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1 **Peer presence elicits task-independent changes within and**
2 **beyond the mentalizing network across children and adults**

3

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16

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23 **This PDF file includes:**

24 Main Text

25 Figures 1 to 6 (in color)

26 Tables 1 to 3

27

28 **Highlight**

- 29 • Basic math and reading skills were measured in children and adults.
- 30 • Participants were alternately observed and unobserved by a familiar peer.
- 31 • Behavior showed that children were as facilitated by peer observation as adults.
- 32 • fMRI data showed task-independent, observation-driven changes in mentalizing, attention,
33 and reward brain regions.
- 34 • All adults' neural changes were also found in children, except one located in right temporo-
35 parietal junction.

36 **Abstract**

37

38 There is ample behavioral evidence that others' mere presence can affect any behavior in human
39 and non-human animals, generally facilitating the expression of mastered responses while
40 impairing the acquisition of novel ones. Much less is known about i) how the brain orchestrates the
41 modulation of such a wide array of behaviors by others' presence and ii) when these neural
42 underpinnings mature during development. To address these issues, fMRI data were collected in
43 children and adults alternately observed and unobserved by a familiar peer. Subjects performed
44 two tasks. One, numerosity comparison, depends on number-processing brain areas, the other,
45 phonological comparison, on language-processing areas. Consistently with previous behavioral
46 findings, peer observation facilitated both tasks, and children's improvement was comparable to
47 adults'. Regarding brain activation, we found virtually no evidence of observation-driven changes
48 within the number- or language-related areas specific to each task. Rather, we observed the same
49 task-independent changes for both numerosity and phonological comparisons. This unique neural
50 signature encompassed a large brain network of domain-general areas involved in social cognition,
51 especially mentalizing, attention, and reward. It was also largely shared by children and adults. The
52 one exception was children's right temporoparietal junction, which failed to show the observation-
53 driven lesser deactivation seen in adults. These findings indicate that social facilitation of some
54 human education-related skills is i) primarily orchestrated by domain-general brain networks, rather
55 than by task-selective substrates, and ii) relatively mature early in the course of education, thus
56 having a protracted impact on academic achievements that may have heretofore been
57 underestimated.

58 1. Introduction

59 The presence of an observer affects behavior. Generally, it facilitates simple or mastered
60 responses while impairing complex or novel ones (Zajonc). A long history of psychology research
61 has demonstrated the ubiquity of this social facilitation-inhibition phenomenon across species,
62 observers, and behaviors (Bond and Titus; Guerin; van Meurs et al.). We share this fundamental
63 form of social influence with many -if not all- other animal species, including other primates such
64 as macaques (Reynaud et al.), but also songbirds (Vignal, Mathevon, et al.) or drosophilas
65 (Chabaud et al.). Actual observers embodied by friends (Ruddock et al.), strangers (Guerin), or
66 humanized robots (Woods et al.) trigger social facilitation-inhibition, but virtual observers
67 (Miyazaki), or even imagined ones (Hazem et al.), can induce it as well. All behaviors can be
68 changed by others' presence (positively or negatively, depending on the difficulty of the task they
69 are embedded into), including, in particular, the very eye movements and attention mechanisms
70 that guide vision, our primary window to the world (Liu and Yu; Tricoche, Ferrand-Verdejo, et al.;
71 Huguet et al.; Wykowska et al.). In contrast with this wealth of behavioral data, there is limited
72 knowledge on the neural mechanisms orchestrating others' presence effects on such a wide variety
73 of behaviors in so many species (Belletier et al.; Monfardini, Reynaud, et al.). Even less is known
74 about the emergence of the neural correlates of social facilitation-inhibition in children, although
75 others, especially peers, might be particularly important during development (Somerville;
76 Steinberg).

77 Social facilitation-inhibition is a lifelong phenomenon detectable as early as one year of age in
78 humans (Pearcey and Castro). Therefore, understanding the neural correlates of social facilitation-
79 inhibition during development has potential relevance to several domains including childhood
80 obesity (Higgs and Thomas), adolescent risk-taking (Telzer, Rogers, et al.), and education (van
81 Duijvenvoorde et al.). Because peers' influences can have staggering dramatic consequences on
82 adolescents' health and life, much of the effort has heretofore focused on understanding the neural
83 correlates of peers' influences on adolescent decision making (Hartley and Somerville). Interest is
84 nevertheless emerging for the exploration of peers' influences on cognitive skills relevant to
85 education (Dumontheil et al.). Given peers omnipresence at school, a better understanding of peer
86 presence effects on cognition could provide useful insights to educators about when to minimize,
87 or on the contrary, maximize peers' presence during learning in order to improve academic
88 achievements.

89 At least two different neural mechanisms may explain social facilitation-inhibition remarkable
90 ubiquity across ages, behaviors and species. One is that others' presence might modify neural
91 activity in task-specific networks. All animals having congeners, it could indeed be adaptive for

92 evolution to endow every neural system, whether sensory, motor or cognitive, immature or mature,
93 with some capacity to process relevant social information (Ferrari et al.). Several lines of evidence
94 from research in non-human animals support this hypothesis. In monkeys, for example, a
95 congener's presence changes activity in the fronto-parietal network subserving an attentional task
96 (Monfardini, Redoute, et al.), but also in the dorsolateral prefrontal neurons encoding a visuo-motor
97 task (Demolliens et al.). In songbirds, a congener's presence affects early gene activation in
98 auditory areas when the bird is listening and in motor areas when the bird is singing (Woolley et
99 al.; Ritters et al.; Vignal, Andru, et al.; Menardy et al.; Hessler and Doupe; Woolley). Some human
100 neuroimaging data are also compatible with the idea that peer presence affects task-specific
101 regions. Being observed changes activity in the (adult's) inferior parietal region controlling object
102 grasping during a fine grip motor task (Yoshie et al.), whereas it affects the (adult's and
103 adolescent's) dorsolateral prefrontal region controlling relational integration during a complex
104 reasoning task (Dumontheil et al.). In adolescents, being observed by a peer enhances the
105 pleasure of risk-taking and the associated activity in the ventral striatal region controlling reward
106 processing (Albert et al.; Chein et al.; Van Hoorn et al.). Thus, several studies in human and non-
107 human animals support the hypothesis that peer-presence effects on behavior might be mediated
108 by task-specific neural systems.

109 Another possibility, however, is that others' presence exerts its influence via one or several domain-
110 general neural systems irrespective of the task. This could especially hold for primates, whose
111 brain is thought to include several domain-general networks dedicated to processing social
112 information (Rogier B Mars et al.). Specifically, social presence effects in humans have been
113 associated with our species' outstanding mentalizing abilities (Hamilton and Lind). Mentalizing is
114 the ability to infer others' states-of-mind, such as their desires, intentions, or beliefs (Frith and Frith;
115 Blakemore). Explicit mentalizing is generally considered to mature at around 4 years of age, but
116 implicit mentalizing is present by 15 months of age (Kovács et al.). The core mentalizing network
117 identified in the brain across a variety of tasks and stimuli includes four regions: the medial
118 prefrontal cortex (mPFC), the temporo-parietal junction (TPJ), the precuneus/posterior cingulate
119 cortex (PreC/PCC) and the middle temporal gyrus (MTG) (Preckel et al.; van Veluw and Chance).
120 This network is developing early in life, before school age, and is relatively stable across late
121 childhood, adolescence, and adulthood (Fehlbaum et al.; Richardson et al.). Changes in one or
122 more nodes of this network have been reported in several neuroimaging studies that investigated
123 the effects of peer-presence on various behaviors. This holds true for adolescents observed while
124 taking risks (van Hoorn et al.; Chein et al.; Telzer, Ichien, et al.), making prosocial decisions (Van
125 Hoorn et al.), or engaging in complex reasoning (Dumontheil et al.), as well as for adults observed
126 during risk-taking (Beyer et al.), skilled motor performance (Chib et al.) or embarrassing failures
127 (Müller-Pinzler et al.). It is therefore possible that humans mentalize about the thoughts of the

128 observer, even when such mentalizing is not explicitly required. This would be associated with the
129 systematic recruitment of the brain mentalizing network, irrespective of the task at hand. It is
130 interesting to note that some animal data are also compatible with the idea that neural changes
131 produced by a congener's presence extend beyond task-specific substrates. Chicks, for example,
132 show a dissociation of the brain regions controlling foraging vs. the social facilitation of foraging
133 (Xin et al.). Also, despite its 100,000-neuron brain, the drosophila's uses two distinct brain networks
134 to encode long-lasting olfactory memories, one when flies are tested alone, the other when they
135 are tested in the presence of other flies (Muria et al.). Overall, studies in humans and non-human
136 animals may also support the hypothesis that peer-presence effects on behavior are mediated by
137 a domain-general neural system such as the mentalizing network.

