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2 new naturalistic task of social cognition

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40

41 **Highlights**

- 42 • The DIT ecologically explores neutral and emotional inference, and gaze processing
- 43 • Social situations that require inferences engage temporal areas including the STS
- 44 • The left precuneus was implicated in emotional inferences processing
- 45 • Greater mPFC activation is observed during emotional versus nonemotional inference

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Abstract

Understanding others' intentions requires both the identification of social cues (e.g., emotional facial expressions, gaze direction) and the attribution of a mental state to another. The neural substrates of these processes have often been studied separately, and results are heterogeneous, in part attributable to the variety of paradigms used. The aim of the present study was to explore the neural regions underlying these sociocognitive processes, using a novel naturalistic task in which participants engage with human protagonists featured in videos.

A total of 51 right-handed volunteers underwent functional magnetic resonance imaging while performing the Dynamic Inference Task (DIT), manipulating the degree of inference (high vs. low), the presence of emotion (emotional vs. nonemotional), and gaze direction (direct vs. averted).

High nonemotional inference elicited neural activation in temporal regions encompassing the right posterior superior temporal sulcus. The presence (vs. absence) of emotion in the high-inference condition elicited a bilateral pattern of activation in internal temporal areas around the amygdala and orbitofrontal structures, as well as activation in the right dorsomedial part of the superior frontal gyrus and the left precuneus.

On account of its dynamic, naturalistic approach, the DIT seems a suitable task for exploring social interactions and the way we interact with others, both in nonclinical and clinical populations.

Keywords: mentalizing, dynamic, functional MRI, theory of mind, emotion processing, gaze direction, second-person neuroscience

72 **1. Introduction**

73 *Social cognition* refers to the set of cognitive processes underlying social interactions, such as
74 the perception and interpretation of social cues (gaze, facial expressions, attitudes, etc.), and
75 the generation of responses to the intentions, dispositions, and behaviors of others (Brothers,
76 1990; Frith and Frith, 2012; Happé et al., 2017). One of these components, theory of mind
77 (ToM), also called mentalizing, is a core component of social cognition. It is defined as the
78 ability to infer other people’s mental states (e.g., intentions, desires, thoughts) in order to
79 understand and predict their most probable acts and behaviors (Brüne and Brüne-Cohrs, 2006;
80 Leslie, 2001; Premack and Woodruff, 1978). It entails the causal link between individuals’
81 mental states and their behaviour, and the knowledge that other people may experience
82 different mental states and have different perspectives on the world from ours. ToM is not a
83 single construct, and can be divided into two components, depending on the nature of mental
84 state to be attributed: the cognitive component of ToM encompasses inferences about other
85 people’s beliefs or intentions, while the emotional component of ToM encompasses
86 inferences about other people’s feelings or emotions (e.g., Shamay-Tsoory and Aharon-
87 Peretz, 2007). This distinction is supported by lesion studies, which have found a double
88 dissociation at the neural level, with the dorsal medial prefrontal cortex (mPFC) being
89 involved in cognitive ToM (Kalbe et al., 2010; Sommer et al., 2007), and the ventral mPFC
90 (including the orbitofrontal cortex, OFC) in emotional ToM (Hynes et al., 2006; Shamay-
91 Tsoory and Aharon-Peretz, 2007). Increased activation of the limbic system, including the
92 amygdala, is also observed during ToM tasks when emotional facial expressions are present
93 (Schmitgen et al., 2016; Schnell et al., 2011).

94 ToM ability allows us to adapt our behaviors. Quickly understanding the actions and
95 intentions of others would appear to be crucial for successful social interactions and adequate
96 psychosocial functioning. ToM deficits have been described in a number of psychiatric and

97 neurological diseases (Bora et al., 2016; Brüne, 2005; Henry et al., 2015; Vucurovic et al.,
98 2020) characterized by impaired social functioning. Evidence suggests that social cognition is
99 a strong predictor of social functioning (i.e., interpersonal relationships and other socially
100 focused behaviors) sometimes even stronger than nonsocial cognitive processes in psychiatric
101 populations (Couture et al., 2006; Fett et al., 2011; Vlad et al., 2018).

102 Neuroscientific research has explored the neural substrates of the cognitive processes
103 involved in social cognition and delineated a widespread brain network specific to social
104 reasoning (Abu-Akel and Shamay-Tsoory, 2011; Amodio and Frith, 2006; Yang et al., 2015).

105 Advances in brain imaging, especially functional magnetic resonance imaging (fMRI), have
106 resulted in a large and growing body of evidence in favor of the existence of two distinctive
107 types of brain network supporting social cognition: the *mirror neuron system* (MNS) and the
108 *mentalizing system* (or *ToM system*). The putative MNS includes the premotor cortex, anterior
109 intraparietal sulcus, and posterior part of the inferior frontal gyrus. These regions are recruited
110 during both the execution and observation of actions, including facial expressions (Becchio et
111 al., 2012; Rizzolatti and Sinigaglia, 2010; Spunt and Lieberman, 2012; Van Overwalle and
112 Baetens, 2009; Vogeley, 2017). Some of these regions are also involved in empathy (Alcala-
113 Lopez et al., 2019; Bekkali et al., 2021), but probably in the early stages of social information
114 processing, and may be related more to processes such as the *detection* of bodily signals
115 (Vogeley, 2017). By contrast, the mentalizing system comprises the mPFC, the
116 temporoparietal junction (TPJ), including the posterior superior temporal sulcus (STS), the
117 posterior cingulate cortex/precuneus (PCC/PC), and the anterior temporal lobes. This system
118 is typically activated, irrespective of the task or stimulus, when we infer others' intentions (de
119 Lange et al., 2008; Frith and Frith, 2006; Saxe, 2006). The mentalizing system is also
120 activated during action observation when individuals are explicitly instructed to identify the
121 intentions of the actors they observe (Spunt et al., 2011; Spunt and Lieberman, 2012). In a

122 recent study exploring the neural correlates of self- and other-mentalizing via
123 electrocorticography, Tan et al. (2021) found that both types of mentalizing engaged near-
124 identical neuronal populations in the same spatiotemporal sequence: activation in the visual
125 cortex first, then the temporoparietal regions of the default mode network, and finally the
126 medial prefrontal cortex. Interestingly, the latter showed greater functional specificity for
127 mentalizing and greater self/other differentiation.

