



Task-independent neural bases of peer presence effect on cognition in children and adults[☆]

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ABSTRACT

There is ample behavioral evidence that others' mere presence can affect any behavior in human and non-human animals, generally facilitating the expression of mastered responses while impairing the acquisition of novel ones. Much less is known about i) how the brain orchestrates the modulation of such a wide array of behaviors by others' presence and ii) when these neural underpinnings mature during development. To address these issues, fMRI data were collected in children and adults alternately observed and unobserved by a familiar peer. Subjects performed a numerosity comparison task and a phonological comparison task. While the former involves number-processing brain areas, the latter involves language-processing areas. Consistent with previous behavioral findings, adults' and children's performance improved in both tasks when observed by a peer. Across all participants, task-specific brain regions showed no reliable change in activity under peer observation. Rather, we found task-independent changes in domain-general brain regions typically involved in mentalizing, reward, and attention. Bayesian analyses singled out the attention network as the exception to the close child-adult resemblance of peer observation neural substrates. These findings suggest that i) social facilitation of some human education-related skills is primarily orchestrated by domain-general brain networks, rather than by task-selective substrates, and ii) apart from attention, peer presence neural processing is largely mature in children.

1. Introduction

The presence of an observer affects behavior. Generally, it facilitates simple or mastered responses while impairing complex or novel ones (Zajonc, 1965). A long history of psychology research has demonstrated the ubiquity of this social facilitation-inhibition phenomenon across species, observers, and behaviors (Bond, 1983; Guerin, 2010; van Meurs et al., 2021). We share this fundamental form of social influence with many -if not all- other animal species, including other primates such as macaques (Reynaud et al., 2015), but also songbirds (Vignal et al., 2004) or drosophilae (Chabaud et al., 2009). Actual observers embodied by friends (Ruddock et al., 2019), strangers (Guerin, 2010), or humanized robots (Woods et al., 2005) trigger social facilitation-inhibition, but virtual observers (Miyazaki, 2015), or even imagined ones (Hazem et al., 2017), can induce it as well. All behaviors can be changed by others' presence (positively or negatively, depending on the difficulty of the task they are embedded into), including, in particular, the very eye

movements and attention mechanisms that guide vision, our primary window to the world (Liu and Yu, 2017; Tricoche et al., 2020; Huguet et al., 2014; Wykowska et al., 2014). In contrast with this wealth of behavioral data, there is limited knowledge on the neural mechanisms orchestrating others' presence effects on such a wide variety of behaviors in so many species (Belletier et al., 2019; Monfardini et al., 2017). Even less is known about the emergence of the neural correlates of social facilitation-inhibition in children, although others, especially peers, might be particularly important during development (Somerville, 2013; Steinberg, 2007).

Social facilitation-inhibition is a lifelong phenomenon detectable as early as one year of age in humans (Pearcey and Castro, 1997). Therefore, understanding the neural correlates of social facilitation-inhibition during development has potential relevance to several domains including childhood obesity (Higgs and Thomas, 2016), adolescent risk-taking (Telzer et al., 2017), and education (van Duijvenvoorde et al., 2016). Because peers' influences can have staggeringly dramatic consequences

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on adolescents' health and life, much of the brain research effort has heretofore focused on 13- to 18-year-olds in order to decipher the neural processes responsible for peers' negative influences on cognition (Breiner et al., 2018; Chein et al., 2011; Dumontheil et al., 2016), especially decision making (Hartley and Somerville, 2015). Peers, however, are present at school well before 13 years of age. In fact, we recently showed that, at 10 years of age, basic academic skills that are foundational to math and reading can be facilitated as much as in adults by the presence of a familiar peer (Tricoche et al., 2021). Such positive influences of peers on children's academic performance might be of interest to educators. The present neuroimaging study builds upon these behavioral findings to determine whether the neural bases of social facilitation are the same in 10- to 13-year-olds and in adults.

At least two different neural mechanisms may explain the remarkable ubiquity of social facilitation-inhibition across ages, behaviors and species. One is that others' presence might modify neural activity in task-specific networks. All animals having congeners, it could indeed be adaptive for evolution to endow every neural system, whether sensory, motor or cognitive, immature or mature, with some capacity to process relevant social information (Ferrari et al., 2013). Several lines of evidence from research in non-human animals support this hypothesis. In monkeys, for example, a congener's presence changes activity in the fronto-parietal network subserving an attentional task (Monfardini et al., 2015), but also in the dorsolateral prefrontal neurons encoding a visuo-motor task (Demolliens et al., 2017). In songbirds, a congener's presence affects early gene activation in auditory areas when the bird is listening and in motor areas when the bird is singing (Woolley et al., 2014; Riters et al., 2004; Vignal et al., 2005; Menardy et al., 2014; Hessler and Doupe, 1999; Woolley, 2016). Some human neuroimaging data are also compatible with the idea that peer presence affects task-specific regions. Being observed changes activity in the (adult's) inferior parietal region controlling object grasping during a fine grip motor task (Yoshie et al., 2016), whereas it affects the (adult's and adolescent's) dorsolateral prefrontal region controlling relational integration during a complex reasoning task (Dumontheil et al., 2016). In adolescents, being observed by a peer enhances the pleasure of risk-taking and the associated activity in the ventral striatal region controlling reward processing (Chein et al., 2011; Albert et al., 2013; Van Hoorn et al., 2016). Thus, several studies in human and non-human animals support the hypothesis that task-specific neural systems contribute to peer-presence effects on behavior.

Another possibility, however, is that others' presence exerts its influence via one or several domain-general neural systems irrespective of the task. This could especially hold for primates, whose brain is thought to include several domain-general networks dedicated to processing social information (Mars et al., 2012). Social presence effects in humans have particularly been associated with our species' outstanding mentalizing capacities (de C. Hamilton and Lind, 2016; Beyer et al., 2018). Mentalizing is the ability to infer others' states-of-mind, such as their desires, intentions, or beliefs (Frith and Frith, 2006; Blakemore, 2015). Explicit mentalizing is generally considered to mature at around 4 years of age, but implicit mentalizing is present by 15 months of age (Kovács et al., 2021). The core mentalizing network identified in the brain across a variety of tasks and stimuli includes the medial prefrontal cortex (mPFC), the temporo-parietal junction (TPJ), the precuneus/posterior cingulate cortex (PreC/PCC), and the middle temporal gyrus (MTG) (Preckel et al., 2018; van Veluw and Chance, 2014). This network is developing early in life, before school age, and is relatively stable across late childhood, adolescence, and adulthood (Fehlbaum et al., 2021; Richardson et al., 2018). Changes in one or more nodes of this network have been reported in several neuroimaging studies investigating peer-presence effects on various behaviors. This holds true for adolescents observed while taking risks (Chein et al., 2011; van Hoorn et al., 2018; Telzer et al., 2015), making prosocial decisions (Van Hoorn et al., 2016), or engaging in complex reasoning (Dumontheil et al., 2016), as well as for adults observed during

risk-taking (Beyer et al., 2018), skilled motor performance (Chib et al., 2018) or embarrassing failures (Müller-Pinzler et al., 2015). It has therefore been proposed that performing a task in social presence might automatically recruit the human mentalizing network even when the other's state of mind is irrelevant to the current goal (Beyer et al., 2018). Supporting this proposal are the brain changes associated with (passive or active) participation in live social interaction (Beyer et al., 2018; Redcay et al., 2010; Warnell et al., 2018; Rice et al., 2016; Iacoboni et al., 2004). For example, believing that a human presence is live, rather than video-recorded or computer-generated, suffices to change activity in mentalizing, motivation, and attention brain regions (Redcay et al., 2010; Warnell et al., 2018; Rice et al., 2016). It is therefore possible that several domain-general neural networks contribute to peer-presence effects, at least in humans.

Critically, the two possible neural accounts of social facilitation-inhibition make different predictions when different tasks have non-overlapping neural substrates. According to the task-specific theory, the effect of peer presence on brain activity depends on the task at hand and is localized in task-specific brain regions. According to the domain-general theory, the effect of peer presence on brain activity is independent of the task at hand and is localized in a domain-general network (such as the mentalizing network). To the best of our knowledge, such a paradigm with two different tasks was used in only one previous neuroimaging study of peer presence effects (Smith et al., 2018). Adolescents (15 to 17-year-old) alternatively performed a gambling, risk-taking task, and a go/no-go, response inhibition task, either unobserved or under the belief that an anonymous peer was watching. The go/no-go task did not activate, however, the typical brain substrates of response inhibition, making a cross-task comparison difficult. So, a successful two-task comparison of peer presence effects neural underpinnings is still lacking.

To test between the task-specific and domain-general accounts of social facilitation-inhibition, we used here functional magnetic resonance imaging (fMRI) to compare brain activity in children and adults. We chose a familiar peer as the observer because known peers, being more frequent than unknown peers at school or at work, are more representative of daily life. Also, close others capture attention (Chauhan et al., 2017), elicit pleasure (Fareri et al., 2012) and induce social facilitation (Monfardini et al., 2017; Herman, 2015; Sugimoto et al., 2016) more than strangers. Building on previous behavioral (Tricoche et al., 2021) and neuroimaging data (Prado et al., 2011; Prado et al., 2014), we measured the effect of peer presence on the neural mechanisms underlying two education-related skills, numerosity comparison and phonological comparison (Phillips et al., 2008; Starr et al., 2013). Numerosity comparison consists of comparing quantities using approximate representations of numbers without relying on counting or numerical symbols (Dehaene, 2001). It is an early-developing numerical skill, detectable as early as 6 months of age, that has been found to predict mathematics achievement (Starr et al., 2013; Hyde et al., 2014). Phonological comparison consists in comparing the sound structure of words (Phillips et al., 2008). It is an early-acquired language skill, taught in preschool (Qi and O'Connor, 2000), that predicts reading achievement (Ehri et al., 2001). In both the developing and the mature brain, numerosity comparisons involve brain areas supporting the representation of magnitudes in the intraparietal sulcus and posterior superior parietal lobule, while phonological comparison involves language-related areas in the inferior frontal and the middle temporal gyri (Prado et al., 2011; Prado et al., 2014). Our earlier findings indicated that, by age 9 or 10, children optimize their response strategy in presence of a peer, thus displaying shorter and less variable reaction times resembling adults' for both types of comparisons (Tricoche et al., 2021).