138 Critically, the two possible neural accounts of social facilitation-inhibition make different predictions
139 when different tasks have non-overlapping neural substrates. According to the task-specific theory,
140 the effect of peer presence on brain activity depends on the task at hand and is localized in task-
141 specific brain regions. According to the domain-general theory, the effect of peer presence on brain
142 activity is independent of the task at hand and is localized in a domain-general network (such as
143 the mentalizing network). To the best of our knowledge, such a paradigm with two different tasks
144 was used in only one previous neuroimaging study of peer presence effects (Smith et al.).
145 Adolescents (15 to 17-year-old) alternatively performed a gambling, risk-taking task, and a go/no-
146 go, response inhibition task, either unobserved or under the belief that an anonymous peer was
147 watching. The go/no-go task did not activate, however, the typical brain substrates of response
148 inhibition, making a cross-task comparison difficult. So, a successful two-task comparison of peer
149 presence effects neural underpinnings is still lacking.

150 To test between the task-specific and domain-general accounts of social facilitation-inhibition, we
151 used here functional magnetic resonance imaging (fMRI) to measure the effect of peer presence
152 on the neural mechanisms underlying two basic tasks in children and adults: numerosity
153 comparison and phonological comparison. Both tasks are foundational to humans' math and
154 reading skills (Phillips et al.; Starr et al.). Numerosity comparison consists in comparing quantities
155 using approximate representations of numbers without relying on counting or numerical symbols
156 (Dehaene). It is an early-developing numerical skill, detectable as early as 6 months of age, that
157 has been found to predict mathematics achievement (Starr et al.; Hyde et al.). Phonological
158 comparison consists in comparing the sound structure of words (Phillips et al.). It is an early-
159 acquired language skill, taught in preschool (Qi and O'Connor), that predicts reading achievement
160 (Ehri et al.). In both the developing and the mature brain, numerosity comparisons involve brain
161 areas supporting the representation of magnitudes in the intraparietal sulcus and posterior superior
162 parietal lobule, while phonological comparison involves language-related areas in the inferior

163 frontal and the middle temporal gyri (Prado, Mutreja, Zhang, et al.; Prado, Mutreja, and Booth). In
164 addition, these two types of comparison are at least as much facilitated by the presence of a peer
165 in 8 to 10-year-old fourth-graders as in adults (Tricoche, Monfardini, et al.).

166 The fact that both numerosity and phonological comparisons are sensitive to peer presence,
167 despite distinct neural substrates, makes them well suited to test between the task-specific and
168 domain-general accounts of social facilitation-inhibition. Furthermore, testing children and adults
169 provides us with the opportunity to evaluate whether the neural mechanism underlying effects of
170 peer presence change with age and expertise with the task. Here we compare 10 to 13-year-olds
171 to young adults to determine whether the neural correlates of peer presence effects are already
172 mature during the pivotal period between elementary and middle school, i.e., between the end of
173 childhood and the beginning of adolescence. Neural changes elicited by familiar peer presence
174 were analyzed across tasks and ages using regions-of-interest (ROI) analyses to assess changes
175 within task-specific substrates, as well as whole-brain analyses to assess changes in domain-
176 general networks, especially those dedicated to mentalizing (Amft et al.; Frith and Frith;
177 Blakemore).

178 2. Materials and Methods

179

180 2.1. Participants

181 Participants were pairs of familiar, non-kin, age-mates (± 2 years), recruited *via* web posting. They
182 included 17 pairs of children (15/34 females) with a mean age of 11 years (range: 10-13 years) and
183 12 pairs of adults (16/24 females) with a mean age of 23 years (range: 20-29 years). Standardized
184 Intellectual Quotient (IQ) was as assessed by the Nouvelle Echelle Métrique de l'Intelligence
185 (Cognet and Bachelier) in children and by the average of the matrix reasoning and similarities
186 subtests of the Wechsler Abbreviated Scale of Intelligence (*WAIS-IV Wechsler Adult Intelligence*
187 *Scale 4th Edition*) in adults. IQs were in the normal to superior range (children, mean: 114.3, range:
188 76-141; adults, mean: 99.8, range: 83-115). Closeness scores, as assessed by the 7-point,
189 Inclusion of Other in the Self scale (Aron et al.), reached scores ≥ 4 (children, mean: 5.94, range:
190 3-7; adults: mean: 5.54, range: 3-7), typical of close partners such as best friends (Gächter et al.;
191 Myers and Hodges).

192 Nine children and one adult were discarded due to claustrophobia, sleepiness, joystick malfunction,
193 misunderstood instructions, or excessive motion in the scanner. One of the remaining children had
194 missing fMRI data and one of the remaining adult had missing behavioral data due to recording
195 issues. The final samples of subjects therefore comprised 25 children and 22 adults for behavioral
196 analyses, and 24 children and 23 adults for fMRI analyses. All participants were native French

197 speakers, had no visual deficit, no MRI contra-indications and no history of neurological and
198 psychiatric disorder. The study was conducted according to the guidelines of the Declaration of
199 Helsinki, and approved by the CPP Sud Est II Ethics Committee on November 7, 2018
200 (ClinicalTrials.gov Identifier: NCT03453216). Informed consent was obtained from all subjects
201 involved in the study or their parents. Each participant received a 20€-per-hour compensation for
202 her/his time.

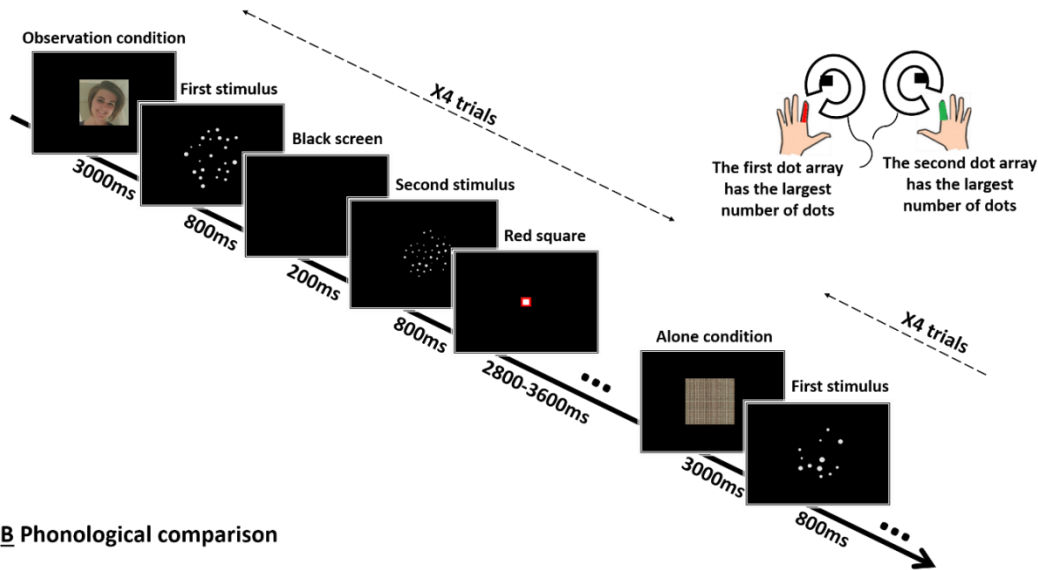
203 **2.2. Session timeline**

204 During the scanning session, participants first performed the numerosity comparison task (Figure
205 1A), and then the phonological comparison task (Figure 1B), in two successive functional runs of
206 approximatively 12 minutes each. A pause was provided halfway through each functional run,
207 which the participant ended at her/his convenience by pressing a button on one of the joysticks.
208 The two functional runs were separated by an 8-minute anatomical T1 scan, and followed by a 9-
209 minute resting state scan that is not analyzed in the present paper. Eight blocks of fixation, during
210 which participants had to look at a fixation cross for 16,800ms, were randomly interspersed among
211 the task blocks of each functional run.

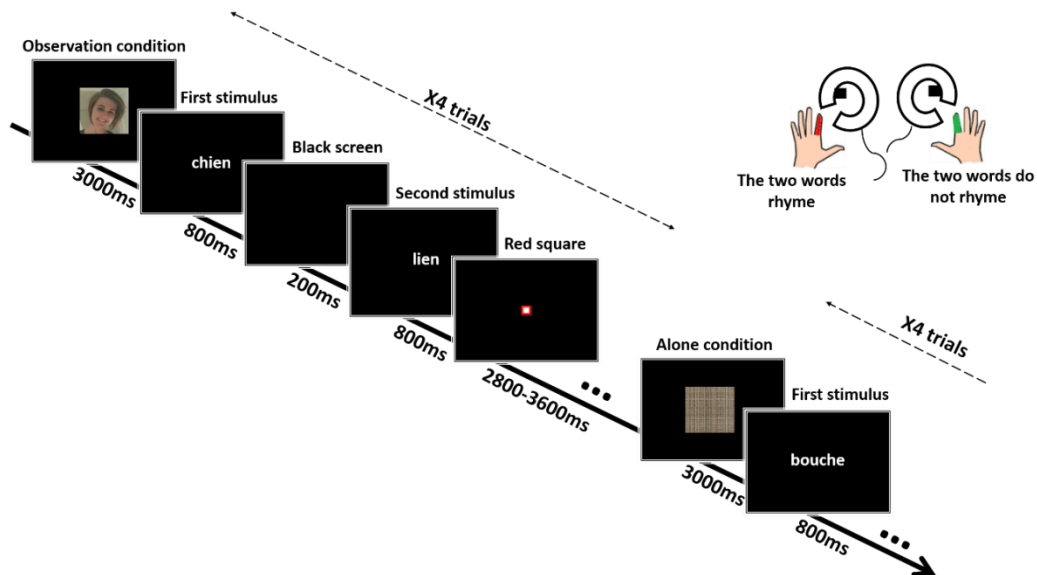
212 **2.3. Trial sequence**

213 Both tasks were programmed using the Presentation® software (www.neurobs.com accessed on
214 15 December 2021). The stimuli were projected onto a screen viewed by the participant through a
215 mirror attached to the head coil. For each trial, two stimuli (two dot arrays for numerosity
216 comparisons; two words for phonological comparisons) appeared one after the other for 800ms
217 each, with a 200ms delay in between. A red square then appeared for a randomly varying duration
218 of 2,800ms, 3,200ms or 3,600ms. Participants had to decide which array contained the largest
219 number of dots (numerosity comparison; Figure 1A) or whether the two words rhymed or not
220 (phonological comparison; Figure 1B). They were asked to respond as fast and accurately as
221 possible as soon as the second stimulus appeared and before the red square turned off.
222 Participants pressed a button of the joystick in their left hand if the first dot array had the largest
223 number of dots or if the two words rhymed. They pressed a button of the joystick in their right hand
224 if the second dot array had the largest number of dots, or if the two words did not rhyme.