128 Although both the MNS and the mentalizing system may be elicited in everyday social
129 situations, few studies have explored them together. Furthermore, while some authors have
130 argued that they are functionally independent (e.g., Saxe et al., 2006; Van Overwalle and
131 Baetens, 2009), others support the existence of concurrent activation during the observation of
132 complex social stimuli (Spunt et al., 2011; Zaki and Ochsner, 2011). The discrepant results
133 can also be explained by the experimental paradigms designed to isolate these systems and the
134 processes in which they are involved and by the complexity of developing a naturalistic task
135 that is compatible with fMRI constraints. For these reasons, neural correlates of social
136 cognition, especially inferential processes, have been explored using situations where
137 participants observe an interaction between protagonists (third-person perspective). However,
138 we can assume that when we observe-rather than interact with-someone, the processing is
139 fundamentally different at both behavioral and neural levels. This is the assumption of
140 second-person neuroscience, and in their seminal paper, Schilbach et al. (2013) encouraged
141 researchers to focus on the neural mechanisms of social interaction, which they referred to as
142 the *dark matter* of social neuroscience. According to Schilbach (2015), *social observation*
143 refers to an intra-individual mental process leading to the inference of others' mental states by
144 adopting a third-person perspective, whereas *social interaction* implies joint (i.e.,
145 interindividual) attention between two or more individuals. Social interaction therefore differs
146 from social observation on the individual's degree of involvement in the social situation: the

147 individual actively participates in a social interaction and/or feels emotionally engaged with a
148 social partner (for a review, see Schilbach et al., 2013). Social interaction may be real or
149 perceived, but it must be reciprocal and in real time. *Engagement* refers to the perception that
150 a social partner is interacting directly with the participant. Studies adopting a second-person
151 approach use experimental paradigms with at least one of these criteria. Several studies have
152 investigated the influence of this fundamental distinction between social interaction and social
153 observation, and their results suggest that self-involvement may modulate the recruitment of
154 both the MNS and the mentalizing system (e.g., Ciaramidaro et al., 2014). Thus, the
155 mentalizing network is not only involved in the later stages of social information processing,
156 but may also be concurrently activated with the MNS during social interaction (for a review,
157 see Redcay et al., 2019). Second-person approach studies have shown that the mentalizing
158 system is recruited during perceived realtime interactions with no explicit mental inference
159 demand, such as a gaze-based interaction with a social partner (e.g., Alkire et al., 2018;
160 Redcay et al., 2010). They have also highlighted simultaneous recruitment of mentalizing and
161 mirror networks during live social exchanges based on reciprocal imitation (Sperduti et al.,
162 2014). These differences in the neural processing of social stimuli according to social
163 observation versus interaction conditions underline the importance of adopting a second-
164 person perspective approach. These differences have been confirmed in gaze processing
165 paradigm: Schilbach et al. (2006) found stronger activation of the ventral mPFC and STS in
166 social interactions with self-directed facial expressions. In particular, the right posterior STS
167 may play an essential role in social interactions associated with a direct gaze, by allowing for
168 the continuous temporal integration of environmental stimuli (Haxby et al., 2000; Pelphrey et
169 al., 2003; Tylén et al., 2012). While studies with second-person paradigms have found brain
170 activation similar to that observed with classic third-person mentalizing tasks, they have also
171 revealed a more distributed network, probably reflecting the recruitment of cognitive

172 processes associated with real-world social stimuli (Redcay et al., 2020; Wolf et al., 2010).
173 Using a naturalistic paradigm makes it possible to reproduce some of the richness of real-
174 world social interactions and their underlying cognitive processes.

175 The aim of the present study was to investigate the neural correlates of social inference
176 processing using a more naturalistic task that elicited the different components of social
177 inference: identifying observed behaviors from body motion (e.g., hands, bust, facial
178 emotional expressions, gaze direction); and attributing a mental state to an inferred social
179 cause (e.g., situational event).

180 Such a task could be useful for identifying the neural regions involved in real-life social
181 situations (for a recent review, see Redcay et al., 2020). To address these challenges, we
182 developed the Dynamic Inference Task (DIT), an ecological task inspired by Kim et al.
183 (2009). In the original virtual reality social cognition task (Kim et al., 2009), participants
184 undergo fMRI while viewing short video clips simulating real-world social interactions, in
185 which the degree of inference (high vs. low) and the presence versus absence of emotions
186 (i.e., anger, happiness, neutral) are manipulated. Participants are asked to attribute possible
187 reasons for the situations displayed by virtual humans (avatars) from verbal and nonverbal
188 (facial) expressions. We adapted this task by creating scenarios played by male/female actors
189 that were closer to real-world social situations. In half the situations, the context was not
190 clearly explained, thus requiring a higher level of inference, whereas in the other half, the
191 context was given, thus requiring a low level of inference. In order to elicit a feeling of
192 engagement with others, the male/female actor verbally engages the participant at the
193 beginning of and during each video. In a further attempt to elicit a feeling of engagement, we
194 manipulated the actors' gaze direction, so that it was either participant-directed (direct) or
195 other-directed (averted). Although gaze direction had previously been manipulated for action
196 goals (e.g., Tylén et al., 2012) or facial expressions (e.g., Schilbach et al., 2006), to our

197 knowledge, this had never been done for mental state attribution. We tested three predictions:
198 during trials requiring nonemotional mental state inference, the brain regions belonging to the
199 mentalizing system would be preferentially engaged (mPFC, STS, TPJ, PCC/PC) in situations
200 requiring high versus low inference (Hypothesis 1); trials requiring high inference would
201 elicit the joint activation of the MNS and mentalizing system, and the amygdala would be
202 activated in emotional versus nonemotional situations (Hypothesis 2); and direct-gaze trials
203 would elicit stronger activation within the ventral mPFC and premotor cortex than averted-
204 gaze trials (Hypothesis 3). In addition to these three predictions, we expected to observe
205 activation in other brain regions or in a broader brain network than that traditionally found for
206 mentalizing processes. Second-person studies using naturalistic tasks have highlighted the
207 activation of regions that are usually observed in mentalizing, but also of a more extensive
208 network (Redcay et al., 2010, 2019). Thus, as the DIT adopts a second-person approach, it
209 might also elicit a broader or slightly different brain network. As studies using such
210 naturalistic paradigms are still scarce, we could not form more specific predictions about
211 activation patterns, apart from there being a broader brain network encompassing regions
212 associated with motor movements, language, and emotion (e.g., Iacobini et al., 2004; Redcay
213 et al., 2020; Wolf et al., 2010).

214

215 **2. Method**

216 **2.1. Participants**

217 Participants were 51 healthy, right-handed adult volunteers, recruited from the local
218 community through an advertisement. The inclusion criteria were as follows: a) native French
219 speaker, b) right-handed (as assessed with the Edinburgh Handedness Inventory; Oldfield,
220 1971), c) normal or corrected-to-normal vision and hearing, and d) compliance with health
221 and safety regulations regarding MRI use. Exclusion criteria included a) past or present

222 history of psychiatric disorders according to the DSM-5 (American Psychiatric Association,
223 2013), and b) first-degree relatives with psychiatric disorders or severe general medical illness
224 (including neurological disorders or head trauma) that might influence brain function.
225 Participants were screened for eligibility in interviews by trained psychiatrists.
226 Prior to fMRI acquisition, verbal intelligence was estimated using the Mill Hill Vocabulary
227 Scale, which has consistent test–retest reliability in excess of 0.90 for several normal adult
228 populations (Deltour, 2005; Raven, 2000).
229 The study was approved by the regional ethical committee (CPP Grand Est I no.: 2016-
230 A00275-46), and conducted in accordance with the Declaration of Helsinki. All participants
231 gave their written informed consent after the experimental procedure had been explained to
232 them and were compensated for their participation (\$85).