The fact that both numerosity and phonological comparisons are facilitated by peer presence at behavioral level while depending on distinct neural substrates makes them well suited to test the task-specific versus domain-general accounts of social facilitation. We compared children aged 10 to 13 to determine whether the child brain codes

peer presence and implements social facilitation differently from the adult brain. In addition to whole-brain analyses, we conducted regions-of-interest (ROI) analyses within task-specific (i.e., numerosity processing, phonological processing) and task-independent (i.e., mentalizing, attention, motivation) substrates. Frequentist statistics were complemented by Bayesian statistics to quantify the evidence in favor of or against the null hypothesis (H0) and its alternative (H1).

2. Materials and methods

2.1. Participants

Participants were pairs of familiar, non-kin, age-mates (± 2 years), recruited via web posting. They included 17 pairs of children (15/34 females) with a mean age of 11 years (range: 10–13 years) and 12 pairs of adults (16/24 females) with a mean age of 23 years (range: 20–29 years). Standardized Intellectual Quotient (IQ) was assessed by the Nouvelle Echelle Métrique de l'Intelligence (Cognet and Bachelier, 2017) in children and by the average of the matrix reasoning and similarities subtests of the Wechsler Abbreviated Scale of Intelligence (WAIS-IV Wechsler Adult Intelligence Scale 2021) in adults. IQs were in the normal to superior range (children, mean: 114.3, range: 76–141; adults, mean: 99.8, range: 83–115). The IQ difference across dyad members averaged 7.8 points in children and 7.5 points in adults, such that the two peers generally fell within the same intelligence level (i.e. their IQs stood less than 10 points apart). Closeness scores, as assessed by the 7-point, Inclusion of Other in the Self scale (Aron et al., 1992), reached scores ≥ 4 (children, mean: 5.94, range: 3–7; adults: mean: 5.54, range: 3–7), typical of close partners such as best friends (Gächter et al., 2015; Myers and Hodges, 2012).

Nine children and one adult were discarded due to claustrophobia, sleepiness, joystick malfunction, misunderstood instructions, or excessive motion in the scanner. One of the remaining children had missing fMRI data and one of the remaining adult had missing behavioral data due to recording issues. The final samples of subjects therefore comprised 47 subjects, 25 children and 22 adults for behavioral analyses, and 24 children and 23 adults for fMRI analyses.

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

2.2. Justification of sample size

In a behavioral study demonstrating greater social inhibition of difficult relational reasoning in adolescents than adults, Wolf et al. (2015) reported an Age \times Condition \times Difficulty interaction of medium size ($\eta_p^2=0.09$, Cohen's $f = 0.3$). According to a power analysis using G*Power 3.1.9.7 (for repeated measures within factors and $\alpha=0.05$), an overall sample size of 22 participants is required to detect an Age \times Condition interaction of the same medium size as Wolf et al.'s (2015) effect with a standard power of 80%. Therefore, our overall sample size of 47 participants (25 children and 22 adults) appears appropriate to fulfill our objective and detect age influence on peer presence effects. In terms of fMRI data, the few previous papers comparing peer presence effects across two age groups did not specify the size of their Age or/and Condition effects. Therefore, as suggested by Lakens (Lakens, 2022), we plotted the sensitivity curve corresponding to an ANOVA with a between \times within-subject interaction for an α of 0.05 and a sample size of 47 participants (see Supplementary Material 1). It indicates that with our design a standard power of 80% can be reached with a medium-size Cohen's f of 0.21, or its equivalent, a Cohen's d of 0.42. This criterion

seems fulfilled here as the average d obtained for the changes revealed by the whole brain analysis reached a medium size of 0.55.

2.3. Session timeline

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

2.4. Trial sequence

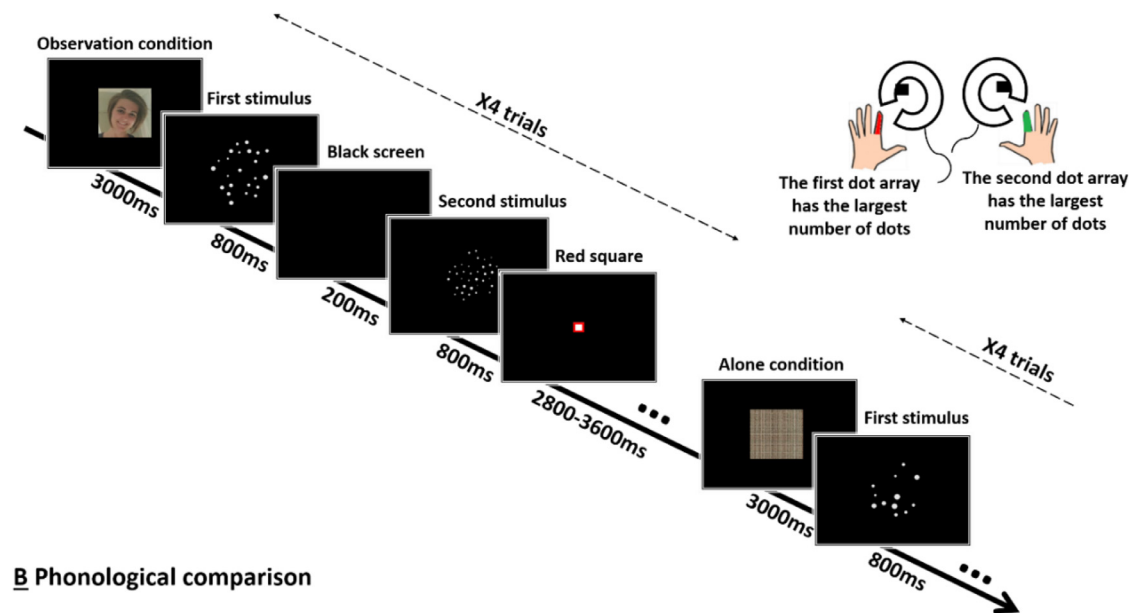
Both tasks were programmed using the Presentation® software (www.neurobs.com accessed on 15 December 2021). The stimuli were projected onto a screen viewed by the participant through a mirror attached to the head coil. For each trial, two stimuli (two dot arrays for numerosity comparisons; two words for phonological comparisons) appeared one after the other for 800 ms each, with a 200 ms delay in between. A red square then appeared for a randomly varying duration of 2800 ms, 3200 ms or 3600 ms. Participants had to decide which array contained the largest number of dots (numerosity comparison; Fig. 1A) or whether the two words rhymed or not (phonological comparison; Fig. 1B). They were asked to respond as fast and accurately as possible as soon as the second stimulus appeared and before the red square turned off. Participants pressed a button of the joystick in their left hand if the first dot array had the largest number of dots or if the two words rhymed. They pressed a button of the joystick in their right hand if the second dot array had the largest number of dots, or if the two words did not rhyme.

2.5. Stimuli

Dot arrays were created while controlling for differences in the cumulative surface area and in the distribution of dot sizes (Gebuis and Reynvoet, 2011). An array could contain 12, 18, 24 or 36 dots. Comparison difficulty varied with the ratio of the number of dots between the two arrays. The higher the ratio, the greater the difficulty. Comparisons involved a 0.33 ratio (12 dots vs. 36 dots), a 0.5 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 dots), or a 0.75 ratio (18 dots vs. 24 dots). The task was divided into 24 blocks of 4 trials each, for a total of 96 trials. There were 12 easy blocks involving small ratios (i.e., 0.33 and 0.5) and 12 hard blocks involving large ratios (i.e., 0.67 and 0.75), pseudo-randomly ordered during the task. The first dot array contained the larger number of dots in half of the trials, while in the other half of the trials it contained the smaller number of dots. A given pair of stimuli was presented only once. The task began with 8 practice trials (4 per ratio) that were not included in the analyses.