A Numerosity comparison



B Phonological comparison



225

226 **Figure 1: Experimental tasks.** Trial time course (from top to bottom) was the same for numerosity
227 (A) and phonological comparisons (B). At the beginning of each block of 4 trials, an original or
228 scrambled version of a headshot of the observer indicated the condition for the block: observation
229 or alone condition, respectively. Two stimuli were successively presented for 800ms each,
230 separated by a 200ms-interval. Participants had to decide which of the dot arrays had the largest
231 number of dots (A) or whether the two words rhymed or not (B), and to respond as fast and

232 accurately as possible, using either the left or the right index finger, as soon as the second stimulus
233 appeared and before the red square turned off.

234

235 **2.4. Stimuli**

236 Dot arrays were created while controlling for differences in the cumulative surface area and in the
237 distribution of dot sizes (Gebuis and Reynvoet). An array could contain 12, 18, 24 or 36 dots.
238 Comparison difficulty varied with the ratio of the number of dots between the two arrays. The higher
239 the ratio, the greater the difficulty. Comparisons involved a 0.33 ratio (12 dots vs. 36 dots), a 0.5
240 ratio (18 dots vs. 36 dots or 12 dots vs. 24 dots), a 0.67 ratio (24 dots vs. 36 dots or 12 dots vs. 18
241 dots), or a 0.75 ratio (18 dots vs. 24 dots). The task was divided into 24 blocks of 4 trials each, for
242 a total of 96 trials. There were 12 easy blocks involving small ratios (i.e., 0.33 and 0.5) and 12
243 difficult blocks involving large ratios (i.e., 0.67 and 0.75), pseudo-randomly ordered during the task.
244 The first dot array contained the larger number of dots in half of the trials, while in the other half of
245 the trials it contained the smaller number of dots. A given pair of stimuli was presented only once.
246 The task began with 8 practice trials (4 per ratio) that were not included in the analyses.

247 Words contained 3 to 8 letters. Comparison difficulty varied with the congruence or incongruence
248 of the spelling and phonology of the two successively presented words. In half of the trials, the two
249 words had congruent orthography and phonology, i.e., they had identical spelling and sounded the
250 same (e.g., sac-lac [sak-lak]), or they had a different spelling and sounded different (e.g., jeu-doux
251 [ʒœ-du]). In the other half of the trials, the two words had incongruent orthography and phonology,
252 i.e., they had a different spelling and sounded the same (e.g., dos-taux [do-to]), or they had identical
253 spelling and sounded different (e.g., tapis-iris [tapi-iris]). The phonological comparison task was,
254 like the numerosity comparison task, divided in 24 blocks of 4 trials each, for a total of 96 trials.
255 There were 12 easy blocks involving congruent trials and 12 difficult blocks involving incongruent
256 trials, pseudo-randomly ordered during the task. Each word was presented only once during the
257 task. Words presented over two successive trials could not have the same phonology, orthography
258 or be semantically related. The two words rhymed in half of the trials, while they did not rhyme in
259 the other half of the trials. As for numerosity comparison, the task began with 8 practice trials (4
260 congruent, 4 incongruent) that were not included in the analyses.

261 **2.5. Observation versus Alone conditions**

262 For each pair, each subject alternatively took the actor and the observer roles. While the actor was
263 lying inside the MR scanner, the observer was sitting in an adjacent room, facing a computer
264 screen. The observer's computer screen displayed filler videos (Alone condition) or the live video
265 streams of three cameras placed inside the scanner: one filming the actor's body, one filming the

266 actor's eyes, and one filming what the actor saw on her/his screen (Observation condition). The
267 two conditions alternated every other 4-trial block, always starting with the Alone condition, up to a
268 total of 24 blocks (96 trials) per task.

269 The actor was informed about the forthcoming condition at the beginning of each 4-trial block by
270 displaying the observer's picture for 3,000ms, either in a scrambled version (Alone condition), or in
271 its original form (Observation condition). During the 8-minute anatomical T1 scan in between the
272 two tasks, actor and observer could see each other via video cameras as a reminder for the actor
273 of the observer's actual presence in the adjacent room. During acquisition, the experimenters
274 remained out of sight in the scanner's monitoring room (whose window overlooking the scanner
275 was obstructed by a curtain) and refrained from any unnecessary verbal contact with either the actor
276 or the observer during the scanning session in order to minimize third-party presence.

277 **2.6. Behavioral analyses**

278 R (RStudio, v.1.0.136) and SYSTAT (v13) were used to analyze the subjects' accuracy (% of
279 correct responses) and their speed during correct responses (reaction times, RTs, calculated as
280 the time separating the appearance of the second stimulus from the button press). Scores for each
281 task were averaged across all 24 blocks of four trials. These averages were then analyzed using
282 three-way ANOVAs with the between-subject factor Age (Children, Adults) and the within-subject
283 factors Condition (Observation, Alone) and Task (Numerosity comparison, Phonological
284 comparison). We also calculated, for each subject and each task, the performance gain produced
285 by observation in accuracy and speed relative to the alone condition ($(\text{Observation}-$
286 $\text{Alone})/\text{Alone} \times 100$). We then used one-tailed Student's t-tests to determine whether the group mean
287 gain was significantly greater than 0, i.e., reflected the expected social facilitation. Peer presence
288 effect size was estimated as earlier (Tricoche, Monfardini, et al.), using Cohen's d (d_z for dependent
289 samples) and common language effect size (CL).

290 **2.7. MRI data acquisition**

291 MRI scans were obtained from a MAGNETOM Prisma 3.0 T scanner (Siemens Healthcare,
292 Erlangen, Germany) at the Lyon Primage neuroimaging platform (CERMEP, Imagerie du vivant,
293 Lyon, France). The fMRI blood oxygenation level-dependent (BOLD) signal was measured with a
294 susceptibility weighted single-shot echo planar imaging (EPI) sequence. The following parameters
295 were used: TR = 2,000 ms, TE = 24 ms, flip angle = 80°, matrix size = 128 x 120, field of view =
296 220 x 206 mm, voxel size = 1.72 x 1.72 mm, slice thickness = 3 mm (0.48 mm gap), number of
297 slices = 32. Between the two functional runs, a high resolution T1-weighted 3D structural image
298 was acquired for each participant (TR = 3,000 ms, TE = 2.93 ms, flip angle = 8°, matrix size = 320
299 x 280 mm, field of view = 280 x 320 mm, slice thickness = 0.8 mm, number of slices = 160).

300 **2.8. fMRI data analyses**

301 *2.8.1. Preprocessing*

302 Data analysis was performed using SPM12 (www.fil.ion.ucl.ac.uk/spm accessed on 15 September
303 2021). Functional images were corrected for slice acquisition delays, spatially realigned to the first
304 image of the first run to correct for head movements, and spatially smoothed with a Gaussian filter
305 equal to twice the voxel size (4 x 4 x 7 mm³ full width at half maximum). Functional image runs
306 were inspected using ArtRepair ([cibsr.stanford.edu/tools/human-brain-project/artrepair-
307 software.html](http://cibsr.stanford.edu/tools/human-brain-project/artrepair-software.html) accessed on 15 September 2021); functional volumes with a global mean intensity
308 greater than 3 standard deviations from the average of the run or a volume-to-volume motion
309 greater than 2 mm were identified as outliers and substituted by the interpolation of the 2 nearest
310 non-repaired volumes. Finally, functional images were coregistered with the segmented anatomical
311 image and normalized into the standard Montreal Neurological Institute (MNI) space (normalized
312 voxel size: 2 x 2 x 3.5 mm³).