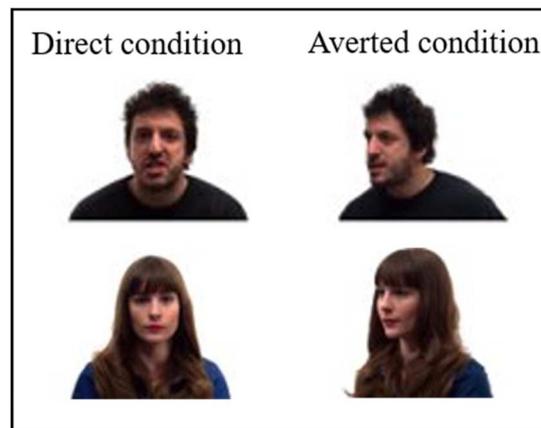
233 **2.2. Experimental design**

234 **2.2.1. DIT stimuli**

235 Stimuli consisted of 24 video clips, each lasting 12-15 seconds, showing a male/female actor
236 talking about a personal experience. We manipulated three variables: a) degree of inference
237 (high-inference condition vs. low-inference condition), b) emotional expression (emotional
238 condition vs. nonemotional condition), and c) gaze direction (direct condition vs. averted
239 condition).

240 There were 12 high-inference trials and 12 low-inference trials. In the high-inference video
241 clips, the male/female actors shared their mental state but not the triggering event, which was
242 emotionally valenced (angry, happy, and neutral). As the context of the situation was not
243 clearly explained, the reasons for the mental state remained ambiguous, and thus required a
244 higher level of inference. In the low-inference video clips, the male/female actors shared clear
245 information about what had happened them without any emotion (for examples of stories, see
246 online supplementary material S1).

247 In the high-inference trials, the actors and the scripts conveyed an emotion in half the trials
248 (emotional condition), but not in the other half (nonemotional condition).
249 To manipulate gaze direction, in half the videos, the actors directly faced the participant (i.e.,
250 camera; direct condition), while in the other half, the actors faced approximately 30--35°
251 away from the camera, in the direction of an inferred other (averted gaze condition; see Fig.
252 1).



253
254 Figure 1. Example of stimuli

255 In each video clip, a male/female actor shared his/her mental state, which was emotionally
256 valenced (angry, happy, and neutral), with either a participant-directed (direct gaze condition)
257 or other-directed (averted gaze condition) gaze.

258
259 To assess the quality of the clips, we first conducted a pilot study in which 60 healthy
260 participants (30 females; mean age = 33.85 years, $SD = 11.9$ years) viewed the clips while
261 seated in front of a computer screen. For each clip, participants rated a short sentence that
262 suggested a potential reason (inference sentence) for the character's emotion (forced-choice:
263 true or false), the nature of the emotion expressed by the character (anger, happy, or neutral),
264 the intensity of the character's emotional facial expression on a Likert scale ranging from 0 to
265 10, and perceived social self-involvement on a Likert scale ranging from 0 (*No involvement*)
266 to 10 (*High social involvement*).

267 Statistical results showed that sentences constituted plausible inferences for the character's
268 emotion (mean accuracy = 91%). Emotion identification was satisfactorily high (min =
269 96.56%), and the intensity ratings confirmed a bias toward emotional clips over neutral ones
270 ($p < .001$). Moreover, the direct gaze condition induced greater self-involvement than the
271 averted one ($p < .001$). Detailed results of analyses are available in supplementary material.

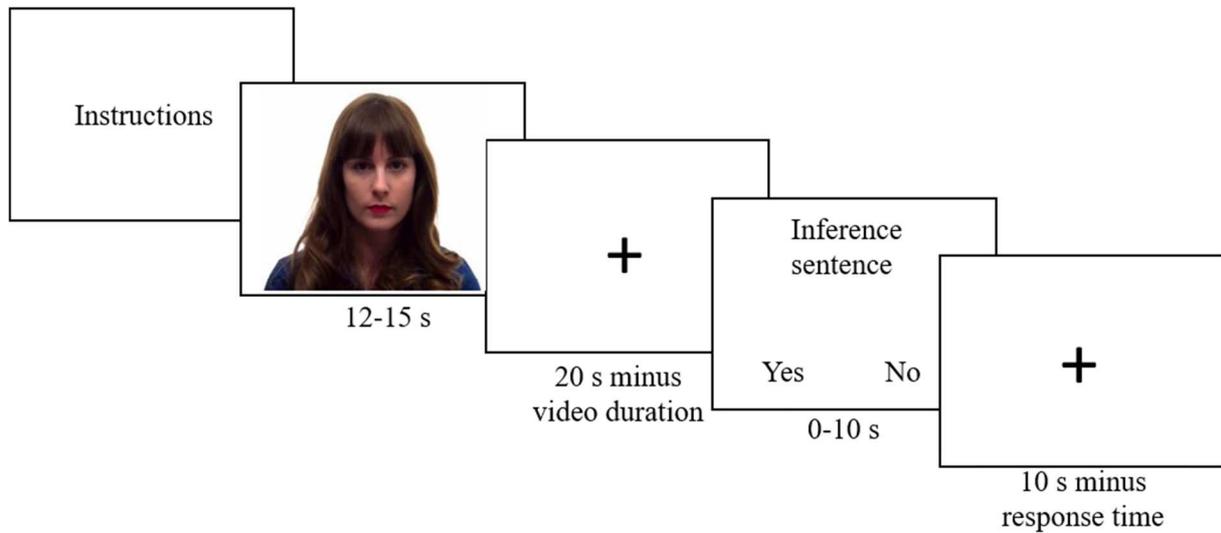
272 **2.2.2. DIT task and procedure**

273 Before participating, all participants received standardized instructions: they were told they
274 would observe individuals telling stories that had happened to them, and would have to find
275 out what had happened. After each clip, a sentence would appear, and they would have to
276 decide whether this sentence matched the described situation by answering “yes” or “no”.

277 To familiarize participants with the task, the MRI environment (MRI table, screen, response
278 pad), and the experiment's time constraints, we ran a training session at the beginning of the
279 fMRI session, once the participants had been installed on the MRI table. We used two video
280 clips that were not included in the fMRI task.

281 During the fMRI scanning, each trial began with a reminder of the instructions, followed by a
282 video clip (duration: 12-15 s), then a centered fixation cross (duration: 5-8 s, depending on
283 video clip duration), followed by the inference sentence, which participants had to rate as
284 either “true” or “false”, by pressing on an MRI-compatible button response pad within 10 s.
285 Each trial was separated by a period of variable duration (2-10 s), depending on response
286 duration and jitter, which featured a white screen with a centered fixation cross (see Fig. 2).