Words contained 3 to 8 letters. Comparison difficulty varied with the congruence or incongruence of the spelling and phonology of the two successively presented words. In half of the trials, the two words had congruent orthography and phonology, i.e., they had identical spelling and sounded the same (e.g., sac-lac [sak-lak]), or they had a different spelling and sounded different (e.g., jeu-doux [ʒœ-du]). In the other half of the trials, the two words had incongruent orthography and phonology, i.e., they had a different spelling and sounded the same (e.g., dos-taux [do-to]), or they had identical spelling and sounded different (e.g., tapis-iris [tapi-iris]). The phonological comparison task was, like the numerosity comparison task, divided in 24 blocks of 4 trials each, for a total

A Numerosity comparison



B Phonological comparison

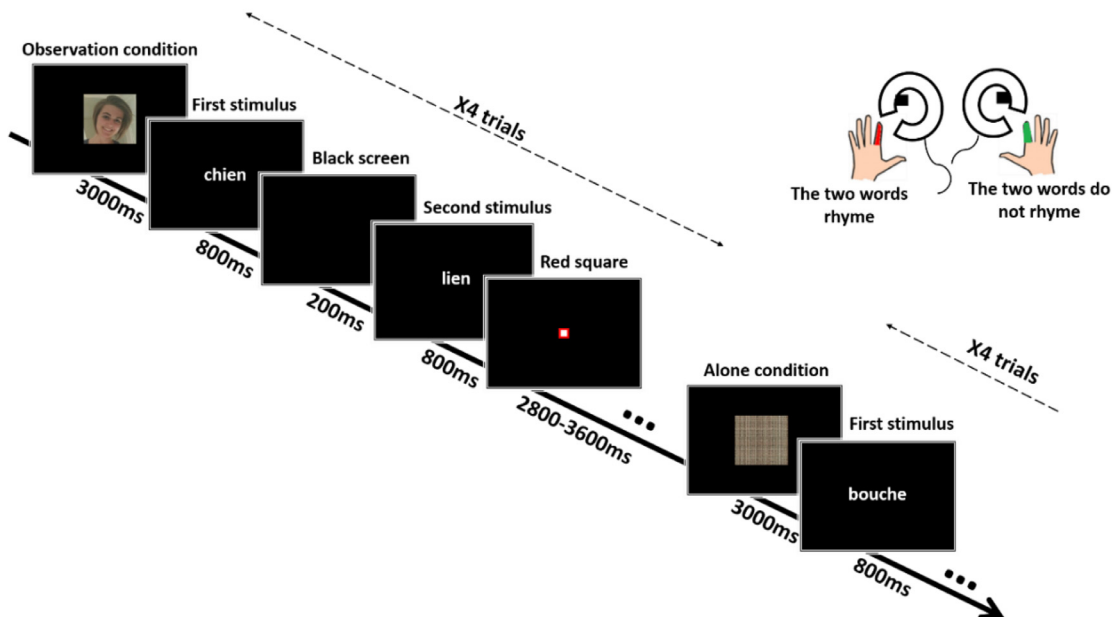


Fig. 1. Experimental tasks. Trial time course (from top to bottom) was the same for numerosity (A) and phonological comparisons (B). At the beginning of each block of 4 trials, an original or scrambled version of a headshot of the observer indicated the condition for the block: observation or alone condition, respectively. Two stimuli were successively presented for 800 ms each, separated by a 200ms-interval. Participants had to decide which of the dot arrays had the largest number of dots (A) or whether the two words rhymed or not (B), and to respond as fast and accurately as possible, using either the left or the right index finger, as soon as the second stimulus appeared and before the red square turned off.

of 96 trials. There were 12 easy blocks involving congruent trials and 12 hard blocks involving incongruent trials, pseudo-randomly ordered during the task. Each word was presented only once during the task. Words presented over two successive trials could not have the same phonology, orthography or be semantically related. The two words rhymed in half of the trials, while they did not rhyme in the other half of the trials. As for numerosity comparison, the task began with 8 practice trials (4 congruent, 4 incongruent) that were not included in the analyses.

2.6. Observation versus alone conditions

Upon arrival to the testing site, the two peers were kept together while they received the testing instructions and visited the scanner room and the nearby observation room. A head model was positioned inside the scanner to help them mentalize the subject's point of view. In the observation room, the real-time images from the three cameras monitoring the scanner room were displayed for them to experience the observer's

point of view. Then, each subject alternatively took the actor and the observer roles. While the actor was lying inside the MR scanner, the observer was sitting in an adjacent room, facing a computer screen. The observer's computer screen displayed filler videos (Alone condition) or the live video streams of three cameras placed inside the scanner: one filming the actor's body, one filming the actor's eyes, and one filming what the actor saw on her/his screen (Observation condition). The two conditions alternated every other 4-trial block, always starting with the Alone condition, up to a total of 24 blocks (96 trials) per task.

The actor was informed about the forthcoming condition at the beginning of each 4-trial block by displaying the observer's picture for 3000 ms, either in a scrambled version (Alone condition), or in its original form (Observation condition). During the 8-minute anatomical T1 scan in between the two tasks, actor and observer could see each other via video cameras as a reminder for the actor of the observer's actual presence in the adjacent room. During acquisition, the experimenters remained out of sight in the scanner's monitoring room (whose window overlooking the scanner was obstructed by a curtain) and refrained from any unnecessary verbal contact with either the actor or the observer during the scanning session in order to minimize third-party presence.

2.7. Behavioral analyses

R (RStudio, v.1.0.136) and SYSTAT (v13) were used to analyze the subjects' accuracy (% of correct responses) and their speed during correct responses (reaction times, RTs, calculated as the time separating the appearance of the second stimulus from the button press). Scores for each task were averaged across all 24 blocks of four trials. ANOVAs were first used to determine whether Testing order (being actor first versus second) and Difficulty level (easy versus hard trials) mattered for social facilitation. As they did not, behavioral data were then analyzed using three-way ANOVAs with the between-subject factor Age (Children, Adults) and the within-subject factors Condition (Observation, Alone) and Task (Numerosity comparison, Phonological comparison). Given that a standard frequentist approach indicated several lacks of difference between children and adults, Bayesian ANOVAs and Student t-tests were also conducted in order to lower the risk of false negatives (Keyes et al., 2020). The Bayes Factor (BF_{incl} or BF_{10}) was calculated using JASP (<https://jasp-stats.org/>) to quantify the relative plausibility of alternative hypotheses H_0 and H_1 . As described by Wagenmakers and collaborators (2018), extreme, strong, moderate or anecdotal evidence for the null hypothesis (H_0) were set for a $BF < 0.001$, < 0.01 , < 0.33 , < 1 respectively; whereas extreme, strong, moderate or anecdotal evidence for the alternative hypothesis H_1 were set for a $BF > 100$, > 10 , > 3 and > 1 (Wagenmakers et al., 2018).

We also calculated, for each subject and each task, the performance gain produced by observation in accuracy and speed relative to the alone condition ((Observation-Alone)/Alone*100). We then used one-tailed Student's t-tests to determine whether the group mean gain was significantly greater than 0, i.e., reflected the expected social facilitation. Peer presence effect size was estimated as earlier (Tricoche et al., 2021), using Cohen's d (d_z for dependent samples) and common language effect size (CL).

2.8. MRI data acquisition

MRI scans were obtained from a MAGNETOM Prisma 3.0 T scanner with a 64-channel head coil (Siemens Healthcare, Erlangen, Germany) at the Lyon Primage neuroimaging platform (CERMEP, Imagerie du vivant, Lyon, France). The fMRI blood oxygenation level-dependent (BOLD) signal was measured with a susceptibility weighted single-shot echo planar imaging (EPI) sequence. The following parameters were used: TR = 2000 ms, TE = 24 ms, flip angle = 80° , matrix size = 128×120 , field of view = 220×206 mm, voxel size = 1.72×1.72 mm, slice thickness = 3 mm (0.48 mm gap), number of slices = 32. Between the two functional runs, a high resolution T1-weighted 3D structural image was

acquired for each participant (TR = 3000 ms, TE = 2.93 ms, flip angle = 8° , matrix size = 320×280 mm, field of view = 280×320 mm, slice thickness = 0.8 mm, number of slices = 160).

2.9. fMRI data analyses

2.9.1. Preprocessing

Data analysis was performed using SPM12 (www.fil.ion.ucl.ac.uk/spm accessed on 15 September 2021). Functional images were corrected for slice acquisition delays, spatially realigned to the first image of the first run to correct for head movements, and spatially smoothed with a Gaussian filter equal to twice the voxel size ($4 \times 4 \times 7$ mm³ full width at half maximum). Functional image runs were inspected using ArtRepair (cibsr.stanford.edu/tools/human-brain-project/artrepair-software.html accessed on 15 September 2021); functional volumes with a global mean intensity greater than 3 standard deviations from the average of the run or a volume-to-volume motion greater than 2 mm were identified as outliers and substituted by the interpolation of the 2 nearest non-repaired volumes. Note that, for participants who were not excluded due to high motion (more than 20% of interpolated images), we suppressed on average 8.7 scans per child (min=0, max=60) and 5.1 scans per adult (min=0, max=16), corresponding to 2.4% and 1.4% of suppressed scans for each population, respectively. Statistical analyses of movement parameters did not reveal any significant Age effect, nor any interaction between age and tasks' run (all p 's > 0.05 , all BF_{incl} 's ≤ 0.10). Finally, functional images were coregistered with the segmented anatomical image and normalized into the standard Montreal Neurological Institute (MNI) space (normalized voxel size: $2 \times 2 \times 3.5$ mm³).

2.9.2. Processing

Event-related statistical analysis was conducted using the general linear model (GLM). Activation was modeled as epochs with onset time locked to the presentation of the first stimulus in each trial and with a duration of 2 s. Fixation periods were modeled as 16 s blocks. All trials (including correct, incorrect and miss trials) were sorted according to Task, Condition and trial type (e.g., ratio for numerosity comparison, congruency for phonological comparison). Fixation blocks were modeled in a separate regressor for each task. Finally, two regressors of no-interest (one per task, including instructions, breaks, and picture display of the observation/alone conditions) were added in the model. To explore the link between brain activity and social facilitation, we created a second GLM in which an additional regressor coded the RT associated with each trial (separately for each task and condition). All epochs were convolved with a canonical hemodynamic response function (HRF). The time series data were high-pass filtered (1/128 Hz), and serial correlations were corrected using an autoregressive AR (1) model.