313 *2.8.2. Processing*

314 Event-related statistical analysis was conducted using the general linear model (GLM). Activation
315 was modeled as epochs with onset time locked to the presentation of the first stimulus in each trial
316 and with a duration of 2 seconds. Fixation periods were modeled as 16 seconds blocks. All trials
317 (including correct, incorrect and miss trials) were sorted according to Task, Condition and trial type
318 (e.g., ratio for numerosity comparison, congruency for phonological comparison). Fixation blocks
319 were modeled in a separate regressor for each task. Finally, two regressors of no-interest (one per
320 task, including instructions, breaks, and picture display of the observation/alone conditions) were
321 added in the model. All epochs were convolved with a canonical hemodynamic response function
322 (HRF). The time series data were high-pass filtered (1/128 Hz), and serial correlations were
323 corrected using an autoregressive AR (1) model.

324 *2.8.3. Whole-brain analyses*

325 Voxel-wise parameter estimates obtained for each subject were entered into random effect (RFX)
326 analyses in order to identify regions exhibiting main effects and interactions involving the Age, Task,
327 and/or Condition factors. Group-wise statistical maps were thresholded for significance using a
328 voxel-wise probability threshold of $p < 0.001$ (uncorrected) and a cluster-wise probability threshold
329 of $p < 0.05$ (FWE corrected for multiple comparisons).

330 *2.8.4. ROI analyses of the task-specific substrates*

331 Task-specific ROIs were defined across groups and condition based on the main effect of task at
332 the whole-brain level. Specifically, numerosity ROIs were defined using the contrast of numerosity
333 comparison versus phonological comparison, while phonology ROIs were defined using the

334 contrast of numerosity comparison versus phonological comparison. For each map, we excluded
335 voxels for which task-related activity was not also significantly greater than activity during fixation.
336 ROIs were defined as the intersection of 10 mm radius spheres centered on the local maximum of
337 each cluster (using the SPM toolbox Marsbar) with the corresponding thresholded statistical map.
338 Activity (calculated with respect to the fixation baseline) was averaged across all voxels of each
339 ROI. These average values were then analyzed using four-way ANOVAs to assess the effects on
340 task-specific neural activity of the between-subject factor Age (Children, Adults) and the within-
341 subject factors Task (Numerosity comparison, Phonological comparison), Condition (Observation,
342 Alone) and ROI. Statistical significance was set at $p < 0.05$.

343 *2.8.5. Complementary psychophysiological interaction (PPI) analysis*

344 Our main analyses identified a right TPJ cluster as the only area that was more activated in adults
345 than children under peer observation (see Results section). Thus, we performed a whole-brain
346 psycho-physiological interaction (PPI) analysis to identify brain regions whose coupling with this
347 region was modulated as a function of Condition (Observation/Alone). The seed was defined as
348 the entire cluster found in the Age x Condition interaction of the whole-brain analysis (coordinates
349 of the peak: 58, -26, 10; Table 3). We estimated a GLM that included 3 regressors for each task: a
350 physiological regressor corresponding to the entire time series of the cluster over the whole task,
351 a psychological regressor for the Observation > Alone contrast, and the PPI regressor reflecting
352 the interaction between the psychological and physiological regressors. The model also included
353 two regressors of no interest (one per task).

354 **3. Results**

355

356 **3.1. Behavioral data: Task and Age effects**

357 Making phonological comparisons took longer than making numerosity comparisons
358 ($F(1,45)=177.3$, $p < 0.001$, $\eta_p^2=0.80$), but accuracy was comparable in the two tasks ($F(1,45)=0.2$,
359 n.s.). Children's expectedly performed worse than adults. Their responses were less accurate
360 ($F(1,45)=5.22$, $p=0.03$, $\eta_p^2=0.10$) and slower ($F(1,45)=10.9$, $p=0.002$, $\eta_p^2=0.19$) than adults'.
361 Children's developmental lag behind adults was more pronounced for phonological than for
362 numerosity comparisons (Age x Task interaction: RTs, $F(1,45)=7.73$, $p=0.008$, $\eta_p^2=0.15$; percent
363 correct responses, $F(1,45)=6.22$, $p=0.02$, $\eta_p^2=0.12$).

364 **3.2. Behavioral data: Condition effect**

365 For accuracy, we found a main effect of Condition ($F(1,45)=7.31$, $p=0.01$, $\eta_p^2=0.14$), indicating that
366 observation improved accuracy. This effect was qualified by a Condition x Age x Task interaction

367 (F(1,45)=4.04, $p=0.05$, $\eta_p^2=0.08$), as this social facilitation was detectable (at least marginally) in
368 all cases, i.e., children's numerosity comparisons (Alone: 90%, Observation: 92%, gain 2%,
369 $t(24)=2.29$, $p=0.03$), children's phonological comparisons (Alone: 88%, Observation: 90%, gain 2%,
370 $t(24)=1.41$, $p=0.08$), and adults' phonological comparisons (Alone: 93%, Observation: 96%, gain
371 4%, $t(21)=3.01$, $p=0.007$), except adults' numerosity comparisons (Alone: 93%, Observation: 91%).
372 Cohen's d_z respectively estimated the three positive peer presence effects as medium- and small-
373 sized effects of 0.52 and 0.28 for children, and as a medium-sized effect of 0.65 for adults. The
374 corresponding CL effect sizes, which give the probability for a score randomly selected from the
375 observed condition to be better than a score randomly selected from the unobserved condition,
376 were: 70% and 61% for children, and 74% for adults.

377 For RTs, we found a Condition x Task interaction (F(1,45)=8.05, $p=0.007$, $\eta_p^2=0.15$). Peer
378 observation had no effect on phonological comparisons (Children: Alone 1324ms, Observation
379 1381ms; Adults: Alone 988ms, Observation 986ms), but did fasten numerosity comparisons. This
380 held true in both children (Alone 894ms, Observation 862ms, gain 3%, $t(24)=1.71$, $p=0.05$) and
381 adults (Alone 689ms, Observation 664ms, gain 3%, $t(21)=3.24$, $p=0.002$). Cohen's d_z estimated
382 these peer presence effects as a small-sized effect of 0.14 for children and a medium-sized effect
383 of 0.73 for adults. The corresponding CL effect sizes amounted to 55% for children and 77% for
384 adults.

385 To summarize, behavioral data showed the expected social facilitation during observed relative to
386 unobserved trials. Irrespective of age, the improvement under peer observation took the form of
387 faster numerosity comparisons and more accurate phonological comparisons. Children additionally
388 showed more accurate numerosity comparisons.

389 **3.3. fMRI data: ROI analyses**

390 The ROI analyses identified seven clusters as task-specific neural substrates (all F 's(1,135)>40,
391 all p 's<0.001, $\eta_p^2>0.23$; Table 1, Figure 2). These clusters were consistent with earlier fMRI data
392 obtained using the same tasks (Prado, Mutreja, Zhang, et al.; Prado, Mutreja, and Booth).

393 There were four numerosity ROIs (see Methods): the right IPS/SPL, the right and left posterior
394 Insula, the left STG, and the left postcentral gyrus. There were two phonological ROIs (see
395 Methods): one in the left IFG, the other in the left ITG. A main effect of Condition was found on
396 ROIs (F(1,1215)=4.43, $p=0.03$), but without any interaction with Task, Age or ROI. Yet, post-hoc

397 tests revealed a significant Condition effect only on the left IFG ($p=0.04$) and a marginal effect on
 398 the left postcentral gyrus ($p=0.07$).

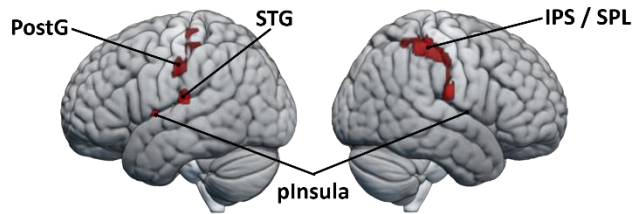
399 To summarize, ROI analyses provided little support to the task-specific account of peer presence
 400 effect. Considered together, ROIs showed an increase in activation under observation, but post-
 401 hoc tests revealed that this effect was significant only for one neural substrate of phonological
 402 comparisons, the left IFG. In absence of Condition x Task interaction, this increase could not be
 403 considered as reliably task-selective, i.e., as significantly greater for phonological than numerosity
 404 comparisons.

405

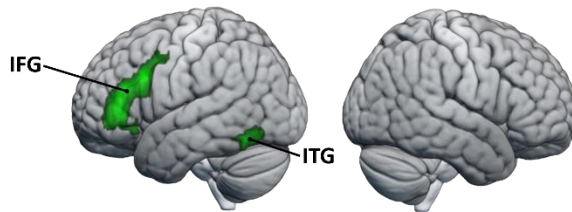
Table 1. MNI (Montreal Neurological Institute) coordinates of the seven brain regions showing a main Task effect.

Anatomical location	MNI coordinates (mm)			Z score	Cluster size (voxels)
	x	y	z		
<i>Numerosity comparison > Phonological comparison</i>					
Right Superior Parietal Lobule / Intra Parietal Sulcus	32	-40	34	4.94	616
Right Posterior Insula	46	-4	13	4.55	108
Left Posterior Insula	-44	-2	10	5.45	207
Left Superior Temporal Gyrus	-58	-24	13	4.64	199
Left Postcentral Gyrus	-38	-26	55	3.93	94
<i>Phonological comparison > Numerosity comparison</i>					
Left Inferior Frontal Gyrus	-48	36	2	6.93	1244
Left Inferior Temporal Gyrus	-50	-56	-15	7.06	317

A Numerosity comparison > Phonological comparison



B Phonological comparison > Numerosity comparison



406

407

408 **Figure 2.** Task-specific substrates selectively activated by (A) numerosity comparisons *versus*

409 (B) phonological comparisons.

