

Brief Report

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Brief Report

Me, Myself, and I: Neural Activity for Self versus Other across Development

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Abstract: Although adults and children differ in self-versus-other perception, the developmental perspective on this discriminative ability is missing. We compared neural activation of self-vs-others in 39 participants of 4 different age groups (4 yo. to adulthood). Two brain regions, the MCC and right postcentral gyrus, exhibited respectively non-linear and gradual gains in discriminative abilities for self-vs-others stimuli. These regions play critical roles in self-referential processing, empathy, and social cognition. Nine brain regions showed linear increase for others-vs-self stimuli. These regions are associated with multisensory processing, somatosensory skills, complex visual stimuli, self-awareness, empathy, theory of mind, and social recognition. Understanding the neural basis of self-vs-others discrimination during development can inform when and how social contexts support learning processes during childhood and adolescence.

Keywords: self-versus-other perception; social cognition; development of neural activity; social processing

Introduction

“Is that my idea or yours?” From playgrounds to boardrooms, the ability to form an accurate self-vs-other representation enables individuals to navigate social interactions by understanding their own thoughts, feelings, and intentions as distinct from others (Ruby & Decety, 2004). It affects the capacity to embrace others’ perspectives and feelings in a non-centered manner and use this information to bind constructive social interactions (Lang & Reschke, 2006). Indeed, our ability to discriminate self from others helps us navigate complex social environments using adequately social cues (Young, 2008) to effectively form and maintain positive relationships (i.e., friendships, romantic partnerships, and professional networks) (Frith, 2008). Impaired discriminative skills across development impact social cognition, from recognizing oneself in the mirror to interpreting the intentions and emotions of others (Berlim De Mello et al., 2023). Given the importance of well-developed self-vs-others discriminative skills, it seems important to unveil underlying brain activations across development, to gain an understanding of needs and capacities at different stages of life. While different studies shed light on either behavioral or neuroimaging markers of this discriminative ability at different ages or by contrasting adults with young children, none report a cross-sectional perspective on the neural activity across development.

The development of self versus other representations is a complex process, influenced by different factors, including genetics, brain maturation, and environmental experiences (Bahrick, 2008; Falk et al., 2020). During the first year of life already, the ability to distinguish the self from the environment and from others starts emerging, at the physical level (Butterworth, 1992). In fact, babies develop their sensorimotor ability while experiencing different perceptual and sensorimotor events, such as self-produced sounds or touching their own faces and bodies. These events contribute to uniquely specifying and separating their own body as differentiated entities from the environment

(Rochat, 1998). Then, discriminative abilities become more abstract. Infants, as young as 20-24 months old, have been shown to display self-recognition in mirror tasks (i.e., touch their own forehead and not their reflection). More interestingly, this ability comes along with the ability to discriminate their own reflection as distinct from other objects or people (Amsterdam, 1972; Platek et al., 2004). As they develop, their brain elaborates increasing preciseness and stability in behavior (Lippé et al., 2009; Posner et al., 2007), while sophisticating their self-concepts, incorporating beliefs and attitudes about their own abilities, personality traits, and social identities (Northoff et al., 2006). At the same time, their understanding of others gives them the ability to recognize others as intentional agents and to take another person's perspective and empathize with them (Decety & Jackson, 2004).

While little is known about the school years' age, more studies have shown that adolescence is a particularly important period for the development of self-vs-others' representations, with significant changes in social and emotional abilities, reflected in new relationships and social roles. In fact, adolescents' brains undergo significant changes during this period, notably in regions involved in social cognition and emotion regulation (i.e., the posterior superior temporal sulcus and the medial prefrontal cortex) (Blakemore, 2008). The development of self-vs-other representations continues to evolve throughout adulthood. The cognitive and emotional processes may change as people age, affecting their ability to understand and adapt to social interactions (Lang & Reschke, 2006).

While there is a gradual gain in social cognitive processing, a deeper understanding of self-vs-others discrimination across the development could shed light on differences in social needs and improve the social dimension of learning environments (e.g., when is peer learning a good strategy?). Indeed, the quality of early social experiences is critical and predictive of the development of self and other representations (Beebe & Lachmann, 2003; Brumariu, 2015). Providing adequate social feedback may help shape emotion recognition and regulation as they develop social skills such as empathy and perspective-taking (Brumariu, 2015).

This study aimed at exploring age-related brain activity differences in the processing of self-vs-others. Overall, we hypothesized increased brain activity associated with self-perception across development in brain regions that have been associated with self-recognition in adults. These regions are located in the frontal, parietal, and occipital areas (Devue & Brédart, 2011), as well as the ACC, and the posterior cingulate cortex (PCC) (Araujo et al., 2013; Hu et al., 2016c; Murray et al., 2012; Qin & Northoff, 2011). Conversely, we expected increased brain activity when observing someone else in the precuneus, and the angular gyrus, as these regions are activated when looking at others more than oneself (Asakage & Nakano, 2022; Farrer & Frith, 2002). Finally, we also expected higher activity for other than self within the temporal cortex and brain regions involved in the recognition of visual stimuli, previously associated with early identification of humans and human movement (Jastorff & Orban, 2009).