2.9.3. Whole-brain analyses

Voxel-wise parameter estimates obtained for each subject were entered into random effect (RFX) analyses in order to identify regions exhibiting main effects and interactions involving the Age, Task, and/or Condition factors, or whose activity was associated with the RT improvement driven by observation on a trialwise basis. Group-wise statistical maps were thresholded for significance using a voxel-wise probability threshold of $p < 0.001$ (uncorrected) and a cluster-wise probability threshold of $p < 0.05$ (FWE corrected for multiple comparisons).

2.9.4. ROI analyses

Observation-related changes of activity in both task-specific and task-independent (i.e., mentalizing) were also assessed in ROI analyses, using both frequentist and Bayesian statistics. ROIs were defined across groups and conditions based on the main effect of task at the whole-brain level. Specifically, numerosity ROIs were defined using the contrast of numerosity comparison versus phonological comparison, while phonology ROIs were defined using the contrast of phonological comparison

versus numerosity comparison. For each map, we excluded voxels for which task-related activity was not also significantly greater than activity during fixation. ROIs were defined as the intersection of 10 mm radius spheres centered on the local maximum of each cluster (using the SPM toolbox Marsbar) with the corresponding thresholded statistical map. Activity (calculated with respect to the fixation baseline) was averaged across all voxels of each ROI.

We also defined ROIs belonging to the mentalizing, attention and motivation networks based on previous meta-analyses (S.J. van Veluw and Chance, 2014; Jauhar et al., 2021; Hongkeun, 2014). We defined 9 ROIs in the mentalizing network (two clusters in the dmPFC, bilateral TPJ-STG, Precuneus, pPCC, bilateral MTG and right MFG), 7 ROIs in the attention network (bilateral aTPJ, right Anterior Insula (AI), left IPS/IPL, bilateral Inferior Frontal Junction (IFG) extending to FEF and ACC/MCC), and 3 ROIs in the motivation network (right VS, aPCC and MFC). ROIs were defined as 10 mm radius spheres centered on the coordinates obtained in the meta-analyses (see Supplementary Material 2).

Average values for each ROI were then analyzed using four-way frequentist and Bayesian ANOVAs to assess the effects on task-specific or task-independent neural activity of the between-subject factor Age (Children, Adults) and the within-subject factors ROIs, Task (Numerosity comparison, Phonological comparison) and Condition (Observation, Alone). For frequentist statistics, statistical significance was set at $p < 0.05$ and post-hoc tests were applied using FDR or Bonferroni corrections when needed. For Bayesian statistics, the Bayes Factor (BF_{incl} or BF_{10}) was interpreted using the benchmarks described above.

3. Results

3.1. Behavioral data: testing order and difficulty

We first investigated whether Testing order (whether participants performed first or observed first) influenced behavior. We found no effect of Testing order on accuracy or RTs, nor any interaction of Testing order with Condition, Age or Task (all p 's > 0.05); all BF_{incl} 's were comprised between 0.43 and 0.001, indicating anecdotal to extreme evidence in favor of H0. Therefore, we pooled all participants regardless of whether they performed first or observed first in all subsequent analyses. We then investigated the effects of Difficulty. These were as expected based on prior results (Tricoche et al., 2021). Namely, hard trials took longer and were less accurate than easy trials (RT: $F(1,45)=147.67$, $p < 0.001$, $BF_{incl} > 100$; percent correct: $F(1,45)=146.13$, $p < 0.001$, $BF_{incl} > 100$), and these costs were greater for phonological than for numerosity comparisons (Task x Difficulty, RT: $F(1,45)=17.08$, $p < 0.001$, $BF_{incl} > 100$; percent correct: $F(1,45)=4.47$, $p = 0.03$, $BF_{incl}=0.87$). We found no reliable influence of Difficulty on either the magnitude or the direction of peer presence effects, as indicated by a marginal Condition x Task x Difficulty interaction ($F(1,45)=3.88$, $p = 0.05$) associated with moderate Bayesian evidence for H0 rather than H1 ($BF_{incl}=0.25$). We therefore did not include Difficulty as factor in the following analyses.

3.2. Behavioral data: task and age effects

We then turned to the effects of task and age. Making phonological comparisons took longer than making numerosity comparisons ($F(1,45)=177.3$, $p < 0.001$, $\eta_p^2=0.80$, $BF_{incl} > 100$), but accuracy was comparable in the two tasks ($F(1,45)=0.2$, n.s., $BF_{incl}=0.96$). In line with earlier results (Tricoche et al., 2021), children performed worse than adults. Their responses were less accurate ($F(1,45)=5.22$, $p = 0.03$, $\eta_p^2=0.10$, $BF_{incl}=3.55$) and slower ($F(1,45)=10.9$, $p = 0.002$, $\eta_p^2=0.19$, $BF_{incl} > 100$) than adults'. Children's developmental lag behind adults was more pronounced for phonological than for numerosity comparisons (Age x Task interaction: RTs, $F(1,45)=7.73$, $p = 0.008$, $\eta_p^2=0.15$,

$BF_{incl} > 100$; percent correct responses, $F(1,45)=6.22$, $p = 0.02$, $\eta_p^2=0.12$, $BF_{incl}=4.51$).

3.3. Behavioral data: condition effect

Finally, more central to our current interest, we evaluated the effect of condition. For accuracy, a main effect of Condition ($F(1,45)=7.31$, $p = 0.01$, $\eta_p^2=0.14$, $BF_{incl}=0.60$) reflected improved correct responses under observation. A lack of Condition x Age interaction ($F(1,45)=1.18$, $p = 0.28$) and anecdotal Bayesian evidence for H0 rather than H1 ($BF_{incl}=0.46$) suggested that this observation effect was comparable in children and adults. Further confirming the resemblance across age groups was a Condition x Age x Task interaction ($F(1,45)=4.04$, $p = 0.05$, $\eta_p^2=0.08$, $BF_{incl}=1.13$) showing that, in children and adults alike, social facilitation predominantly occurred for one of the two tasks. Specifically, observation reliably improved children's numerosity comparisons (Alone: 90%, Observation: 92%, gain 2%, $t(24)=2.29$, $p = 0.03$, $BF_{10}=1.6$), and adults' phonological comparisons (Alone: 93%, Observation: 96%, gain 4%, $t(21)=3.01$, $p = 0.007$, $BF_{10}=6.33$), but not children's phonological comparisons (Alone: 88%, Observation: 90%, gain 2%, $t(24)=1.41$, $p = 0.08$, $BF_{10}=0.54$) or adults' numerosity comparisons (Alone: 93%, Observation: 91%, loss: 2%, $t(21)=1.16$, $p = 0.26$, $BF_{10}=0.41$). Cohen's d_z respectively estimated the two positive peer presence effects as medium-sized effects of 0.52 for children and 0.65 for adults. The corresponding CL effect sizes, which give the probability for a score randomly selected from the observed condition to be better than a score randomly selected from the unobserved condition, were: 70% for children, and 74% for adults.

For RTs, there was a Condition x Task interaction ($F(1,45)=8.05$, $p = 0.007$, $\eta_p^2=0.15$, $BF_{incl}=0.18$) as, in children and adults alike, observation speeded up numerosity comparisons (Children: Alone 894 ms, Observation 862 ms, gain 3%, $t(24)=1.71$, $p = 0.05$, $BF_{10}=1.32$; Adults: Alone 689 ms, Observation 664 ms, gain 3%, $t(21)=3.24$, $p = 0.002$, $BF_{10}=22.87$), but not phonological comparisons (Children: Alone 1324 ms, Observation 1381 ms; Adults: Alone 988 ms, Observation 986 ms). A non-significant Condition x Age interaction ($F(1,45)=2.95$, $p = 0.09$) that was associated with moderate Bayesian evidence for H0 over H1 ($BF_{incl}=0.12$) further supported the idea of similar observation-driven changes in children and adults. Cohen's d_z estimated these peer presence effects as a small-sized effect of 0.14 for children and a medium-sized effect of 0.73 for adults. The corresponding CL effect sizes amounted to 55% for children and 77% for adults.

To summarize, behavioral data (Supplementary Result 1) showed the expected social facilitation during observed relative to unobserved trials. Irrespective of age, being observed by a peer improved speed (of adults' and children's numerosity comparisons) and accuracy (of adults' phonological comparisons and children's numerosity comparisons). Comparison of children and adults using the Bayesian approach yielded evidence toward H0, that is, supported the idea of an absence of reliable age-related difference in observation behavioral effects.

3.4. fMRI data: whole-brain analyses, condition effect

We found no effect of Testing order on brain activity, nor any interaction with other factors, so, as for behavior, participants were pooled whether they performed first or observed first. Across both groups and both tasks, no main effect of Condition was observed in the Alone > Observation contrast. Rather, the neural correlates of peer presence effects were revealed by the whole-brain Observation > Alone contrast, which identified eleven clusters (Table 1, Fig. 2A). Associated Beta values (Fig. 2B) showed that the most frequent change took the form of a lesser deactivation in the observation than in the alone condition. This concerned the mPFC, the TPJ, and the Prec/PCC region, as well as the left MTG, right precentral gyrus PreG, and right posterior occipital gyrus (POG). Greater activation in the observation condition compared to the alone condition was also observed. This pattern was found in the right

Table 1
MNI coordinates of the brain regions showing a main Condition effect.