410

411 **3.4. fMRI data: Whole-brain analyses, Condition effect**

412 Across both groups and both tasks, no main of effect of Condition was observed in the Alone >
413 Observation contrast. Rather, the neural correlates of peer presence effects were revealed by the
414 whole-brain Observation > Alone contrast, which identified eleven clusters (Table 2, Figure 3A).
415 Associated Beta values (Figure 3B) showed that the most frequent change took the form of a lesser
416 deactivation in the observation than in the alone condition. This concerned the three nodes of the
417 mentalizing network, the mPFC, the TPJ, and the Prec/PCC region, as well as the left MTG, right
418 precentral gyrus PreG, and right posterior occipital gyrus (POG). Greater activation in the
419 observation compared to the alone condition was also observed. This pattern was found in the right
420 VS, the left IFG, the Middle Cingulate Gyrus (MCC), and a cluster involving the left frontal eye field
421 (FEF) and extending into the precentral gyrus (PreG).

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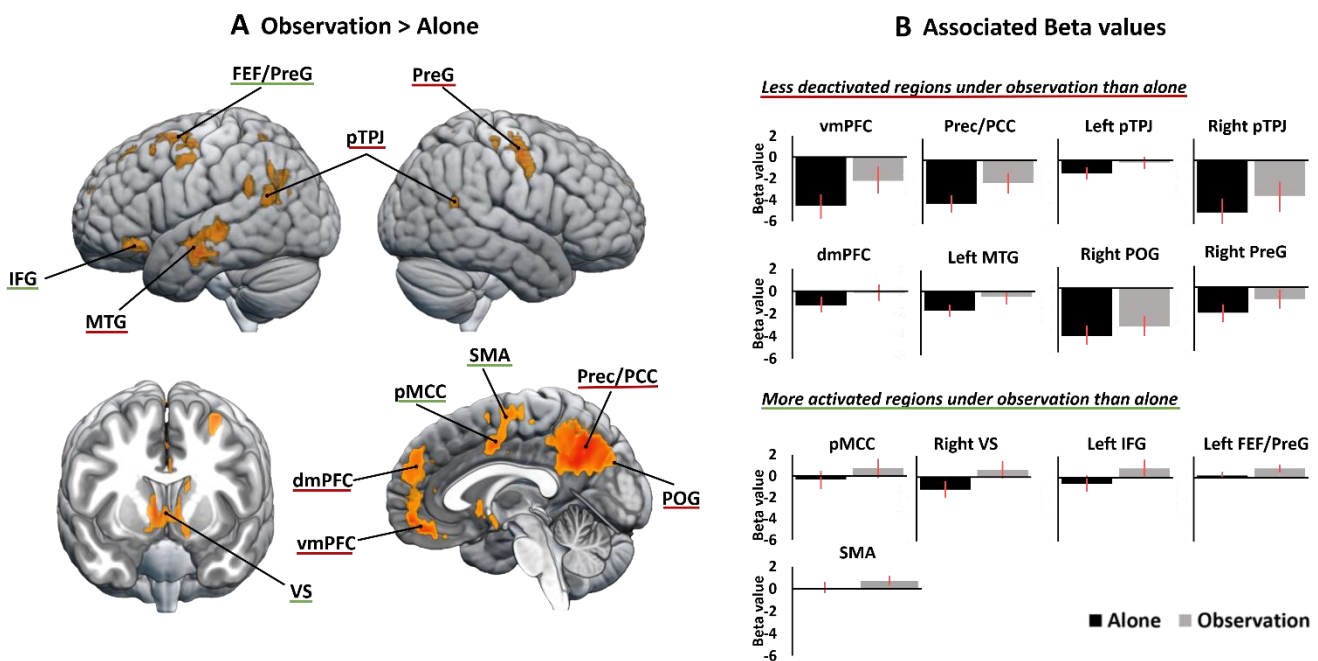
427

428 **Table 2.** MNI coordinates of the brain regions showing a main Condition effect

429

Anatomical location	MNI coordinates (mm)			Z score	Cluster size (voxels)
	x	y	z		
<i>Observation > Alone</i>					
Ventro-Medial Prefrontal Cortex	-2	54	-15	4.93	975
Dorso-Medial Prefrontal Cortex	10	60	24	4.43	
Right Precentral Gyrus	48	-6	52	4.77	403
Precuneus and Posterior Cingulate Cortex	-12	-52	34	5.42	2549
Left posterior Temporo-Parietal Junction	-46	-48	30	4.43	654
Right posterior Temporo-Parietal Junction	56	-50	16	3.87	146
Left Middle Temporal Gyrus	-62	-14	-18	4.92	379
Right Posterior Occipital Gyrus	22	-82	30	3.87	111
Left Inferior Frontal Gyrus	-48	36	-15	4.10	75
Left Frontal Eye Field / Precentral Gyrus	-28	-2	41	4.50	741
Posterior Middle Cingulate Gyrus	-2	0	41	4.33	570
Supplementary Motor Area	10	0	62	4.24	
Right Ventral Striatum	8	6	2	4.47	264

430



431

432

433 **Figure 3:** Brain regions activated in the Observation > Alone contrast across Age and Task. (A)
434 Location of activated brain regions. (B) Associated Beta values of less deactivated regions
435 (vmPFC, dmPFC, Prec/PCC, pTPJ, left MTG, right POG and right PreG) and more activated
436 regions (pMCC, SMA, right VS, left IFG and left FEF/PreG) during observed relative to unobserved
437 trials.

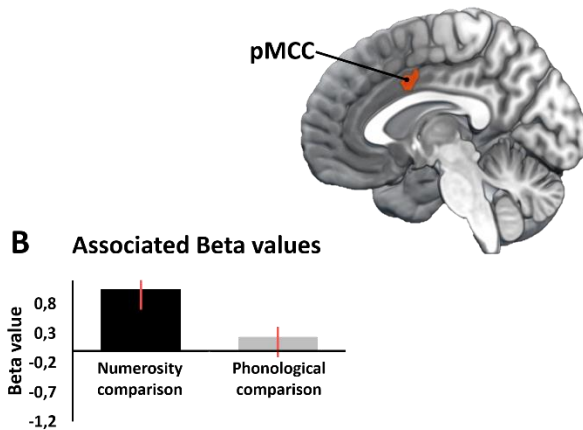
438

439 3.5. fMRI data: Whole-brain analyses, Condition x Task interaction

440 Only one cluster of the large network modulated by peer observation showed a Condition x Task
441 interaction (Figure 4). Located in the posterior part of the MCC ([2 2 41], Z=3.92), it displayed
442 increased activation under observation for numerosity but not phonological comparisons.

443

A Numerosity comparison > Phonological comparison



444

445

446 **Figure 4.** Brain activation in the Observation > Alone contrast interacting with Task. A single area
447 (posterior MCC) showed increased activation under observation for numerosity but not
448 phonological comparisons.

449

450

451 **3.6. fMRI data: Whole-brain analyses, Condition x Age interaction**

452 When adults were considered separately (Table 3), the brain regions identified by the Observation
 453 > Alone were the same as those described above for all subjects taken together. When children
 454 were considered separately, only one cluster survived the threshold: the Prec and nearby SPL
 455 (Figure 5B). This was also the sole cluster revealed by a conjunction analysis across adults and
 456 children for the Observation > Alone contrast (Figure 5B). However, all but one of the adults'
 457 clusters were observed in children with a lower ($p=0.005$) and uncorrected statistic level (Figure
 458 5C).

459 The one exception to the close resemblance between children and adults was a cluster located
 460 close to the right pSTS, in a region defined by Mars et al. in 2012 (Rogier B. Mars, Sallet, et al.) as
 461 the anterior part of TPJ (aTPJ, [58 -26 10], $Z=4.79$). This region stood out as the only node of the
 462 large network modulated by peer observation showing a significant Condition x Age interaction.
 463 Associated Beta values showed that the right aTPJ was less deactivated in observed than
 464 unobserved trials in adults, but not in children (Figure 5A). There was no Condition x Age x Task
 465 interaction, indicating that this developmental difference held for both tasks.