287



288

289 Figure 2. Study design

290 Each participant performed two different sessions, each featuring 12 trials (6 high-inference
 291 and 6 low-inference). The degree of inference (high vs. low), presence/absence of emotion
 292 (emotional vs. nonemotional), and gaze direction (direct vs. averted) were counterbalanced
 293 across participants.

294 After the fMRI scanning, the videos were shown a second time outside the scanner.

295 Participants were asked to identify the facial expressions of emotion (anger, happiness or
 296 neutral), and rate perceived social self-involvement on a 10-point Likert scale.

297

298 **2.2.3. Behavioral data analysis**

299 Participants' response accuracy and reaction times were measured during scanning, and their
 300 perceived social self-involvement after scanning. These variables were summarized and
 301 averaged for each participant and each condition, and condition-related differences were
 302 compared using a within-participants repeated-measures analysis of variance (ANOVA). All
 303 statistical analyses were performed using R and the easieR metapackage (Stefaniak, 2018)
 304 with a threshold at $p < .05$.

305 **2.2.4. Functional MRI data acquisition**

306 Imaging was performed on a 3-T Siemens Skyra (Siemens Healthcare, Erlangen, Germany).
307 For each participant, we acquired anatomical whole-brain T1-weighted images parallel to the
308 AC-PC line with a tilt of -30° , using a 3D gradient-echo pulse sequence with the following
309 parameters: TR = 2800 ms; TE = 6 ms; flip angle = 90° ; 36 slices, slices thickness = 4.50 mm.
310 Functional data were acquired in an ascending-slice 2D-T2-weighted EPI sequence sensitive
311 to blood-oxygen-level-dependent (BOLD) contrast, in the same axial plane as the T1-
312 weighted structural images (2D-T2-FFE-EPI; TR = 2000 ms, TE = 30 ms, flip angle = 90° , 36
313 axial slices, slice thickness = 4.50 mm).

314 **2.2.5. Functional MRI data analysis**

315 Images processing and statistical analyses were conducted using statistical parametric
316 mapping implemented in SPM12 (<http://www.fil.ion.ucl.ac.uk/spm/software/spm12/>). The
317 first six volumes in each session were discarded—leaving 243 volumes in each session—, to
318 allow for T1 equilibration effects. Functional images were spatially realigned to the mean
319 functional image of the series, and a slice-timing correction was then applied. At this step,
320 potential outlier scans were identified using Artifact Detection Tools (ART) algorithms. Scans
321 showing a global BOLD signal more than five standard deviations from the mean, or motion
322 exceeding a 0.9-mm threshold, were marked as outlier scans and included as nuisance
323 regressors. Images were directly segmented and normalized to the standard anatomical space
324 of the Montreal Neurological Institute. Resample resolution was set at 2 mm x 2 mm x 2 mm.
325 Finally, spatial smoothing was performed with an isotropic three-dimensional Gaussian filter
326 with a full width at half maximum of 8 mm.

327 At the first level, a design matrix was defined with separate regressors for each experimental
328 condition resulting from the combination of the three factors: degree of inference (high vs.
329 low), emotion (emotional vs. nonemotional), and gaze direction (direct vs. averted) for both
330 the video clip and the inference sentence. Additional nuisance regressors were added,

331 including motion regressors extracted from the realignment processing and scan outliers,
332 where applicable. From this first level, we computed three contrasts. The first one compared
333 the high-inference condition with the low-inference one in the nonemotional condition. The
334 purpose of this contrast was to assess mental state attribution when no emotional state had to
335 be inferred. The second one compared the emotional condition with the nonemotional one in
336 the high-inference condition. This contrast served to evaluate the effect of emotion processing
337 in the high-inference condition. The last contrast compared the direct gaze condition with the
338 averted gaze one in the nonemotional condition, and was designed to assess the general effect
339 of self-involvement.

340 The resulting first-level images were entered into separate one-sample *t* tests in second-level
341 analyses. We ran a Monte Carlo simulation to determine the cluster extent threshold needed to
342 reach $p < .05$ corrected (Slotnick, 2017; Slotnick et al., 2003). For each contrast, we modelled
343 a functional image matrix below a $p < .001$ voxelwise threshold and an appropriate estimation
344 of the full width at half maximum kernel (high-inference vs. low-inference in the
345 nonemotional condition = 11.25; emotional vs. nonemotional in the high-inference condition
346 = 13.25; direct gaze vs. averted gaze in the nonemotional condition = 10.25). The cluster size
347 for each contrast of interest was determined following 10 000 simulations (high-inference vs.
348 low-inference in the nonemotional condition = 127; emotional vs. nonemotional in the high-
349 inference condition = 168; direct gaze vs. averted gaze in the nonemotional condition = 102).
350 Clusters that were significantly activated were labeled using the Anatomy toolbox (Eickhoff
351 et al., 2005, 2006, 2007).

352 For exploratory purposes, and to provide supporting evidence of the DIT's effectiveness in
353 assessing the mentalizing process, we conducted complementary ROI (region-of-interest)
354 analyses to explore the activation of well-identified mentalizing areas for each experimental
355 condition. Defined according to the recent meta-analysis by Wang et al. (2021), ROIs were 8-

356 mm spheres at the following coordinates: left TPJ (-50 -56 20), right TPJ (46 -46 10), dorsal
357 mPFC (-2 48 22; 6 56 20), ventral mPFC (-4 48 -18; 2 46 -18), precuneus (-2 -56 36; 2 -54
358 40), and left and right anterior parts of the temporal lobe (-50 6 -32; 50 4 -32). For each ROI,
359 the mean activation was extracted and tested for each experimental factor (i.e., degree of
360 inference, emotional expression, and gaze direction) when theoretically justified.

361 **3. Results**

362 **3.1. Behavioral data**

363 Behavioral data obtained during scanning showed that participants had a mean response
364 accuracy of 87% ($SD = 10.7$, range = 57-100). There was a main effect of degree of inference,
365 $F(1.8, 90.3) = 34.28$, $p < .001$, indicating a significantly lower rate of correct answers in the
366 high-inference condition ($M = 82$, $SD = 15.6$) than in the low-inference condition ($M = 98$, SD
367 $= 4.4$). There was no effect of gaze direction, $F(1, 50) = .005$, $p = .94$ (direct gaze: $M = 87.2$,
368 $SD = 12.5$; averted gaze: $M = 87$, $SD = 14$). By contrast, there was a significant interaction
369 between the presence of emotion in the high-inference condition and gaze direction, $F(1.52,$
370 $76.14) = 5.58$, $p = .01$. Participants showed higher response accuracy for high-inference
371 emotional videos when the actor directly faced the participant ($M = 90.7$, $SD = 20.6$) than
372 when the gaze was averted ($M = 81.4$, $SD = 23.4$).