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

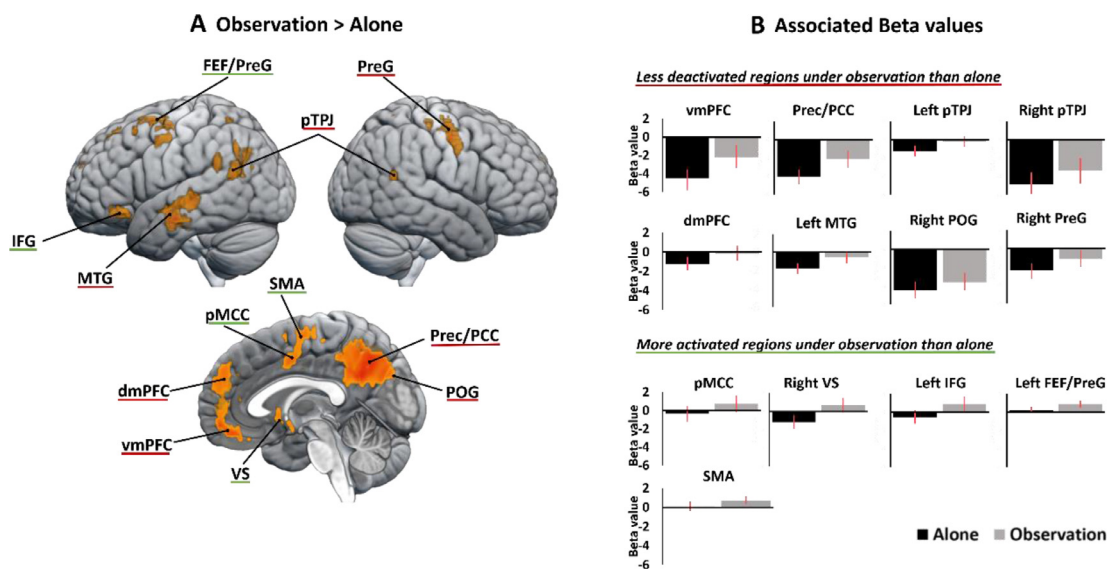


Fig. 2. Brain regions activated in the Observation > Alone contrast across Age and Task. (A) Location of activated brain regions. (B) Associated Beta values of less deactivated regions (vmPFC, dmPFC, Prec/PCC, pTPJ, left MTG, right POG and right PreG) and more activated regions (pMCC, SMA, right VS, left IFG and left FEF/PreG) during observed relative to unobserved trials.

VS, the left IFG, the Middle Cingulate Gyrus (MCC), and a cluster involving the left frontal eye field (FEF) and extending into the precentral gyrus (PreG).

To estimate the link between these anatomical locations and their underlying function(s), we used Neurosynth (<https://www.neurosynth.org>). We entered the coordinates of each of the 11 clusters. We then extracted the posterior probability (pp), that is, the likelihood of a given term to be associated with these coordinates. Based on our hypotheses, we looked for the pp of “Mentalizing”/“Default mode”, “Attention”, and “Motivation”. The mPFC, TPJ and Prec/PCC regions, as well as the left MTG, were mainly associated with “Mentalizing” (all pp’s > 0.70; Table 2). All of these clusters, especially the left MTG, were also frequently associated with “Default mode”. The left FEF and the right POG were predominantly linked to “Attention” (pp’s > 0.65). The VS, but also the vmPFC, and the MCC, were mainly associated with “Motivation” (pp’s > 0.65). The other clusters did not show a clear association with one of the four terms. According to Neurosynth, the SMA is most frequently associated with motor-related terms (pp=0.78), the left IFG with language-related terms (pp’s > 0.75) and the right preG (pp’s > 0.79) with eye movements-related terms.

3.5. fMRI data: whole-brain analyses, condition x task interaction

Among the clusters modulated by peer observation, a single one showed a Condition x Task interaction (Fig. 3). Located in the posterior part of the MCC ([2 2 41], $Z = 3.92$), it displayed increased activation under observation for numerosity but not phonological comparisons. Peer observation also improved RTs only for numerosity comparisons. This behavioral difference, common to children and adults, could explain the neural difference seen across tasks in the MCC.

3.6. fMRI data: whole-brain analyses, condition x age interaction

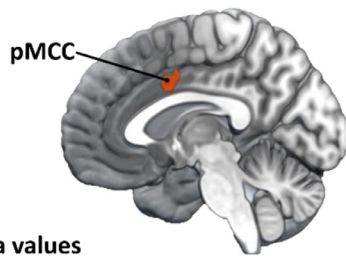
When adults were considered separately, the brain regions identified by the Observation > Alone contrast were the same as those described above for all subjects taken together (Supplementary Result 2A). When children were considered separately, only one cluster survived the threshold: the Prec and nearby SPL (Supplementary Result 2B). This was also the sole cluster revealed by a conjunction analysis across adults and children for the Observation > Alone contrast. However, all but one of the adults’ clusters were observed in children with a lower ($p = 0.005$) and uncorrected voxel-wise probability threshold.

Table 2

Posterior probability for each anatomical location obtained in the Observation>Alone contrast; that is the likelihood of a given term (“Mentalizing”/“Default mode”, “Attention” and “Motivation”) to be used in a study if an activation is observed at particular coordinates (based on Neurosynth).

Anatomical location	Posterior probability for the terms:		
	“Mentalizing” / “Default mode”	“Attention”	“Motivation”
Ventro-Medial Prefrontal Cortex	0.84 / 0.69	0.46	0.68
Dorso-Medial Prefrontal Cortex	0.83 / 0.67	0.56	0.24
Right Precentral Gyrus	0.42 / 0.46	0.49	0.54
Precuneus and Posterior Cingulate Cortex	0.82 / 0.62	0.39	0
Left posterior Temporo-Parietal Junction	0.71 / 0.55	0.46	0
Right posterior Temporo-Parietal Junction	0.79 / 0.40	0.60	0.39
Left Middle Temporal Gyrus	0.71 / 0.76	0.43	0.45
Right Posterior Occipital Gyrus	0.31 / 0.54	0.67	0.60
Left Inferior Frontal Gyrus	0.60 / 0.49	0.35	0.28
Left Frontal Eye Field / Precentral Gyrus	0.57 / 0.39	0.73	0.51
Posterior Middle Cingulate Gyrus	0.53 / 0.48	0.46	0.65
Supplementary Motor Area	0.39 / 0.51	0.47	0.56
Right Ventral Striatum	0.44 / 0.31	0.49	0.73

A Numerosity comparison > Phonological comparison



B Associated Beta values

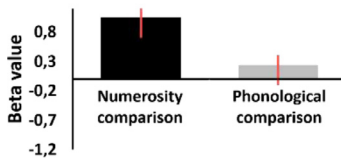


Fig. 3. Brain activation in the Observation > Alone contrast interacting with Task. A single area (posterior MCC) showed increased activation under observation for numerosity but not phonological comparisons. (A) Location of activated brain region. (B) Associated Beta values.

The one exception to the close resemblance between children and adults was a cluster located close to the right pSTS, in a region defined by Mars et al. in 2012 (R.B. Mars et al., 2012) as the anterior part of TPJ (aTPJ, [58 –26 10], $Z = 4.79$). Indeed, this region stood out as the only node of the large network modulated by peer observation showing a significant Condition x Age interaction. Associated Beta values showed that the right aTPJ was less deactivated in observed than unobserved trials in adults but not in children (Supplementary Result 2B). There was no Condition x Age x Task interaction, indicating that this developmental difference held for both tasks.

3.7. fMRI data: ROI analyses of task-specific regions

ROI analyses were conducted on the seven clusters identified as task-specific neural substrates in the whole-brain analyses for the Numerosity > Phonological comparison and Phonological > Numerosity comparison contrasts (all F 's(1135)>40, all p 's<0.001, η_p^2 >0.23; Table 3, Fig. 4). There were five numerosity ROIs (right IPS/SPL, right and left posterior Insula, left STG, and left postcentral gyrus or PostG) and two phonological ROIs (left IFG, left ITG). These clusters were consistent with earlier fMRI data obtained using the same tasks (Prado et al., 2011; Prado et al., 2014).

Unsurprisingly, a main effect of ROI was found ($F(6,1215)=18.72$, $p<0.001$, $BF_{incl}>100$), as well as significant ROI x Task, and ROI x Age interactions ($F(6,1215)=72.86$, $p<0.001$, $BF_{incl}>100$ and $F(6,1275)=4.05$, $p<0.001$, $BF_{incl}=15.81$). Post-hoc analyses confirmed that, in all ROIs,

activity differed between the two tasks (all p 's≤0.005, Bonferroni correction). Concerning the ROI x Age interaction, two differences were found between adults and children using FDR correction, in the left STG ($p = 0.01$) and the right posterior Insula ($p = 0.02$), but neither of them survived Bonferroni correction.

A main effect of Condition ($F(1,1215)=4.43$, $p = 0.03$) indicated that all ROIs were more activated in the Observation than Alone condition, though this main effect was associated with a Bayes of 0.11, which constitutes instead moderate evidence in favor of H_0 . None of the interactions between Condition and other factors reached significance, and all of them displayed Bayesian evidence for H_0 (all BF_{incl} 's<0.13), suggesting a weak homogenous Condition effect across ROIs, ages and tasks. These results provide little to no support to the task-specific account of peer presence effect inasmuch as they did not reveal any observation-driven change in number-related regions selectively occurring for numerosity but not phonological comparisons, and/or changes in language-related regions selectively occurring for phonological but not numerosity comparisons.