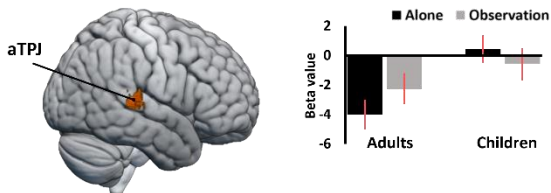
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Table 3. MNI coordinates of the brain regions showing a main Condition effect in analyses conducted separately for Adults and Children

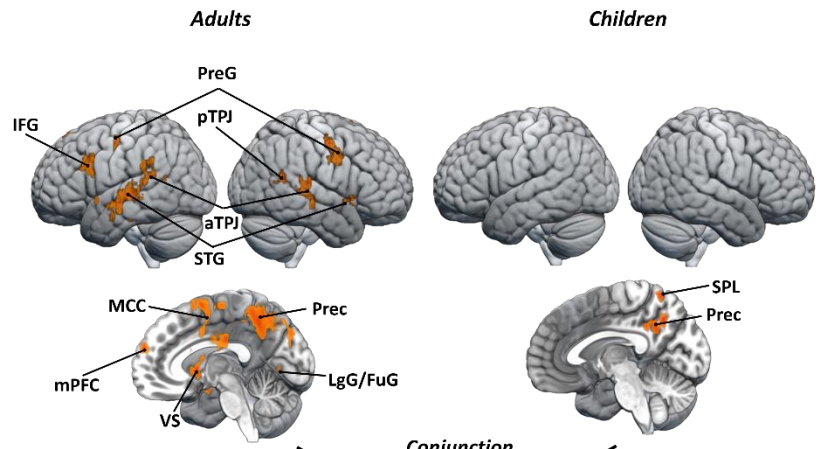
Anatomical location	MNI coordinates (mm)			Z score	Cluster size (voxels)
	x	y	z		
<i>Observation > Alone & Adults > Children</i>					
Right posterior Superior Temporal Sulcus (incl. anterior Temporo-Parietal Junction)	58	-26	10	4.79	126
<i>Observation > Alone in Adults only</i>					
Bilateral Superior Frontal cortex	0	44	30	4.31	235
(incl. medial Prefrontal Cortex) (two clusters)	10	60	24	4.07	54
Left Inferior Frontal Gyrus	-46	18	20	4.01	152
Left Precentral Gyrus	-50	-10	48	3.73	73

Right Precentral Gyrus	40	-22	38	4.39	3067
Middle Cingulate Gyrus	0	-6	30	4.37	4468
Precuneus	-14	-52	38	4.40	1469
Right posterior Temporo-Parietal Junction	56	-50	16	4.19	1090
Left anterior Temporo-Parietal Junction	-66	-24	-1	4.02	5081
Right anterior Temporo-Parietal Junction	60	-26	13	4.39	2422
Left Superior Temporal Gyrus	-50	0	-4	4.02	1223
Right Superior Temporal Gyrus	46	4	-15	3.70	5674
Left Lingual Gyrus / Fusiform Gyrus (two clusters)	-6	-70	-1	4.35	5475
	-24	-70	-4	4.35	6476
Right Ventral Striatum	6	6	-5	4.62	2307
					478
<i>Observation > Alone in Children only</i>					
Precuneus	-6	-62	41	4.29	260
Left Superior Parietal Lobule	-14	-56	62	4.03	114

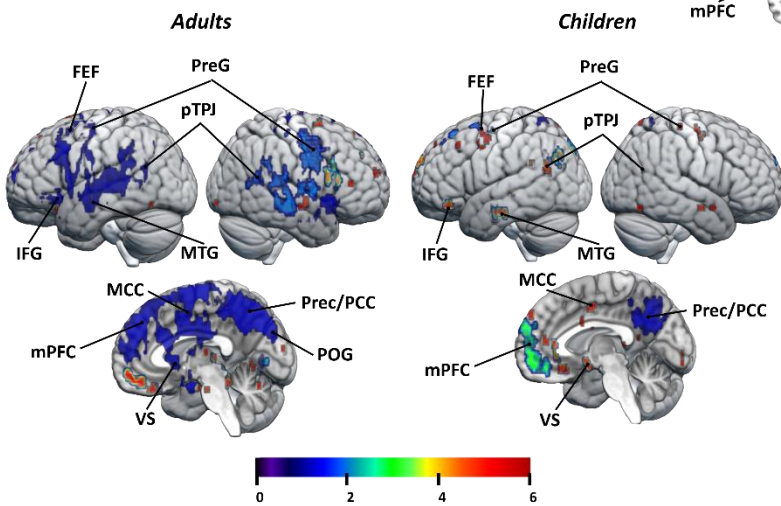
A Observation > Alone & Adults > Children



B Observation > Alone, $p=0.001$ uncorrected voxel-wise probability threshold ($p<0.05$ corrected cluster-wise probability threshold)



C Observation > Alone, $p=0.005$ uncorrected voxel-wise probability threshold



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482

483 **Figure 5:** Brain activation in the Observation > Alone contrast interacting with Task (A) Brain region
484 showing greater activity for the Observation > Alone contrast in adults than children, with associated
485 beta values. (B) Brain regions showing greater activity for the Observation > Alone contrast in adults
486 and children separately using a $p=0.001$ corrected statistic. The conjunction analysis between
487 adults and children for the Observation > Alone contrast is shown at the bottom of the figure. (C)
488 Brain regions showing greater activity for the Observation > Alone contrast in adults and children
489 separately using a $p=0.005$ uncorrected statistic.

490

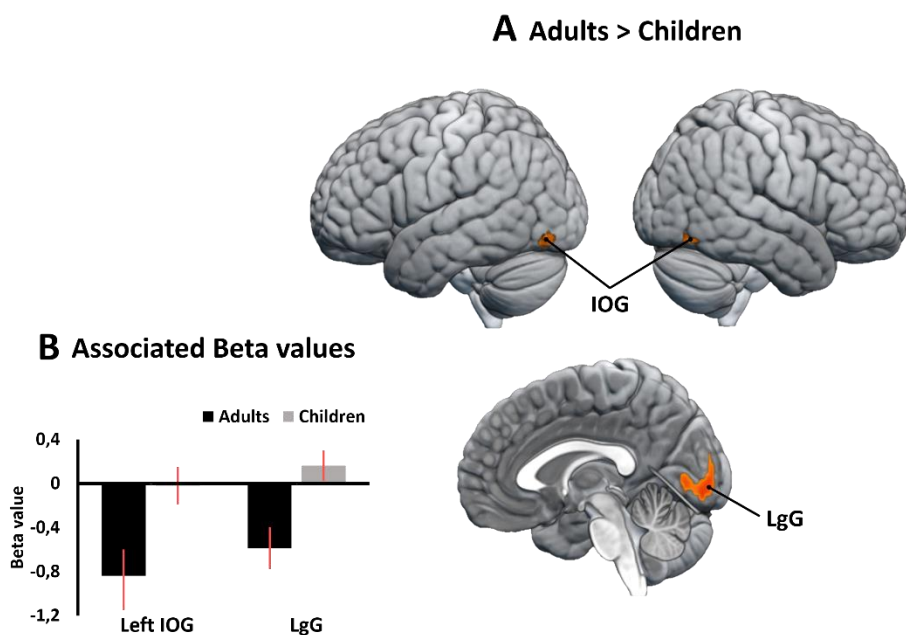
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493 3.7. fMRI data: PPI analysis of right aTPJ connectivity

494 The PPI analysis showed that peer observation decreased the connectivity of the right aTPJ
495 cluster identified above with two visual-information-processing areas in adults, but not in children
496 (Figure 6). These regions were the lingual gyrus (LgG, [10 -82 -8], $Z=4.74$) and the right [26 -70 -
497 12, $Z=4.32$] and left IOG [-34 -80 -15], $Z=4.22$).

498



499

500 **Figure 6:** PPI analysis of the right aTPJ for the Observation > Alone contrast. (A) Brain regions
501 showing a greater decrease of functional connectivity with the right aTPJ for the Observation than
502 Alone condition in adults as compared to children. (B) Associated beta values (Observation > Alone
503 contrast) measured at the peak of these regions as a function of age.

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509 **4. Discussion**

510

511 The present study aimed to uncover the neural mechanisms underlying peer presence effects on
512 human behavior. We investigated adults and children, alternately observed and unobserved by a
513 familiar peer, while they compared either the number of dots in two arrays or the sounds of two
514 written words. Behavioral findings confirmed the social facilitation of these basic skills, which are
515 foundational to humans' math and reading abilities. ROI analyzes revealed virtually no observation-
516 driven change within the numerical and language brain areas forming the task-specific neural
517 substrates of numerosity and phonological comparisons. Rather, whole-brain analyses revealed a
518 unique neural signature of observation, similar for non-symbolic numerosities and words, and
519 largely shared by children and adults. This task-independent signature entailed widespread
520 changes in several brain networks known for their domain-general involvement in social cognition
521 (especially mentalizing), attention, and reward. Children's pattern of observation-driven neural
522 changes largely resembled adults', with one exception, the anterior portion of the right TPJ area.
523 Only in adults did this area show a lesser deactivation in observed relative to unobserved trials,
524 associated with decreased connectivity with visual-information-processing areas.

