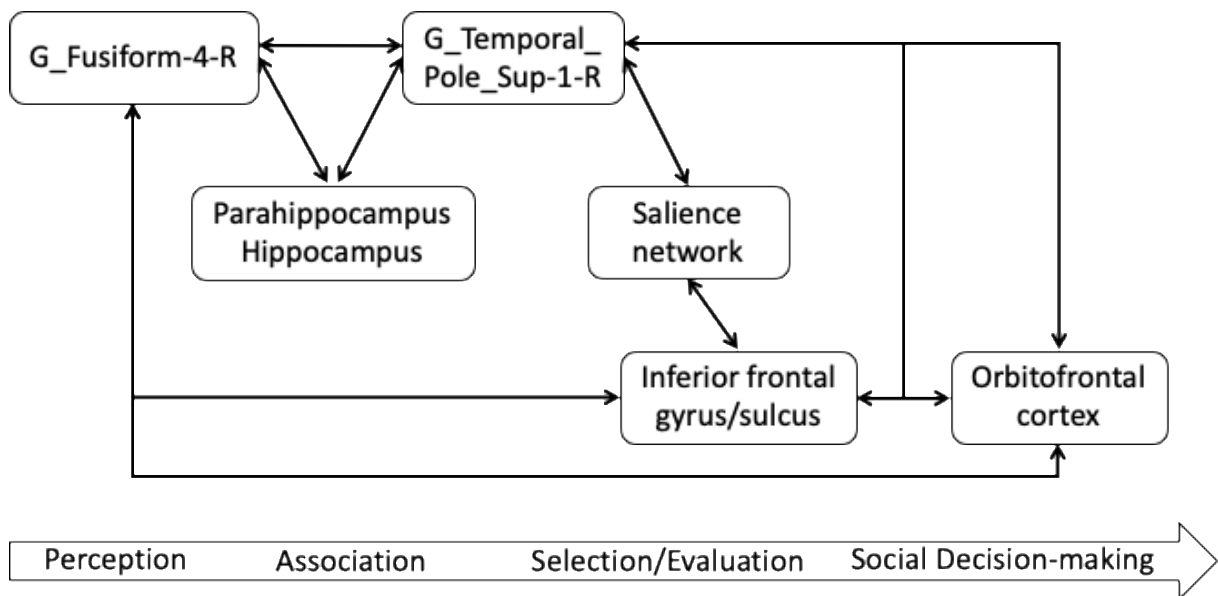
462 Social status attribution elicited activation in the anterior insula, the dorsal anterior cingulate
463 cortex (dACC)/pre-SMA, and subcortical structures, such as the thalamus and the caudate
464 nuclei. These regions constitute the so-called salience network, whose key components are the
465 insula 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**

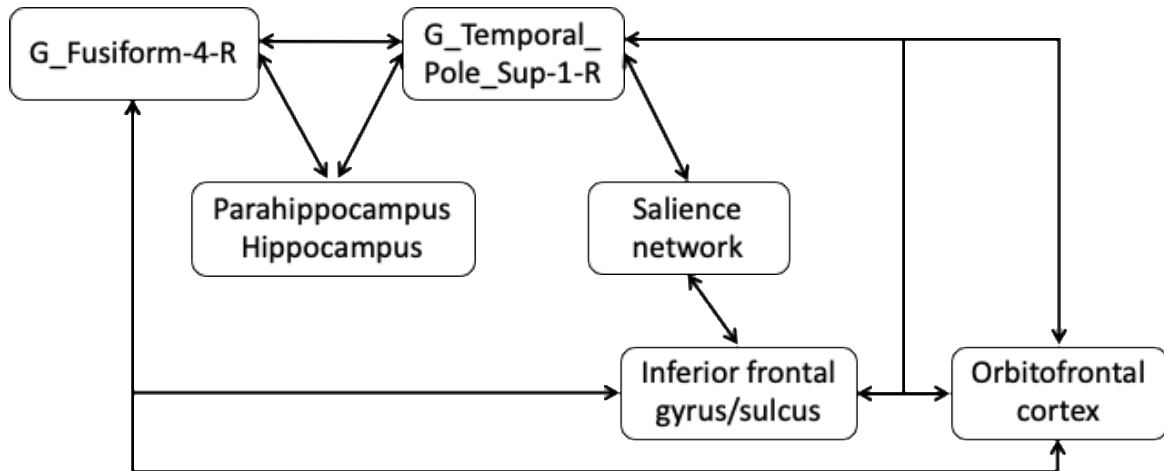
480 Resting-state functional connectivity provides insight into the potential interactions between
 481 neural assemblies activated by the social status assignment task. The G_Fusiform-4-R and the
 482 G_Temporal_Pole_Sup-1-R were characterized by many connections with other activated
 483 regions (