373 For reaction times and perceived social self-involvement, analyses were only run on correct
374 items. For reaction times, there were significant main effects of degree of inference, $F(1.86,$
375 $86.74) = 31.8$, $p < .001$, and gaze direction, $F(1, 46) = 4.13$, $p = .04$, but no significant
376 interaction effect, $F(1.92, 88.14) = 1.76$, $p = .17$. Participants responded more slowly in the
377 high-inference condition ($M = 3256.25$, $SD = 1026.27$) than in the low-inference one ($M =$
378 2551 , $SD = 650.35$), and more slowly in the direct gaze condition ($M = 3103.66$, $SD = 925.26$)
379 than in the averted gaze one ($M = 2938.66$, $SD = 876.66$).

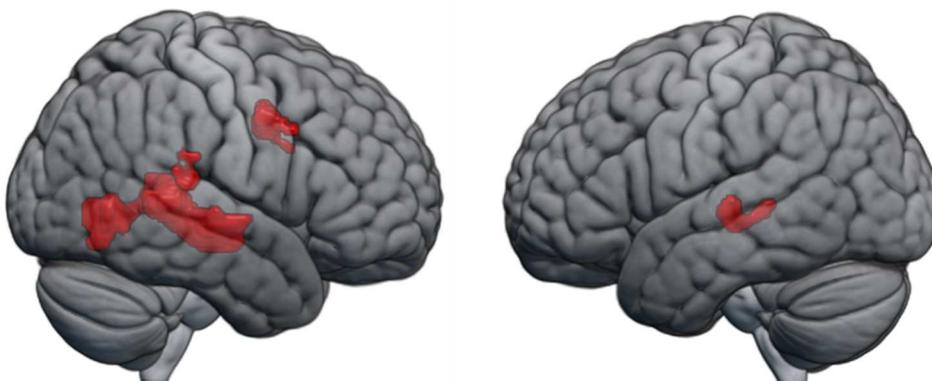
380 Post-scanning data showed a main effect of degree of inference on social self-involvement,
381 $F(1.99, 91.67) = 16.96, p < .001$, indicating that the high-inference condition was more
382 socially self-involving ($M = 49.25, SD = 27.53$) than the low-inference condition ($M = 35.73,$
383 $SD = 24.86$). The main effect of gaze direction was also significant, $F(1, 46) = 47.55, p <$
384 $.001$, indicating that a direct gaze made the video more socially involving ($M = 60.52, SD =$
385 27.21) than an averted gaze ($M = 28.97, SD = 26.07$). We found an interaction effect between
386 degree of inference and gaze direction, $F(1.58, 72.63) = 5.06, p = .01$. Results suggested that
387 participants felt more socially involved in the high-inference condition when the gaze was
388 direct ($M = 69.04, SD = 22.58$) than when it was averted ($M = 31.35, SD = 25.86$).

389 **3.2. Functional MRI data**

390 **3.2.1. High vs. low inference in nonemotional condition**

391 We computed a high > low inference contrast in the nonemotional condition to test our first
392 hypothesis. Results revealed significant activation of the right posterior part of the middle and
393 superior temporal gyrii, encompassing the STS. Additional cluster activation was observed in
394 the temporo-occipital area. Activation was also noted in the left middle temporal gyrus
395 (MTG) and right precentral gyrus (Fig. 3, Table 1 and Table S3 in Supplementary Material).

396



397

398 Figure 3. Activation for the high- > low-inference contrast in the nonemotional condition.

399 $p < .001$ uncorrected, $k = 127$ voxels. Differences were observed in the left and right middle
 400 and superior temporal gyrus, including the superior temporal sulcus and left temporal areas.

401 Color should be used

402

403 Table 1. Whole-brain activation for the high inference > low inference contrast in the
 404 nonemotional condition

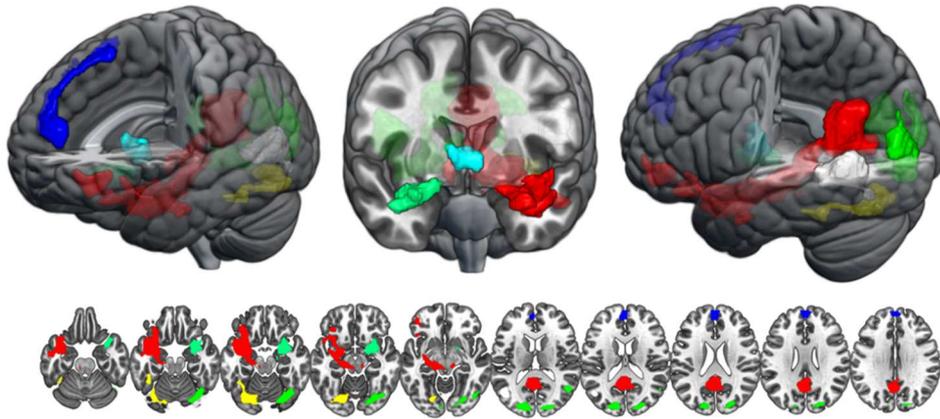
Location		Cluster size	t value	MNI coordinates		
Area	Hemisphere			x	y	z
STG post, MTG post, Occipital cortex	R	1871	8.54	46	-36	2
MFG, IFG oper, precentral	R	287	5.01	40	2	40
STG, MTG	L	165	4.22	-54	-24	-4

405 *Note.* STG: superior temporal gyrus; MTG: middle temporal gyrus; MFG: medial frontal
 406 gyrus; IFG: inferior frontal gyrus. $p < .001$ uncorrected voxelwise; $k = 127$.

407

408 3.2.2. Presence vs. absence of emotion in high-inference condition

409 We computed the emotional contrast in the high-inference condition to test our second
 410 hypothesis. Results revealed a bilateral pattern of activation encompassing cortical and
 411 subcortical areas (Fig. 4, Table 2 and Table S4). Activation was found in bilateral internal
 412 temporal areas around the amygdala and orbitofrontal structures. A cluster in the left
 413 hemisphere included the thalamus and extended to the precuneus. Anteriorly, we noted
 414 activation in the dorsomedial part of the superior frontal gyrus. Activation was also observed
 415 in bilateral posterior areas, including the fusiform and occipital cortex.



416
 417 Figure 4. Activations for the emotional > nonemotional contrast in the high-inference
 418 condition. $p < .001$ uncorrected, $k = 168$ voxels. Differences were notably observed in
 419 the bilateral amygdala, dorsomedial part of the superior frontal gyrus, precuneus, and bilateral
 420 occipital areas.