525

526 Caution should be used in generalizing the above conclusions to all peers as, here and earlier
527 (Tricoche, Monfardini, et al.), we chose to test pairs of familiar peers. First, familiar peers are more
528 representative of daily life as they are more frequent at school or at work than unknown ones.
529 Second, close others capture attention (Chauhan et al.), elicit pleasure (Fareri et al.) and induce
530 social facilitation (Herman; Sugimoto et al.; Monfardini, Reynaud, et al.) more than strangers,
531 accordingly playing a more preeminent role in social cognition (Smith and Mackie). Notwithstanding
532 this limitation, the present behavioral findings provide further proof of the remarkable ubiquity of

533 social facilitation across situations and ages. First, they demonstrate that the social facilitation of
534 numerosity and phonological comparisons reported earlier in the presence of a nearby coactor
535 (Tricoche, Monfardini, et al.) also occurred in the less natural conditions of a live, but remote (via
536 video) and sporadic (every other 4-trial block), observation. In our former paradigm testing
537 numerical and phonological comparisons simultaneously, the improvement concerned speed only
538 whereas, in the present paradigm testing numerical and phonological comparisons successively,
539 the improvement concerned speed and accuracy. Second, the present behavioral findings show
540 that 10 to 13-year-olds are as sensitive to social facilitation as adults, as were 8 to 10-year-olds in
541 our previous study (Tricoche, Monfardini, et al.). Across the two studies, the magnitude of the
542 behavioral changes produced by peer presence or peer observation in children amounted to small-
543 to medium-sized effects (Cohen's d : 0.14 to 0.61) not quite matching, but closely resembling those
544 observed in adults (Cohen's d : 0.21 to 0.73). Testing numerical and phonological comparisons in
545 adolescents is now needed so as to unveil the full developmental trajectory of peer presence effects
546 on these education-related skills. Being observed by a peer induces more self-conscious emotions
547 and greater autonomic arousal in adolescents than in children and adults (Somerville et al.), and
548 adolescence is generally viewed as the period of life with the highest susceptibility to peer influence
549 (Albert et al.). Greater social facilitation of numerical and phonological comparisons in adolescence
550 would indicate that peers' influence on education-related skills follow the same inverted U-shaped
551 trajectory as that reported for peers' influence on reward-related behaviors (Telzer).

552 As detailed in the Introduction, previous studies in both human and non-human animals did
553 describe neural changes in others' presence in the very brain areas underlying the task at hand
554 (Monfardini, Redoute, et al.; Dumontheil et al.; Yoshie et al.). In addition, the changes driven by
555 peer presence in the ventral striatum, orbitofrontal cortex, and amygdala during risk-taking in
556 adolescents can be viewed as a social modulation of the brain areas specialized in processing
557 rewards and emotions (Chein et al.; Hoffmann et al.; Van Hoorn et al.). Yet, as most of these studies
558 rested their conclusions on a single task, proofs of truly task-selective changes (occurring for one
559 task but not the other) were still needed. The present study addressed this issue by using two tasks,
560 respectively dependent on the brain numerical- and language-related areas. The regions
561 selectively engaged by each task were consistent with earlier children's and adults' fMRI data
562 collected with the same tasks (Prado, Mutreja, Zhang, et al.; Prado, Mutreja, and Booth), including,
563 in particular, the right parietal IPS/SPS region for numerosity comparisons, and the left IFG region
564 for phonological comparisons. ROI analyses of these clusters revealed, however, an observation-
565 driven increase in activation in all ROIs when considered together, but with a significant effect only
566 in the left IFG, and no observation \times task interaction in any ROI. In other words, we found only weak
567 evidence of observation-driven changes in task-specific substrates and no evidence of truly task-
568 selective changes in support of the task-specific neural account of peer presence effects. Caution

569 is required, however, in interpreting these negative findings. There is evidence from single-cell
570 recordings that the primate brain harbors intertwined populations of "asocial" and "social" neurons
571 in different brain areas. In the monkey dorsolateral prefrontal cortex, the very same task events are
572 coded by duplicate sets of neurons: one firing when the monkey is alone, the other firing when a
573 congener is present (Demolliens et al.). In the human dorsomedial prefrontal cortex, true and false
574 beliefs are coded by two distinct neuronal populations, one selective for our own beliefs, the other
575 for others' beliefs (Jamali et al.). The local category of neurons responsible for the BOLD response
576 being invisible to fMRI, the relative lack of evidence in support of the task-specific account of peer
577 presence effects, including the present negative findings, might stem from limitations inherent to
578 neuroimaging.

579 The present study provides, by contrast, compelling evidence in support of a domain-general neural
580 account of peer presence effects in humans. The observation-driven changes shared across tasks
581 and ages involved i) the right and left TPJ, a region thought to serve as a hub integrating mentalizing
582 and higher-order attentional control (Patel et al.), together with ii) three regions known for their
583 involvement in mentalizing: the mPFC, Prec/PCC, and left MTG (Fehlbaum et al.), and iii) three
584 regions known for their contribution to higher-order attentional control: the left IFG, MCC, and left
585 and right PreG/FEF (Dosenbach et al.). Observation-driven changes in the Prec/PCC cluster
586 extended into the visual areas of the medial occipital cortex, perhaps due to our use of the peer's
587 picture to signal observed trials. The only other observation-driven changes shared across tasks
588 and ages was found in the VS, a major node of the brain reward system (Haber and Knutson). In
589 the mPFC, Prec/PCC, left MTG, and right and left TPJ, the associated beta values were negative
590 during unobserved trials relative to the fixation baseline, and peer observation lessened this
591 deactivation. This agrees with the fact that these four nodes of the mentalizing network overlap with
592 the default mode network (DMN), whose trademark is to be deactivated during cognitive tasks,
593 presumably to quiet our "default" flow of self-generated thoughts (W. Li et al.; Amft et al.; Hyatt et
594 al.; Rogier B. Mars, Neubert, et al.). The magnitude of such task-induced deactivations tends to
595 increase with task demands, suggesting that DMN deactivation contributes to successful task
596 performance via an efficient reallocation of processing resources from "default" to task-relevant
597 processes (Daselaar et al.). Lessening the magnitude of DMN deactivation necessary to achieve
598 successful task performance could thus be one of the neural mechanisms contributing to social
599 facilitation under peer observation. Attention studies have established that when task demands are
600 too low, the brain becomes vulnerable to task-irrelevant stimuli; increasing task demands, in this
601 case, improves performance by reducing or even eliminating the brain response to distractors
602 (Lavie). Peer presence during easy tasks such as numerosity and phonological comparisons might
603 likewise capture the resources that are left unused by the task, and dedicate them to the observer

604 (e.g. to thoughts about her/his opinion of our performance), thereby protecting the brain from any
605 other task-interfering distraction.

606 As a corollary, task-relevant stimuli might be more efficiently processed. Consistent with this
607 hypothesis, peer observation increased activation in the dorsal frontal gyrus along the precentral
608 sulcus, near or at the FEF, as well as in the IFG, two key nodes contributing to attentional control,
609 usually with a predominant role of the right hemisphere (Corbetta et al.). Here, the increase
610 concerned predominantly the left hemisphere, whose role has been less investigated. One previous
611 study, however, showed that the left FEF and IFG form, together with the left TPJ, a pathway by
612 which a salient contextual (task-irrelevant) cue can be translated into an attentional control signal
613 that facilitates performance in a simple target detection task (DiQuattro and Geng). The
614 engagement of the left FEF-IFG-TPJ pathway in the present study could reflect a similar beneficial
615 effect of the (task-irrelevant) observer's presence on simple responses. The increase in activation
616 observed in a MCC cluster (extending dorsally into the SMA) might concur to improve attentional
617 control as the MCC has been postulated as a hub implementing the higher-order attentional
618 processes necessary for the online monitoring of responses (Procyk et al.), both our own and
619 others' (Apps et al.). Increasing the attentional resources dedicated to task-related information
620 could thus be a second neural mechanism contributing to social facilitation under peer observation.
621 Still another mechanism could be a modulation of affective valuation via the VS. Increased activity
622 in the VS has been associated with enhanced positive valuation in others' presence of, e.g., risk
623 taking in adolescents (Albert et al.), or monetary gain in adults (Fareri et al.). In the present study,
624 no feedback was provided to participants about their accuracy and no reward (praise or money)
625 was given for correct responses. The VS increase in activation under peer observation might
626 therefore reflect an enhancement of the reward intrinsic to live social interactions (Pfeiffer et al.).

627 Overall, the present study provides evidence that peer observation (remote, and episodic, but live),
628 in absence of any reward (save the presence of a friend) and any explicit mentalizing demands,
629 nevertheless triggers widespread neural changes combining attenuated deactivation of
630 mentalizing/DMN nodes with enhanced activation of attentional control and reward-related regions.
631 These findings are consistent with earlier descriptions of the remarkable power of live social
632 interaction on our brain. Specifically, extensive neural changes reminiscent of the present ones,
633 i.e., also including mentalizing, attention, and reward regions, have been reported previously in
634 both adults and children who are (or believe they are) engaged in a real-time interaction with a
635 social (unknown) partner, instead of either watching a recorded version of the same social
636 interaction, or having the same real-time interaction with a computer (Redcay et al.; Rice Warnell
637 et al.; Rice et al.). The engagement of the mentalizing network during peer observation and live
638 social interaction might result, in both cases, from spontaneous mentalizing, that is, from wondering

639 about the observer's thoughts, or a readiness to do so at any moment (Merchant et al.; Hamilton
640 and Lind). Yet, the present observation-driven changes extend beyond the mentalizing network,
641 and live social interaction was previously shown to elicit more extensive activation, both within and
642 outside the mentalizing network, than tasks explicitly requiring to infer another's mental state (Alkire
643 et al.; Rice and Redcay). So, spontaneous conscious mentalizing alone seems insufficient to
644 explain the widespread changes produced by peer observation or live social interaction. Evidence
645 is growing that, starting from infancy, others' representations of the world are automatically coded
646 by our brain, even when irrelevant to our goal, and influence our responses without our awareness
647 (Kampis and Southgate; Steinmetz and Pfattheicher; Smith and Mackie). The resources taken up
648 by such automatic coding inevitably alters the balance between task-dedicated and default mode
649 networks, as well as the distribution of attentional resources to vs. away from the task. This could
650 explain why the mere presence of a social partner can simultaneously affect multiple networks
651 including, in humans, social cognition, attention, and reward, simply by forcing the brain to change
652 the way it harnesses its limited resources.