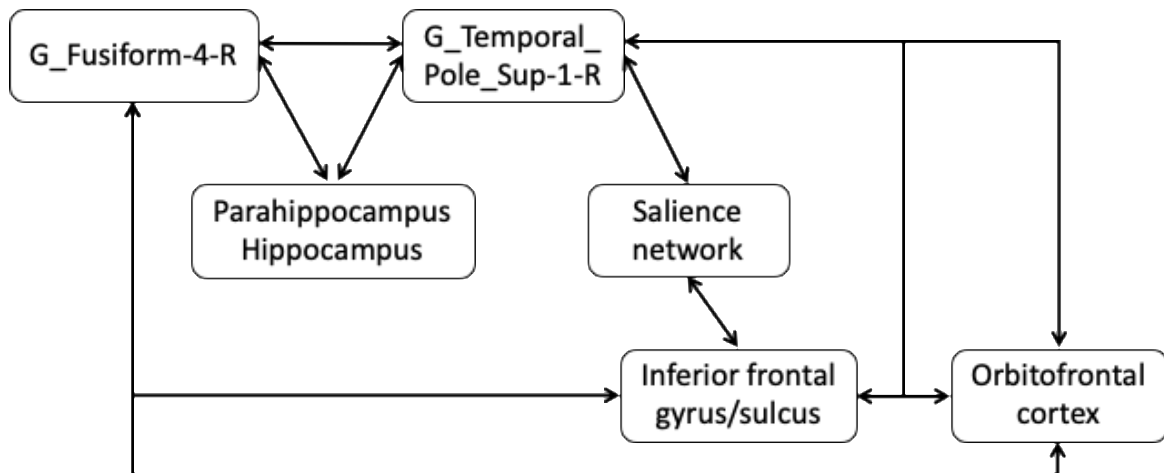
484

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

543 **6. Acknowledgments**

544 We thank the Ginesis Lab (GIN, Fealinks, Labcom Programme 2016, ANR 16LCV2-0006-
545 01) for their help with data management and processing. We are also indebted to Violaine
546 Verrecchia and Marc Joliot for their help in data analysis. Our thanks also go to Marie
547 Guerlain, Annie Bardon-Lay, and her team members for their help with the face painting.
548 Warm thanks also go to all those who agreed to participate in our experiments.

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

555 **8. Fundings**

556 This work was supported by the CNRS project 80 Prime Neurobeads and a grant from the
557 IdEx Bordeaux/CNRS (PEPS 2015). Francesco d'Errico's work is supported by the European
558 Research Council through a Synergy Grant for the project Evolution of Cognitive Tools for
559 Quantification (QUANTA), No. 951388; the Research Council of Norway through its Centres
560 of Excellence funding scheme, SFF Centre for Early Sapiens Behaviour (SapienCE), project
561 number 262618, the Talents Program of the Bordeaux University [grant number:
562 191022_001] and the *Grand Programme de Recherche 'Human Past'* of
563 the *Initiative d'Excellence* (IdEx) of the Bordeaux University.

564 **9. Data Availability**

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

566

567 **10. References**

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

811 **50**, 799–812 (2006).

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

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

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

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

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

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

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

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

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

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

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

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

836