While an overall linear increase in activity is expected across development, non-linear changes are more likely to happen in middle age children (7-10 y.o.) as well as in teenagers (11-19 y.o.). In fact, previous research has shown that brain maturation and connectivity development have both linear and non-linear trajectories. Social cognitive processing is known to follow a non-linear developmental trajectory across the middle age children (Faghiri et al., 2019). In addition, the teenage years are known to be a time window for self-related information (Pfeifer & Berkman, 2018), so we predicted a shift in the pattern of activation for the representation of others.

Method

Participants

In total, 42 healthy participants were recruited for the experiment. Three participants were excluded due to poor MR image quality given by excessive movement, leaving a sample of 39 participants for the final analyses (mean age = 13.54, SD = 8.00). The inclusion criteria were to be healthy and be in the compatible age range studied. The participants were separated into 4 different groups, according to their age: (a) from 4.1 to 6.5 years old, (b) from 7 to 10.5 years old, (c) from 11 to

19 years old, and (d) from 20 years old for the adults (see Table 1). The study was approved by the ethics committee and written and oral informed consent for the course of the experiment was obtained from the participants or their parents (<14 y.o.).

Table 1. Demographics.

Control variable	4.1 to 6.5 y.o. (n = 9)	7 to 10.5 y.o. (n = 10)	11 to 19 y.o. (n = 10)	>20 y.o. (n = 10)	Overall (n = 39)
Age mean (SD)	5.30 (0.73)	7.52 (1.07)	15.85 (2.37)	24.67 (2.75)	13.54 (8.00)
Age min, max	4.10, 6.40	6.60, 9.70	11.90, 19.80	21.17, 31.00	4.10, 31.00
Gender ratio (f/m)	6/4	4/6	5/5	6/4	21/19

fMRI video task

Each participant was initially asked to execute four different movements in front of a camera: hiding their eyes with their hands, turning on themselves, smiling, and plugging their nose (Figure 1a) for ~7-second recordings. These personalized stimuli were then introduced in the fMRI video task, randomly intertwined with similar stimuli from a same-age and same-gender unknown actor. The final fMRI video task was composed of 12 video clips of the four different movements; half performed by the participant, and half performed by the unknown actor. The video clips of the different movements were presented in random order, with at least one presentation of each, and four were randomly presented twice. The 12 video clips of ~7 seconds were separated into 4 parts of 3 video clips with breaks of 20 seconds in between. In total, the video lasted 160 seconds (Figure 1b).

Procedure

Participants were placed in the scanner and asked to simply watch the fMRI video task.