421 Color should be used

422

423 Table 2. Whole-brain activation for the emotional > nonemotional contrast in the high
 424 inference condition

Location		Cluster size	t value	MNI coordinates		
Area	Hemisphere			x	y	z
Lateral occipital cortex	L	646	6.82	-48	-66	12
Lateral occipital cortex, fusiform gyrus	R	2561	5.85	50	-62	8
Temporal pole, amygdala, precuneus, orbitofrontal cortex	L	3949	5.84	-36	2	-22
Amygdala, orbitofrontal cortex, temporal pole, hippocampus	R	522	5.80	22	2	-18
Medial SFG	R	732	5.07	6	58	28
Fusiform	L	483	4.67	-20	-76	-14

Thalamus L 265 4.49 -4 0 0

425 *Note.* SFG: superior frontal gyrus. $p < .001$ uncorrected voxelwise; $k = 168$.

426

427

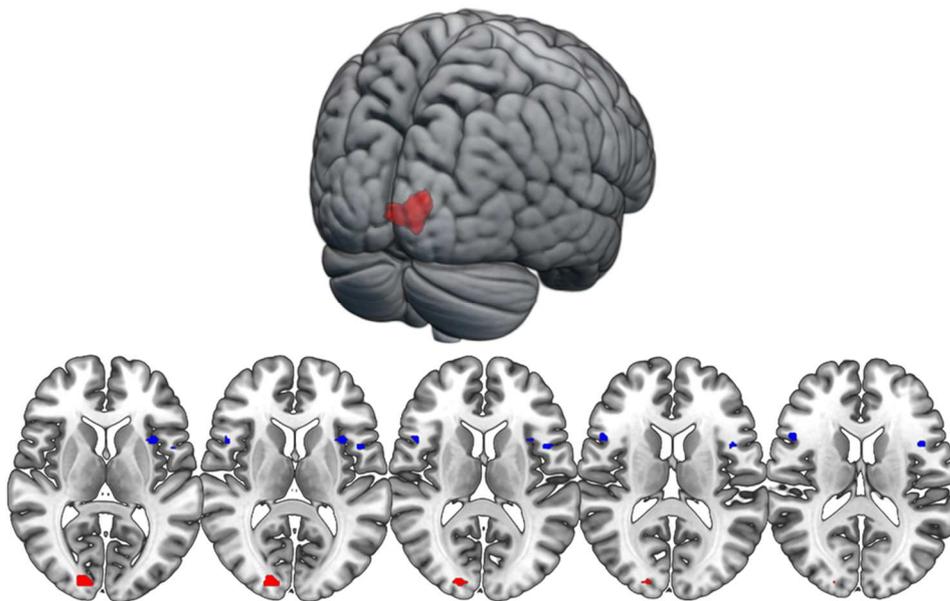
428 3.2.3. Direct vs. averted gaze in nonemotional condition

429 At the initial thresholding, the only significant activation was observed in the posterior

430 occipital area (Fig. 5, Table 3 and Table S5). For exploratory purposes, we therefore used a

431 more liberal threshold ($p < .001$, $k = 20$). Below this threshold, we noted significant activation

432 in the bilateral inferior frontal gyrus and left insular cortex (Fig. 5).



433

434 Figure 5. Activations for the direct > averted gaze condition contrast in the nonemotional

435 condition. In red: activations reaching significance below $p < .001$ and $k = 102$. Differences

436 were observed in the lingual gyrus. In blue: activations below $p < .001$ and $k = 20$.

437 Differences were observed in the bilateral inferior frontal gyrus.

438 Color should be used

439

440 Table 3. Whole-brain activation for the direct > averted gaze contrast in the nonemotional

441 condition

Location		Cluster size	<i>t</i> value	MNI coordinates		
Area	Hemisphere			<i>x</i>	<i>y</i>	<i>z</i>
Occipital pole, lingual gyrus	R	219	4.59	10	-90	-4

442 *Note.* $p < .001$ uncorrected voxelwise; $k = 102$.

443

444 **3.2.4. Additional ROI analyses**

445 Subsequent within-participants ANOVAs comparing the emotional and nonemotional
446 conditions revealed greater activation of all the ROIs in the emotional condition (maximum p
447 $< .01$; see Table S6 for full results), suggesting that mentalizing demands were higher when
448 emotional cues were presented and integrated. Activation of the right TPJ was significantly
449 greater in the high-inference condition than in the low-inference one ($p < .006$). No significant
450 results were noted for the direct versus averted gaze conditions.

451

452 **4. Discussion**

453 The aim of the present study was to investigate the neural correlates of the social inference
454 processing involved in real-life social situations, using a more naturalistic video task (DIT)
455 with a second-person perspective approach that elicited both components of social
456 interactions: identifying observed behaviors from body motion (e.g., shoulders, bust, facial
457 emotional expressions, gaze direction); and attributing mental states to another such as
458 thoughts or emotions in an inferred social situation (e.g., situational event). In real life,
459 individuals do not know the whole context of the social situation, forcing them to make
460 several inferences. In order to recreate these situations, we designed stories in which we
461 manipulated a) the degree of inference: high-inference stories where the reasons for the
462 mental state were ambiguous and involved a higher level of inference because the context of
463 the situation was not clearly explained, and low-inference stories where the context was clear,

464 so the reasons of mental states were unambiguous; b) the presence of emotion in the high-
465 inference stories; and c) the direction of the actor's gaze (direct vs. averted).

466 **4.1. Inference processing in nonemotional condition**

467 We expected the regions belonging to the mentalizing system to be activated during inference
468 processing. Our results did reveal greater activation in the right superior temporal gyrus
469 encompassing the right STS, right precentral gyrus, and bilateral MTG during high inference
470 than during low inference. The right STS is involved in the identification of biological motion
471 and in intention comprehension, regardless of type (Schurz et al., 2014; Van Overwalle and
472 Baetens, 2009). The STS has also been found to be involved in implicit reasoning about
473 mental states in human interaction and joint attention (Redcay et al., 2010; Wolf et al., 2010).
474 The DIT elicits all these processes through videos featuring human characters. Although the
475 demand for mental state reasoning is explicit in our task, the ambiguity of the high-inference
476 condition may require the recruitment of implicit processes such as the decoding of facial
477 expressions and biological motion.