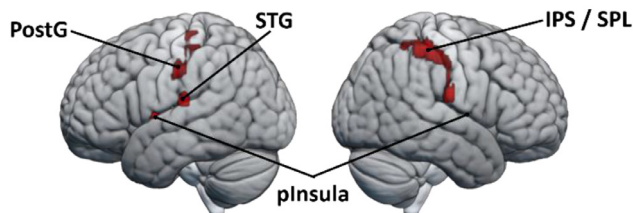
3.8. fMRI data: ROI analyses of mentalizing, motivation and attention regions

As mentioned earlier, following van Velum and Chance, 2014 (S.J. van Veluw and Chance, 2014), we identified nine ROIs as components of the mentalizing network: the Precuneus, pPCC, and two dmPFC clusters, medially, the TPJ-STG and MTG, bilaterally, and the right MFG.

Table 3
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

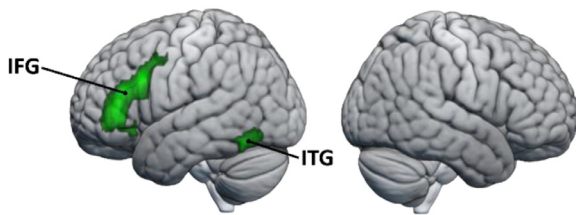


Fig. 4. Task-specific substrates selectively activated by (A) numerosity comparisons versus (B) phonological comparisons.

Following Hongkeun, 2014 (Hongkeun, 2014), we identified three ROIs as parts of the reward-based motivation network: the aPCC and MFC, medially, plus the right VS. Following Jauhar et al., 2021 (Jauhar et al., 2021), we identified seven ROIs as contributing to the attention network: the ACC/MCC, medially, the aTPJ and Inferior Frontal Junction (IFJ, extending to FEF), bilaterally, together with the right Anterior Insula (AI) and left IPS/IPL.

3.8.1. Mentalizing network

Results for mentalizing ROIs revealed extreme Bayesian evidence in favor of H1 for the three main effects (Condition, Age and ROI, all $BF_{incl} > 100$), and also for the Age x ROI interaction ($BF_{incl} > 100$), as children globally showed less activity than adults in all ROIs but the bilateral MTG (particularly in the right hemisphere; Supplementary Result 3). For all other interactions, Bayesian evidence was moderately to extremely in favor of H0. This held true for the Condition x Age x ROI interaction ($BF_{incl} < 0.01$), the Condition x ROI interactions ($BF_{incl} = 0.03$), and also for the Condition x Age interaction ($BF_{incl} = 0.24$). The latter finding constitutes decisive evidence in favor of a close resemblance in the contribution of mentalizing regions to peer observation effects in children and adults.

3.8.2. Motivation network

Results for motivation ROIs also revealed extreme Bayesian evidence in favor of H1 for the three main effects (Condition, Age and ROI, all

$BF_{incl} > 26$), as well as for the Age x ROI interaction ($BF_{incl} = 131.86$), due to high differences between children and adults in MFC compared to the two other regions (rVS and aPCC) (see Supplementary Result 4). For all other interactions, we found anecdotal to moderate Bayesian evidence in favor of H0: Condition x Age x ROI interaction ($BF_{incl} = 0.05$), Condition x ROI interaction ($BF_{incl} = 0.20$), and Condition x Age interaction ($BF_{incl} = 0.72$). The latter finding suggests that, like mentalizing regions, motivation regions encode peer observation effects in comparable ways in the children and adult brains.

3.8.3. Attention network

Results for attentional ROIs likewise revealed strong to extreme Bayesian evidence in favor of H1 for the three main effects (Condition, Age and ROI, all $BF_{incl} > 7.94$), and either anecdotal evidence toward H1 or evidence toward H0 ($BF_{incl} < 1,35$) for the interactions of ROI with Age and/or Condition. This time, however, the Condition x Age interaction revealed strong evidence toward H1 and against H0 ($BF_{incl} = 24.99$). As shown in Supplementary Result 5, children showed none of the observation-driven change characterizing adults in all attention nodes including the medial ACC-MCC and IPL-IPS, the right AI, and the bilateral aTPJ and FEF regions. This represented the second neural exception to child-adult resemblance. Like the first one (the lack of change in children's right aTPJ in the whole-brain approach), it concerned attention brain substrates. Child-adult neural differences therefore outlined a potential developmental asynchrony between late developing neural bases of peer presence effects in the attention network, on the one hand, and early maturing ones in the mentalizing and reward networks, on the other hand.

3.9. fMRI data: relation between brain activity and social facilitation

A GLM with RT data as regressors identified one cluster whose activity for the Social>Alone contrast of numerosity comparisons increased on a trialwise basis when RT decreased (Fig. 5). This cluster associated with observation-driven improvement of performance, i.e., social facilitation, was located in the ventral part of the left angular gyrus, at the posterior tip of the superior temporal sulcus, in a region defined by Igelström, et al. in 2015 (Igelström et al., 2015) as the dorsal part of TPJ (dTPJ, $[-46 -60 30]$).

4. Discussion

The present study aimed to explore the changes occurring in the child and adult brains when the presence of a peer facilitates the execution of familiar responses. We compared adults and 10- to 13-year-old children, alternately observed and unobserved by a familiar peer, while they compared either the number of dots in two arrays or the sounds of two written words, i.e., drew from mastered skills foundational to either math or reading. Behaviorally, observation improved the speed

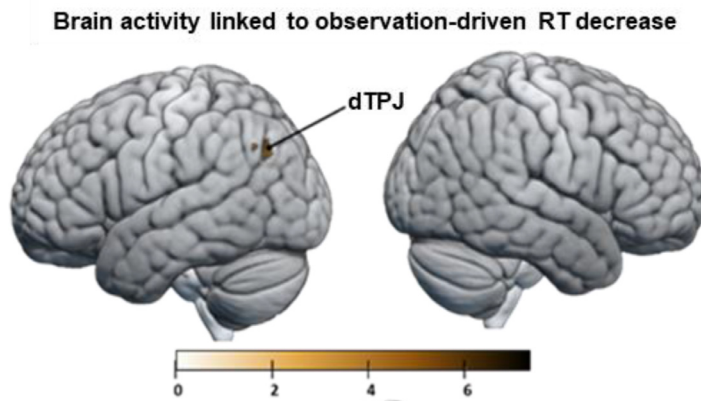


Fig. 5. Cluster in the dorsal part of the left TPJ whose change of activity during observed relative to unobserved numerosity comparisons was positively related to the improvement of behavioral performance on a trialwise basis.

of adults' and children's numerosity comparisons, while for accuracy, it improved adults' phonological comparisons and children's numerosity comparisons. Bayesian evidence was in favor of an absence of age-related difference in both instances, in agreement with earlier findings (Tricoche et al., 2021). ROI analyses revealed virtually no observation-driven change within the numerical and language brain areas identified as the task-specific neural substrates of numerosity and phonological comparisons in earlier studies (Prado et al., 2011; Prado et al., 2014). Rather, whole-brain analyses revealed a unique neural signature of observation, similar for non-symbolic numerosities and words, and largely shared by children and adults. This task-independent signature entailed widespread changes in brain regions that Neurosynth posterior probabilities predominantly associated with the domain-general functions of mentalizing, reward-based motivation, and attention. Whole-brain analyses unveiled a single exception to child-adult close neural resemblance. In the anterior portion of the right TPJ, only adults exhibited a less pronounced deactivation during observed compared to unobserved trials. ROI-based Bayesian analyses confirmed that neural responses to peer observation was largely similar in children and adults in the mentalizing and motivation networks, but not in the attention network. Children's neural reactivity to peer observation actually lagged behind adults' in an array of attention nodes including not only the right aTPJ, but also the left aTPJ, right AI, bilateral FEF, ACC-MCC and IPL-IPS.

4.1. Similar social facilitation induced by peer presence in children and adults

Caution should be used in generalizing the above conclusions to all peers as, here and earlier (Tricoche et al., 2021), we chose to test pairs of familiar peers. First, familiar peers are more representative of daily life as they are more frequent at school or at work than unknown ones. Second, close others capture attention (Chauhan et al., 2017), elicit pleasure (Fareri et al., 2012) and induce social facilitation (Monfardini et al., 2017; Herman, 2015; Sugimoto et al., 2016) more than strangers, accordingly playing a preeminent role in social cognition (Smith and Mackie, 2016). Notwithstanding this limitation, the present behavioral findings provide further proof of the remarkable ubiquity of social facilitation across situations and ages. First, they show that the social facilitation of numerosity and phonological comparisons seen earlier in the actual presence of a coactor (Tricoche et al., 2021) is also triggered by in-scanner remote (via video) and sporadic (every other 4-trial block) live observation. Second, they show that 10 to 13-year-olds are as sensitive to social facilitation as adults, as were 8 to 10-year-olds in our previous study (Tricoche et al., 2021).

Across the two studies, the behavioral changes produced by the presence of, or observation by a peer amounted to small- to medium-size effects in children (Cohen's d : 0.14 to 0.61), not quite matching, but closely approaching those observed in adults (Cohen's d : 0.21

to 0.73). Another similarity between children and adults is that current in-scanner subjects performed better than subjects in our previous behavior-only study (Tricoche et al., 2021). Their RTs were systematically (regardless of age or condition) about 200 ms shorter. Their social facilitation concerned both accuracy and speed, rather than speed only, as we found earlier (Tricoche et al., 2021) along most other social facilitation studies of well-mastered skills (Bond, 1983). More anxiogenic than behavior-only, fMRI scanning tends to attract the more confident / less anxious individuals among research volunteers, thus potentially fostering sampling biases (Charpentier et al., 2021). An over-representation of high-performers in the current sample could explain subjects' faster responses and atypical social facilitation of accuracy. Being observed improved current children's accuracy in the easier task (numerosity comparisons) and current adults' accuracy in the harder task (phonological comparisons), as if some extra-competitiveness led each age group to favor the task that offered them the most room for improvement and chance for success.