653 Regarding development, the present study provides new insights into children's peer presence
654 effects, which have been much less investigated than adults'. A conjunction analysis identified the
655 Prec/PCC as the region presenting the most robust observation-driven change shared by children
656 and adults. This region is a core mentalizing node (Schurz et al.). It stands out, in addition, as a
657 unique hub distinguishing between task and rest states in both the developing and adult human
658 brain (R. Li et al.). Its engagement in the present 10 to 13-year-olds is in agreement with previous
659 findings demonstrating that precuneal mentalizing and DMN networks are already present and
660 functional by the time children reach school age (R. Li et al.). The conjunction analysis did not
661 identify the other observation-driven changes identified in adults at the $p < 0.001$ corrected level
662 (TPJ, mPFC, Prec/PCC, MTG, IFG, MCC, and PreG/FEF) as shared with children. None of these
663 clusters showed, however, a reliable Age x Condition interaction. In fact, all of them were present
664 in children at a more lenient $p < 0.005$ uncorrected statistical threshold, likely resulting from the
665 development noisiness that typically makes children's behavior more variable and neural networks
666 less functional specialized than adults' (Richardson et al.). Thus, although development likely
667 sharpens them thereafter (see below), brain changes mediating peer presence effects are already
668 present and functional by 10-13 years of age. This neural resemblance of children and adults
669 parallels the comparable behavioral magnitude of peer presence effects that we observed here and
670 earlier (Tricoche, Monfardini, et al.) across childhood and adulthood.

671 An abundant developmental literature has established that children's mentalizing capacities,
672 despite their early presence in life, do undergo continuous refinement over development, evolving
673 from relatively simple insights into others' perceptions and goals in infants and toddlers to a

674 sophisticated understanding of others' sarcasm and irony in early adolescence (Richardson et al.).
675 Given its dependence upon the brain mentalizing networks, response to others' presence likely
676 undergoes similar refinement over development. This hypothesis is corroborated by the results of
677 the present Age x Condition interaction analysis, which did identify one reliable age-dependent
678 difference in observation-driven neural changes. It concerned the right TPJ, a region associated
679 with attention and social cognition (Carter and Huettel), two intertwined functions as early
680 attentional capacities predict later social cognition abilities during development (Mundy and
681 Newell). In adults, there is evidence that the right TPJ harbors two functional entities: a posterior
682 region exclusively dedicated to social cognition, especially mentalizing, and an anterior region,
683 bridging attention and social cognition through its role in shifting attention between both stimuli and
684 mental states (Krall et al.; Rogier B. Mars, Sallet, et al.). In the present study, observation-driven
685 changes encompassed both TPJ regions, but the cluster identified by the interaction analysis as a
686 specifically adult change seem to more closely correspond to the anterior portion of rTPJ. This
687 raises the possibility that, because of its sophisticated integrative functions, the anterior portion of
688 rTPJ stands out as having not yet reached its mature role in the control of peer presence effects
689 by late childhood.

690

691 **5. Conclusions**

692 The present study tested the hypothesis that peer presence effects rely on a neural combination of
693 task-selective changes and domain-general modulations using a developmental approach
694 comparing children to adults. The results did not reveal any reliable task-selective changes, but the
695 possibility remains that such changes occur at levels invisible to fMRI. They did, by contrast,
696 provide compelling evidence for widespread task-independent changes in domain-general brain
697 networks that are already in place in late childhood. Putting together phylogenetic and ontogenetic
698 perspectives is the challenge awaiting future studies in order to explain the neural implementation
699 of all social presence effects, from the rudimentary ones shared by infants and animals to the most
700 sophisticated ones that are the privilege of healthy human adults.

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707

708 **Data Availability**

709 Data supporting the results will be available on the Open Science Framework website at

710 <https://osf.io/nspkx/>.

711

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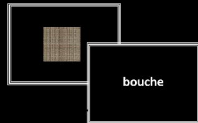
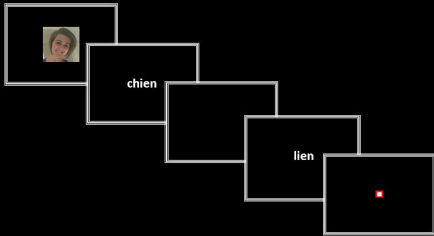
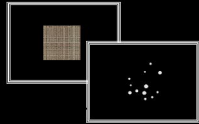
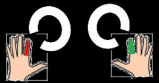
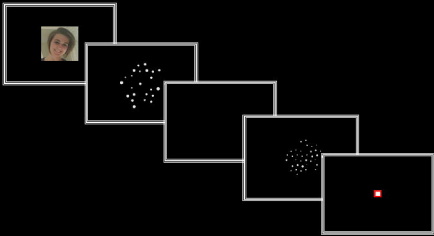
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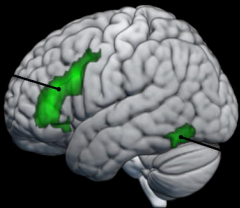
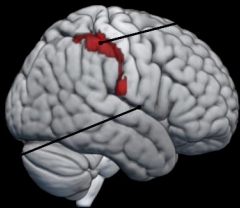
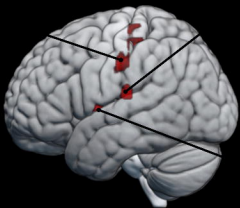
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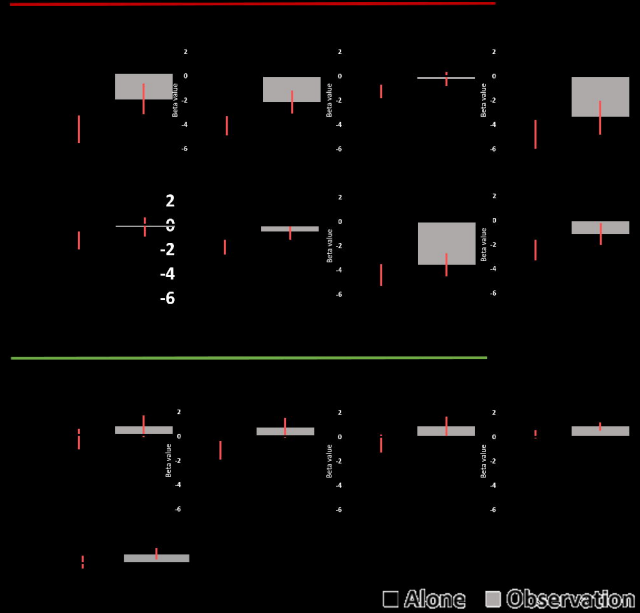
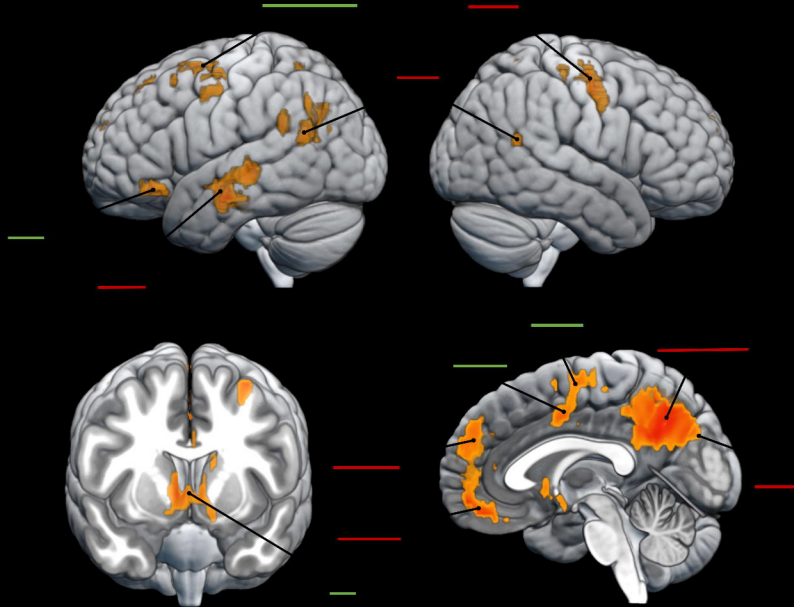
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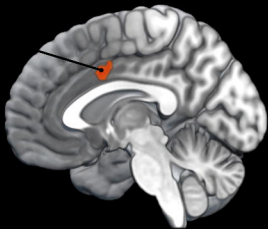
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□ Alone ■ Observation