478 In our study, we observed bilateral MTG activation. The latter has already been reported in
479 studies using ToM tasks (Carrington and Bailey, 2009; Schurz et al., 2014; van Veluw and
480 Chance, 2014). The MTG's role in inference tasks is classically associated with verbal
481 processing, rather than with mental state attribution processing. Kobayashi et al. (2007) found
482 increased activity in the right MTG during the presentation of a ToM cartoon compared with
483 a ToM story condition. One possible explanation provided by these authors is that the thought
484 bubbles added complexity, and the increased MTG activation reflected the implementation of
485 linguistic strategies to perform the task. We could draw the same parallel with our results
486 concerning the more anterior part of MTG activation: an ambiguous context in the high-
487 inference condition may have been more verbally demanding for the attribution of a mental
488 state than the low-inference condition. Our behavioral results support this hypothesis, with

489 lower response rates and longer response times for the high-inference condition than for the
490 low-inference one suggesting a higher level of complexity in social inference processing. In
491 real life, individuals are often confronted with social situations where they make inferences
492 without having all the contextual information, and therefore without knowing which of their
493 inferences is the correct one. The temporal lobes are generally associated with a store of
494 personal semantic and episodic memories (Frith and Frith, 2003; Gallagher and Frith, 2003).
495 Research in social cognition has suggested that the anterior part of the temporal lobes is
496 important for the storage and retrieval of social semantic scripts. In our study, the high-
497 inference condition required participants to remember past episodes with behavior similar to
498 that which they were then observing, in order to retrieve the associated mental state. The
499 greater MTG activation may have reflected the retrieval of social scripts and their comparison
500 with the observed situation in order to make the inference.

501 We also observed greater activation of the left MTG during high inference than during low
502 inference. Left MTG activation has also been found in several other types of task, including
503 social animation, rational actions and reading the mind in the eyes, which all feature
504 depictions of human action or behavior (Schurz et al., 2014). Our finding of increased
505 activation of the left MTG may have reflected the observation of the character's behavior that
506 was necessary to make the inference.

507 The greater activation of the occipitotemporal area in the high-inference condition may also
508 be related to multisensory integration. The DIT requires combined analysis of social signals
509 from multiple sensory cues (biological motion, language, auditory processing), and inference
510 processing in an ambiguous social context may require further cognitive processing of
511 multiple types of sensory information.

512 Interestingly, we also found greater activation in the right precentral gyrus in the high-
513 inference condition than in the low inference condition. The right precentral gyrus is

514 classically involved in voluntary movement control, as well as in higher cognitive processes
515 such as motor imagery, language processing, and even emotion/empathic processing (e.g.,
516 Guo et al., 2012). According to Tomasino et al. (2016), the involvement of this brain region in
517 cognitive processing may reflect “mental simulation processing triggered by the task either
518 implicitly or explicitly” (p. 15). This precentral area has also been found to be activated in
519 multisensory attention and the orientation of auditory attention (Huang et al., 2012). In our
520 study, this activation may also have reflected the recruitment of the attentional network.
521 We expected to observe more activation in the mPFC in the high-inference condition, given
522 the strong demand for the attribution of nonemotional mental states in this condition. While
523 many studies have reported activation of the mPFC in the attribution of mental states, the
524 specific role of this structure in belief reasoning has been questioned by lesion and imaging
525 studies (Bird et al., 2004; Saxe et al., 2006). The mPFC appears to be involved more in
526 processing socially relevant information about others (Aichhorn et al., 2006; Saxe and Powell,
527 2006) than in belief-desire reasoning. In their meta-analysis, Van Overwalle and Baetens
528 (2009) suggested that the mPFC is mainly involved in the attribution of ‘more enduring
529 personality traits about the self and other people’. The fact that the DIT elicits the attribution
530 of transitory mental states might explain the absence of activation in the mPFC.

531 **4.2. Emotional contrast in high-inference condition**

532 The second aim of this study was to explore the neural processing of inferences (i.e., high-
533 inference condition) from emotional facial expressions. Compared with the nonemotional
534 condition, inferences in the emotional condition elicited greater activation of the bilateral
535 temporal areas encompassing the amygdala, dorsal mPFC, and left precuneus, suggesting
536 joint activation of the amygdala and the mentalizing system. Activation was also observed in
537 bilateral posterior areas, including the fusiform and occipital cortex.

538 The greater activation of the bilateral amygdala during emotional versus nonemotional
539 inference trials is in line with previous studies and this structure's role in the detection of
540 stimuli with emotional and social salience (e.g., Adolphs, 2009). Our results are also
541 consistent with those of Schmitgen et al. (2016) and Schnell et al. (2011), who observed
542 increased activation of the amygdala during affective ToM judgments. However, Schnell et
543 al. (2011) reported activation of the left amygdala for affective ToM judgements, whereas
544 Schmitgen et al. (2016) reported right amygdala activation during affective ToM when
545 emotional facial expressions were presented. These authors therefore suggested the existence
546 of a stimulus-dependent lateralization of amygdala activation: the left amygdala for affective
547 ToM judgments, and the right amygdala in the presence of emotional facial expressions
548 during affective ToM. Unlike Schmitgen et al. (2016), we used dynamic facial expressions of
549 human individuals during the ToM task, and observed bilateral amygdala activation. Our
550 results are more in line with the notion that bilateral activation of the amygdala is a general
551 effect of emotional stimuli (Fusar-Poli et al., 2009; Sergerie et al., 2008) than with the
552 hypothesis of stimulus-dependent lateralization of amygdala activation.

553 Bilateral activation of the MTG was also observed in the emotional condition, in contrast to
554 the nonemotional condition. As for the high- versus low-inference comparison, this result may
555 reflect the retrieval of social scripts and the observation of the character's behavior needed to
556 make the inference. Again, the greater activation of the occipitotemporal area in the emotional
557 condition may also be related to multisensory integration.

558 In addition, we observed greater activation in the mPFC in the emotional versus nonemotional
559 inference condition. The mPFC has been shown to be involved in many cognitive processes,
560 although its specific role in reasoning about beliefs remains subject to debate. The mPFC
561 seems to be particularly engaged in reasoning about the stable mental states of others, such as
562 personality traits (Aichborn et al., 2006), and in processing emotionally or socially relevant

563 information about others (Van Overwalle et al., 2009). The activation in our study seemed to
564 concern the dorsal part of the mPFC. The greater activation in this structure in the emotional
565 inference condition may reflect the making of judgments about another person's emotional
566 states. Ochsner et al. (2004) demonstrated involvement of the dorsal mPFC in the emotional
567 assessment of self and others. This region has also been found to be activated during the
568 observation of or engagement in social interaction and, to a lesser extent, during joint
569 attention (e.g., Iacoboni et al., 2004; Saxe et al., 2006). Redcay et al. (2010) observed weak
570 activation of the dorsal mPFC during joint attention, but no differential recruitment during a
571 live social interaction relative to a video. Consistent with previous research, our findings
572 suggest that the dorsal mPFC is recruited when the social situation requires judgments to be
573 made about the emotional mental states of self and others.