Testing numerical and phonological comparisons in adolescents is now needed so as to unveil the full developmental trajectory of peer presence effects on these education-related skills. Being observed by a peer induces more self-conscious emotions and greater autonomic arousal in adolescents than in children and adults (Somerville et al., 2013), and adolescence is generally viewed as the period of life with the highest susceptibility to peer influence (Albert et al., 2013). Greater social facilitation of numerical and phonological comparisons in adolescence would indicate that peers' influence on education-related skills follow the same inverted U-shaped trajectory as that reported for peers' influence on reward-related behaviors (Telzer, 2016).

4.2. Lack of evidence in favor of an involvement of task-specific brain substrates in peer presence effects

As detailed in the Introduction, previous studies did describe neural changes in others' presence in the very brain areas underlying the task at hand (Dumontheil et al., 2016; Yoshie et al., 2016). In addition, the changes driven by peer presence in the ventral striatum, orbitofrontal cortex, and amygdala during risk-taking in adolescents can be viewed as a social modulation of the brain areas specialized in processing rewards and emotions (Chein et al., 2011; Van Hoorn et al., 2016; Hoffmann et al., 2018). Yet, as most of these studies rested their conclusions on a single task, proofs of truly task-selective changes (occurring for one task but not the other) were still needed. The present study addressed this issue by using two tasks, respectively dependent on the brain numerical- and language-related areas. The regions selectively engaged by each task were consistent with earlier children's and adults' fMRI data collected with the same tasks (Prado et al., 2011; Prado et al., 2014), including, in particular, the right parietal IPS/SPS region for numerosity comparisons, and the left IFG region for phono-

logical comparisons. Frequentist and Bayesian analyses both failed to find a reliable influence of peer observation on activity in task-specific regions. The former identified a marginal effect of observation without any interaction with other factors; the latter provided, moderate evidence in favor of the null hypothesis. So, at the very best, observation yielded a weak homogenous change in all task-specific networks, irrespective of the task and regardless of age. In other words, there was little evidence of observation-driven changes in the regions that we identified as task-specific substrates, and no evidence of truly task-selective changes to support the task-specific neural account of peer presence effects. Caution is required, however, in interpreting these negative findings. There is evidence from single-cell recordings that the primate brain harbors intertwined populations of "asocial" and "social" neurons in different brain areas. In the monkey dorsolateral prefrontal cortex, the very same task events are coded by duplicate sets of neurons: one firing when the monkey is alone, the other firing when a congener is present (Demolliens et al., 2017). In the human dorsomedial prefrontal cortex, true and false beliefs are coded by two distinct neuronal populations, one selective for our own beliefs, the other for others' beliefs (Jamali et al., 2021). The local population of neurons responsible for the BOLD response being invisible to fMRI, the relative lack of evidence in support of the task-specific account of peer presence effects, including the present negative findings, might stem from limitations inherent to neuroimaging.

4.3. Evidence for the involvement of three domain-general (mentalizing, attention, and motivation) networks in peer observation effects

The present study provides, by contrast, compelling evidence in support of a domain-general neural account of peer presence effects in humans. The observation-driven changes shared across tasks and ages involved i) the right and left TPJ, a region thought to serve as a hub integrating mentalizing and higher-order attentional control (Patel et al., 2019), together with ii) three regions known for their involvement in mentalizing: the mPFC, Prec/PCC, and left MTG (Fehlbaum et al., 2021), and iii) three regions known for their contribution to higher-order attentional control: the left IFG, MCC, and left and right PreG/FEF (Dosenbach et al., 2006). Observation-driven changes in the Prec/PCC cluster extended into the visual areas of the medial occipital cortex, perhaps due to our use of the peer's picture to signal observed trials. The only other observation-driven changes shared across tasks and ages was found in the VS, a major node of the brain reward-based motivation system (Haber and Knutson, 2010). In the mPFC, Prec/PCC, left MTG, and right and left TPJ, the associated beta values were negative during unobserved trials relative to the fixation baseline, and peer observation lessened this deactivation. This agrees with the fact that these four nodes of the mentalizing network overlap with the default mode network (DMN), whose trademark is to be deactivated during cognitive tasks, presumably to quiet our "default" flow of self-generated thoughts (Li et al., 2014; Amft et al., 2015; Hyatt et al., 2015; R.B. Mars et al., 2012). The magnitude of such task-induced deactivations tends to increase with task demands, suggesting that DMN deactivation contributes to successful task performance via an efficient reallocation of processing resources from "default" to task-relevant processes (Daselaar et al., 2004). Lessening the magnitude of DMN deactivation necessary to achieve successful task performance could thus be one of the neural mechanisms contributing to social facilitation under peer observation. Attention studies have established that when task demands are too low, the brain becomes vulnerable to task-irrelevant stimuli; increasing task demands, in this case, improves performance by reducing or even eliminating the brain response to distractors (Lavie, 2010). Peer presence during easy tasks such as numerosity and phonological comparisons might likewise capture the resources that are left unused by the task, and dedicate them to the observer (e.g. to thoughts about her/his opinion of our performance), thereby protecting the brain from any other task-interfering distraction.

As a corollary, task-relevant stimuli might be more efficiently processed. Consistent with this hypothesis, peer observation increased activation in the dorsal frontal gyrus along the precentral sulcus, near or at the FEF, as well as in the IFG, two key nodes contributing to attentional control, usually with a predominant role of the right hemisphere (Corbetta et al., 2008). Here, the increase concerned predominantly the left hemisphere, whose role has been less investigated. One previous study, however, showed that the left FEF and IFG form, together with the left TPJ, a pathway by which a salient contextual (task-irrelevant) cue can be translated into an attentional control signal that facilitates performance in a simple target detection task (DiQuattro and Geng, 2011). The engagement of the left FEF-IFG-TPJ pathway in the present study could reflect a similar beneficial effect of the (task-irrelevant) observer's presence on simple responses. The increase in activation observed in a MCC cluster (extending dorsally into the SMA) might concur to improve attentional control as the MCC has been postulated as a hub implementing the higher-order attentional processes necessary for the online monitoring of responses (Procyk et al., 2016), both our own and others' (Apps et al., 2013). Increasing the attentional resources dedicated to task-related information could thus be a second neural mechanism contributing to social facilitation under peer observation. Still another mechanism could be a modulation of affective valuation via the VS. Increased activity in the VS has been associated with enhanced positive valuation in others' presence of, e.g., risk taking in adolescents (Albert et al., 2013), or monetary gain in adults (Fareri et al., 2012). In the present study, no feedback was provided to participants about their accuracy and no reward (praise or money) was given for correct responses. The VS increase in activation under peer observation might therefore reflect an enhancement of the reward intrinsic to live social interactions (Pfeiffer et al., 2014).

4.4. Teasing apart observation-driven neural changes responsible for the facilitation of performance from those merely coding the social context

We start out in life as altercentric infants privileging others' perspectives over their own (Southgate, 2020). As adults, we are, without being aware of it, under the influence of others' viewpoints that are totally irrelevant to our goals (Smith and Mackie, 2016; Steinmetz and Pfattheicher, 2017). With limited brain resources, such compulsory processing of others' perspectives can but force the brain to reshape its resource allocation in social contexts. This includes attention and valuation sharing between task and observer, as well as cognition sharing between task-dedicated and DMN networks. A whole-brain resource reshuffling could explain why even the most minimalist social contexts, with no discernible behavioral consequence, nevertheless generate widespread neural changes (Iacoboni et al., 2004; Rice and Redcay, 2016). It complicates, however, data interpretation when the social context does modify behavior. Here, as in at least one other human study (Beyer et al., 2018), behavior improved, making it difficult to tease apart the neural responses underlying the mere detection of another's presence from those actually facilitating performance by enhancing the fluency of task-related decisions and actions. In the earlier social facilitation study by Beyer and colleagues (Beyer et al., 2018), subjects had to stop inflating a balloon as late as possible before it burst in order to avoid heavy losses. The presence of a passive second player improved performance in this high-cost game (reducing participants' losses by about 35% compared to solo playing) and led to activity changes in the very same mentalizing/DMN nodes (TPJ, precuneus, and MFG) as the presence of a passive peer in the present counting and reading tasks. Engagement of these mentalizing/DMN nodes may therefore reflect the mere detection of another's presence across tasks and environments.