574 Moreover, we found left precuneus activation specific to emotional ToM, compared with
575 nonemotional ToM. The precuneus seems to be involved in a variety of higher-order
576 cognitive functions. Beyond its role in visuospatial mental imagery and episodic memory
577 retrieval, it has recently been suggested that the precuneus is involved in social perspective
578 taking (Cavanna and Trimble, 2006; Schurz et al., 2014). In their meta-analysis, Schurz et al.
579 (2014) found stronger activation of the precuneus for false belief, trait judgments and rational
580 action, all of which elicit mental imagery, than for control tasks. Furthermore, this structure
581 was not activated by either social animation or reading the mind in the eyes. Taken together,
582 these results confirmed the involvement of the precuneus in mental imagery. At first glance,
583 our results seem to contradict these data, given that we found activation of the left precuneus
584 for visual material requiring less recourse to mental imagery. However, it may be not so much
585 the nature of the material as the nature of the task that determines the involvement of the
586 precuneus. Petrini et al. (2014) postulated that the precuneus, through its widespread
587 connectivity, is all the more activated 'when the social situation is not easily interpretable'. In

588 our task, the activation of the left precuneus in the emotional condition may have reflected
589 greater difficulty interpreting a social situation where both the inference and the emotion had
590 to be processed. Several studies directly contrasting affective and cognitive ToM have
591 reported strong activation of the precuneus/cuneus region when participants think about
592 others' cognitive mental states, but not their affective mental states (Schlaffke et al., 2015;
593 Schurz et al., 2014). However, this functional distinction was not found in the study by
594 Bodden et al. (2013). The material used in these different studies varied widely in terms of
595 complexity (e.g., stimuli, inference demand) which could explain the discrepancies in the
596 results. Further research manipulating these factors is needed to determine their influence on
597 the recruitment of the ToM brain network.

598 Activation of the visual cortex can be seen in the light of recent evidence of a third visual
599 pathway for processing social cues, notably moving faces, in connection with the STS
600 (Pitcher et al., 2021). Through this pathway, visual input is integrated with other sensory
601 modalities to enable humans to understand and interpret the actions of others.

602 The emotional inference condition may increase cognitive demands, owing to the richness of
603 the stimuli. However, the general difficulty of the task does not appear to be sufficient to
604 explain our results, as increases in cognitive load are often associated with the recruitment of
605 the dorsolateral prefrontal and parietal cortices, which were not activated here (Tomasini et
606 al., 2007).

607 **4.3. Gaze direction in nonemotional condition**

608 The third aim of this study was to explore the brain regions involved in social interaction (i.e.,
609 direct gaze) versus social observation (i.e. averted gaze) in a ToM task where the human
610 character looked either directly at the participant or at someone else. Although we failed to
611 find any strong evidence of an effect of social interaction in our study, there was some
612 evidence of greater activation of anterior frontal (posterior OFC) and bilateral insula

613 activation during social interaction than during social observation. These data are in line with
614 those of Ciaramidaro et al. (2014), who observed joint activation of both the MNS and
615 mentalizing system. At the behavioral level, participants felt more socially involved when the
616 gaze was directed toward them. The direct gaze may have had a facilitating effect, for despite
617 longer response times, response accuracy was higher in the emotional high-inference
618 condition. Previous studies assessing social interactions had shown that the mPFC is involved
619 in highly demanding social interactions (Ciaramidaro et al., 2014; Schilbach et al., 2006;
620 Tylén et al., 2012). Contrary to our hypothesis, the direct gaze condition did not significant
621 activate the mPFC. In their study, Zillekens et al. (2019) also failed to find an effect of gaze
622 direction on brain activation. This result could be due to methodological differences. For
623 instance, some authors have postulated the differential involvement of core nodes of the ToM
624 system. For instance, in their meta-analysis, Schurz et al. (2014) showed that the mPFC is
625 preferentially engaged in situations where individuals are asked to make judgments about
626 others. The participants in our study were asked to infer a mental state from what a
627 male/female actor was doing or saying in a given situation, and not to make judgments
628 directly about the actor. Finally, contrary to most of the studies assessing the directness of
629 social interaction, our participants could rely on other features (e.g., emotional faces and
630 prosody) to perform mentalizing processes. Further studies are needed to gauge the respective
631 influence and neural correlates of social directedness and emotional cues in ecological social
632 interactions.

633 **4.4. Limitations**

634 Our study has several limitations. First, the experimental design did not include a physical
635 inference condition, thus preventing us from directly contrasting cognitive and physical
636 inference processing. We made this choice to limit the number of conditions, in order to focus
637 on other factors such as the degree of inference required and the emotional aspects of social

638 inference processing. Nevertheless, the task's duration and ecological nature make it suitable
639 for evaluating mentalizing processes in clinical populations.

640 Second, our results should be interpreted with caution, as the naturalistic approach we chose
641 limited our ability to isolate and manipulate specific processes. Nevertheless, the richness of
642 this approach yielded insights into brain functioning in a dynamic, multimodal and complex
643 social context.

644 Third, several questions remained unanswered, such as the functional connectivity between
645 and within core nodes of both the MNS and the mentalizing system (Begliomini et al., 2017;
646 Ciaramidaro et al., 2014; Sperduti et al., 2014; Spunt and Lieberman, 2012). Although the
647 DIT was not designed to test functional connectivity hypotheses, ecological designs are
648 needed to capture the dynamic interplay between the MNS and the mentalizing system.

649 Finally, although manipulating gaze direction is the first step in studying the difference
650 between an observational situation and a social interaction situation, it cannot reproduce the
651 full complexity of a social interaction (Schilbach, 2015). fMRI coupled with an eye-tracking
652 device could resolve the question of the processing associated with an actor's gaze direction
653 during the mentalizing process.

654 **4.5. Conclusion**

655 The strength of the present study is that it featured a dynamic task associating the different
656 processes of social cognition with human protagonists, in order to reproduce real-life
657 situations as closely as possible in fMRI. It elicited anatomically circumscribed activation in
658 healthy human brains that is frequently associated with social cognitive processes in the
659 literature on the social cognition brain network. It also highlighted the role of the precuneus
660 and left mPFC in the attribution of emotional mental states based on dynamic visual stimuli.
661 Social cognition appeared to be a strong predictor of real-life social functioning (e.g., Fett et
662 al., 2011). Deficits in social cognition have been highlighted in several pathologies (including

663 neurological, psychiatric, and developmental disorders) and are even a core symptom of some
664 psychiatric disorders (e.g., Cotter et al., 2018; Derntl & Habel, 2011). At the neuroimaging
665 level, transdiagnostic analyses of several severe mental illnesses such as major depressive
666 disorder and schizophrenia have revealed both shared (e.g., between precuneus and bilateral
667 superior parietal lobe) and specific dysconnectivity patterns in the resting state (Schilbach et
668 al., 2016). We believe that the DIT, a more naturalistic task, could be helpful for investigating
669 the neural correlates of social cognition across clinical groups that are adversely affected.

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675 any part of this article.

676 **Conflict of interest**

677 The authors declare that there is no conflict of interest that could be perceived as prejudicing
678 the impartiality of the research reported.

679 **Data and code availability statement**

680 All anonymized behavioral data are shared on the OSF project page (<https://osf.io/qnjrt/>) and
681 fMRI uncorrected statistical maps are available at <https://neurovault.org/collections/10920/>.

682 Any other materials or information the reader may require is available from the authors on
683 reasonable request.

684

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