Here, social facilitation took mainly the form of faster numerosity comparisons. We showed earlier (Tricoche et al., 2021) that, in both children and adults, this RT improvement is made possible by a strategy shift towards anticipatory guesses (subjects preselect a response during the presentation of the first stimulus so as to answer faster at the onset of the second stimulus). Whole-brain analyses revealed two neural

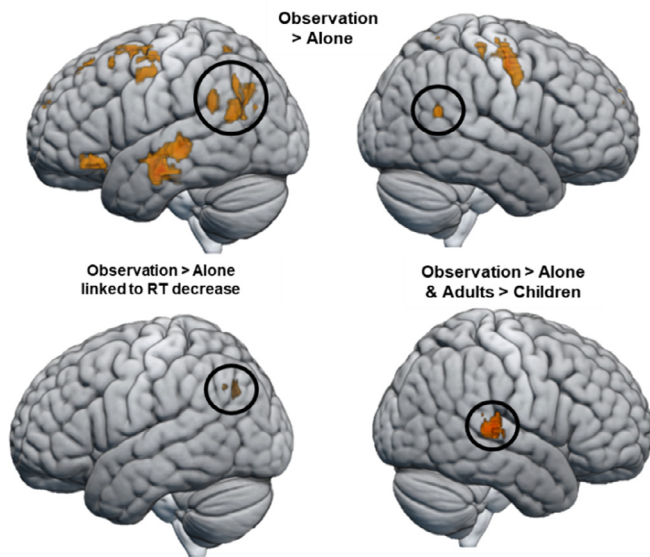


Fig. 6. Overview of the distinct task-independent neural changes in the region of the temporoparietal junction (circled regions) characterizing observed relative to unobserved trials: the bilateral ones including pTPJ common to children and adults (Observation > Alone), the right one in aTPJ specific to adults (Observation > Alone & Adults > children), and the left one with a trialwise link to observation-driven speedup of behavioral responses in dTPJ (Observation > Alone linked to RT decrease).

changes with a potential link with this specific performance improvement. One change was located in the MCC. It showed an increase of activation under observation that was greater for speeded-up numerosity comparisons than non-speeded-up phonological comparisons. MCC neurons are thought to possess the capacity, possibly unique among frontal regions, of monitoring information over long periods of time and large numbers of trials, so as to signal any need for a change in strategy (Procyk et al., 2021). This singularity could explain why MCC was involved in the present observation-driven RT improvement, which depended on an adaptive change of response strategy.

The second neural change with a link to behavior (Fig. 5) was located in the ventral part of the left angular gyrus $[-46 -60 30]$, also identified as the dorsal portion of TPJ (Igelström et al., 2015). Within the domain of arithmetic, the left angular/dTPJ region $[-54, -61, 36]$ is associated with fast problem solving using already known answers stored in memory, and is opposed to the frontoparietal network underlying slower calculation-based arithmetic strategies (Sokolowski et al., 2023). In the domain of therapeutics, transcranial magnetic stimulation of the left angular/dTPJ region $[-45, -67, 38]$ improves both language and memory in patients suffering from mild cognitive impairment or Alzheimer's disease (Chen et al., 2023). Here, trialwise reactivity to peer observation in a left angular/dTPJ cluster $[-46 -60 30]$ was negatively related to reaction time during numerosity comparisons, the greater the observation-driven neural change, the faster the behavioral response. Beyer and colleagues (Beyer et al., 2018) also found a left angular cluster $[-36 -69 45]$ whose trial-by-trial activity was negatively linked to reaction time. In their case, the greater the activity in this left cluster, the less responsible the subjects felt for the outcome of their action, and the better their strategic management of the balloon inflation rate. In this earlier study, the angular/dTPJ cluster whose activity was linked to behavior improvement was distinct from the aTPJ cluster whose activity was associated with social presence. Such was the case also in the present adults.

As recapitulated in Fig. 6, the TPJ region actually harbored several distinct task-independent observation-driven changes: a bilateral one common to children and adults in pTPJ, a right one specific to adults in

aTPJ, and a left one, also common to children and adults, linked to behavior; in dTPJ. TPJ is an approximate term used to design a large brain hub involved in attention, memory, and social cognition (Ahmad et al., 2021). Its anatomical parcellation is a matter of ongoing research and whether its subdivisions subserve a single core computation or separate functions remains debated (R.B. Mars et al., 2012; Igelström et al., 2015). The distinct clusters observed here do support the latter hypothesis. Note, however, that our allocating the bilateral cluster $[56 -50 16 \text{ \& } -46 -48 30]$ to pTPJ, the right cluster $[58 -26 10]$ to aTPJ, and the left cluster $[-46 -60 30]$ to dTPJ is but a tentative proposal to be reassessed as our knowledge about TPJ heterogeneity advances.

4.5. A similar neural signature in children and adults in mentalizing and motivation but not attention regions

Identifying child-adult similarities and dissimilarities is always a challenge. Development is known for its "noisiness" making children's behavior more variable and their neural networks less functionally specialized than adults' (Richardson et al., 2018). In addition, neural responses to cognitive tasks are attenuated in children who show both weaker task-evoked activation and less pronounced DMN deactivation than adults (Chen et al., 2022). We addressed this challenge here with a combination of whole-brain and ROI-based analyses using both frequentist and Bayesian statistics.

The whole-brain conjunction analysis identified the Prec/PCC as the region presenting a robust observation-driven change shared by children and adults. It consisted in a marked deactivation in unobserved trials that was reduced by observation (Supplementary Result 2B). The Prec/PCC is a core mentalizing node (Schurz et al., 2014). It stands out, in addition, as a unique hub distinguishing between task and rest states in both the developing and mature human brain (Li et al., 2019). Its engagement in the present 10 to 13-year-olds is in agreement with previous findings demonstrating that precuneal mentalizing and DMN networks are already present and functional by the time children reach school age (Li et al., 2019). By contrast, the whole-brain Age x Condition interaction analysis identified a cluster within the right aTPJ as the region whose observation-driven change reliably differed between children and adults (Fig. 6). Only adults showed a deactivation during unobserved trials that diminished during observed trials. Both changes were absent in children (Supplementary Result 2B). The lack of aTPJ engagement in the present 10 to 13-year-olds is in agreement with previous findings demonstrating the gradual development of TPJ over adolescence in parallel with the late refinement of human perspective-taking abilities (Crone and Dahl, 2012). Attention and social cognition are tightly intertwined functions during development, early attentional capacities predicting later social cognition abilities (Mundy and Newell, 2013). The rTPJ has been associated with many aspects of social functions (Ahmad et al., 2021). pTPJ, its posterior portion, is thought to be exclusively dedicated to social cognition, especially mentalizing, whereas aTPJ, its anterior portion, is thought to contribute to both attention and social cognition by shifting attention across either stimuli or mental states (R.B. Mars et al., 2012; Krall et al., 2015). The right cluster identified here as specific to adults $[58 -26 10]$ seemed to more closely correspond to attention-shifting aTPJ.

The above findings suggest that, despite the undistinguishable behavioral effects of peer presence observed over age here and earlier (Tricoche et al., 2021), neural observation-driven changes exhibit both common and distinct features in children and adults. We gained further evidence in favor of this hypothesis using Bayesian statistics quantifying child-adult similarities and dissimilarities in nine mentalizing-related ROIs (Precuneus, pPCC, two dmPFC clusters, right and left TPJ-STG and MTG, right MFG), three motivation-related ROIs (aPCC, MFC, right VS), and seven attention-related ROIs (ACC/MCC, right and left aTPJ and IFJ-FEF, right AI and left IPS/IPL). We found strong to extreme evidence for an Age influence on activity in all three networks in line with children's known weaker activation and less pronounced

deactivation relative to adults (Chen et al., 2022). Notwithstanding this amplitude lag, strong to extreme evidence for a Condition effect indicated that, peer observation did exert an overall influence on activity in all three networks. Quantifying evidence for or against a Condition x Age interaction identified distinct and common observation-driven neural changes in children and adults. Anecdotal to moderate evidence of a lack of Condition x Age interaction generalized the child-adult neural resemblance described above in the Prec/PCC mentalizing node to the entire mentalizing and motivation networks. Likewise, strong evidence in favor of a Condition x Age interaction extended the age-related difference obtained above for the right aTPJ to all attention nodes. This developmental heterogeneity is reminiscent of that recently reported using a working memory task whose neural bases reach maturity earlier in default mode regions than in fronto-parietal regions (Chen et al., 2022). The present findings might reflect a similar asynchrony where default mode and motivation regions provide a scaffold for an immature cognitive network to support peer presence effects during development.

4.6. Limitations

Because we selected two tasks that are facilitated by peer presence, our conclusions apply only to social facilitation. Future studies should thus use a task mixing facilitated and inhibited trials to compare the neural signatures of the two directions of peer presence effects, i.e., to identify the changes that predicts the direction of the behavioral outcome.

The second limitation concerns our sample size of 47 participants. It provided sufficient power to detect behavioral effects and brain activity modulations due to peer presence. However, methodological challenges inherent to child neuroimaging studies (variability of brain activity and propensity to move), which led to our discarding 9 children (compared to 1 adult) and reduced our final sample size to 24 children, might have hampered our ability to detect statistically robust neural changes in the children group. Also, our study was designed to compare groups and conditions and explore trialwise intra-individual brain-behavior links. It was not adequately powered to conduct brain-behavior correlations at the inter-individual level, which require larger sample sizes (Marek et al., 2022).

5. Conclusions

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

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Declaration of Competing Interest

The authors declare no competing interest.

Credit authorship contribution statement

Leslie Tricoche: Investigation, Formal analysis, Writing – review & editing. **Denis Péllisson:** Conceptualization, Writing – review & editing. **Léa Longo:** Investigation. **Eric Koun:** Investigation. **Alice Poisson:** Investigation. **Jérôme Prado:** Conceptualization, Formal analysis, Funding acquisition, Writing – review & editing. **Martine Meunier:** Conceptualization, Formal analysis, Funding acquisition, Writing – review & editing.

Data availability

Data supporting the results will be available on the Open Science Framework website at <https://osf.io/nspkx/>.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:[10.1016/j.neuroimage.2023.120247](https://doi.org/10.1016/j.neuroimage.2023.120247).

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