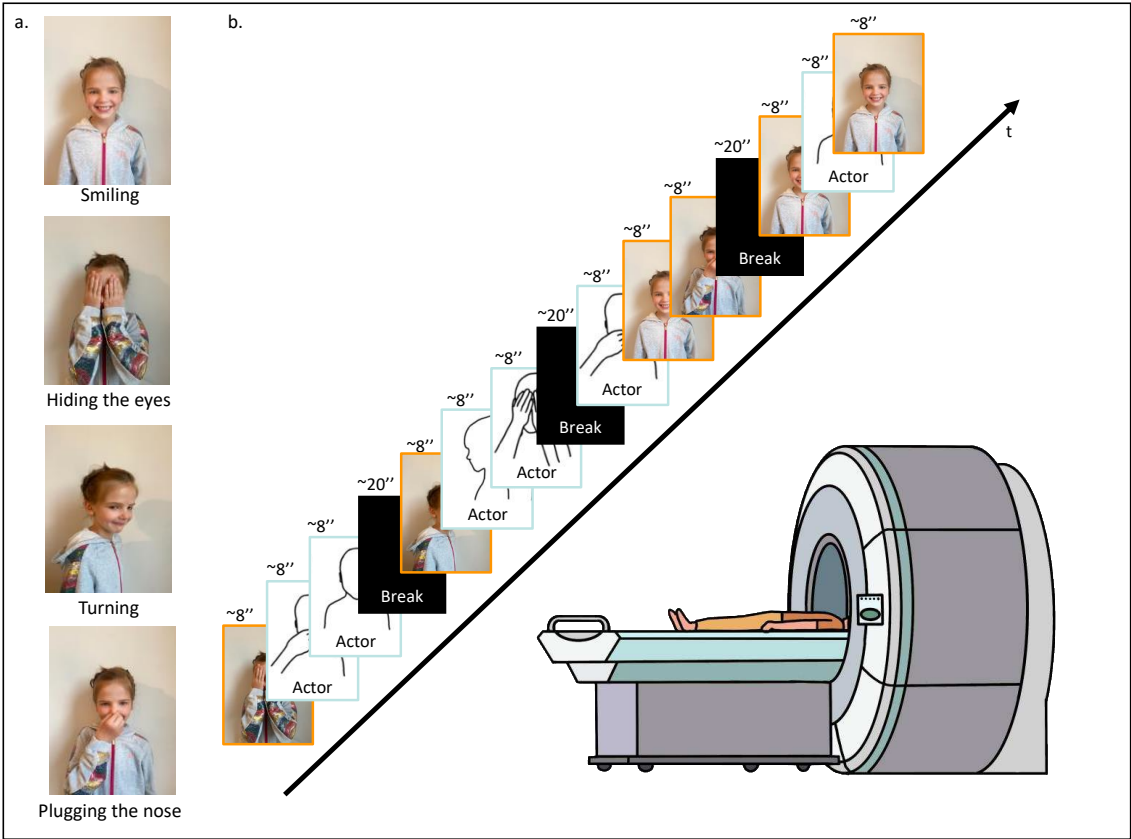


Figure 1. fMRI task design. (a) First, the participant was asked to execute four different movements in front of a camera: hiding their eyes with their hands, turning on themselves, smiling, and plugging their nose. (b) Second, while being placed in the scanner, the participant was asked to watch the video-

based fMRI task; 12 video clips randomly arranged displaying the four different movements performed by the participant or a same-age and same-gender unknown actor.

MRI data acquisition

Anatomical and functional images were collected using a Siemens (Siemens Healthineers, Erlangen, Germany, VE11E Software version) 3T Prisma-Fit MR scanner with a 64-channel head coil at the Lausanne University Hospital. MRI sessions were conducted with two different acquisitions for each subject: (i) 3-dimensional T1 weighted MP-RAGE (Magnetization Prepared - Rapid Gradient Echo) (TR = 2000 ms, TE = 2.47 ms, 208 slices; voxel size=1×1×1 mm³, flip angle=8°), used as an anatomical reference for brain extraction and surface reconstruction, and (ii) a functional MRI (fMRI) acquired continuously using a standard echo-planar gradient echo sequence, with simultaneous multislice (SMS) imaging technique. This technique allows to cover the whole brain with an isotropic voxel size of 2 mm ([TR] = 1000 ms; echo time [TE] = 30 ms; 64 axial slices; slice thickness = 2 mm, no gap between slices, flip angle = 80°, matrix size = 100 × 100, a field of view [FOV] = 200 mm, SMS factor = 4, parallel imaging acceleration factor = 2). The total fMRI acquisition time was 3 min and 12 seconds.

To prevent head movement and noise, foam pads were placed around the participants' heads inside the coil.

MRI data processing

MRI data were preprocessed using SPM12 software (Wellcome Department of Cognitive Neurology, London, UK), run on Matlab (Mathworks, Natick, MA, USA Version 7.13). To correct the motion of the functional images, the first scan was used as a reference, using a 6-parameter rigid-body realignment. The realigned images were then slice-timing corrected, and both the functional images and the high-resolution T1-weighted (T1w) anatomical image of the participant were co-registered, using mutual information. Using the anatomical images as an estimation basis, functional images were normalized to the MNI template and spatially smoothed using an 8-mm Gaussian filter.

Data visualization and figure preparation were done using the xjView Toolbox for SPM (<http://www.alivelearn.net/xjview>). An aal atlas was used to label and describe anatomical locations (Rolls et al., 2020).

Neural activation analyses

In statistical single-subject analysis, performed by applying a general linear model, neural activities while watching self-vs-other perception stimuli were retrieved; onsets were video clips' starting times, and durations were the 7 seconds of the video clips. The realignment parameters were included in the model as a nuisance variable. A frequency threshold of 121 Hz was used as a high pass filter cutoff to filter the amplitude of signals, allowing the removal of the low-frequency noise or interference. A visual inspection of estimated motion parameters was conducted for each participant. Several recording images of 4 participants were excluded according to the artifact repair procedure performed with ArtRepair (Mazaika et al., 2009). Statistical inference from the acquired group was performed using the first-level contrasts of interest as input values. First, a mixed model ANOVA was performed with, as intra-subject variables, the contrasts representing brain activity during perception of self and other (2 levels) at the whole-brain level across age groups as inter-subject variables (four levels). A threshold of $p < 0.05$ (FDR corrected) was used for the selection of the significant clusters. In order to investigate and reveal the effect of self-vs-other perception between the different age groups, we performed a post-hoc comparison using paired t-tests on BOLD signal changes extracted from significant clusters. The paired t-tests were conducted to compare the activation of the brain region during self-vs-other perception, between age groups.

Results

Neural activation analyses

First, the positive effect of condition (self-vs-other) revealed regions that show significant increases in their involvement in the processing of self-vs-other stimuli independently from the age group. These regions included the midcingulate cortex (MCC) and the right postcentral gyrus. The opposite contrast (other-vs-self) revealed regions that show significant increases in their involvement in the processing of other-vs-self stimuli independently from the age group. These regions included the right angular gyrus, left angular gyrus, right inferior temporal gyrus, left middle temporal gyrus, right rectus, right precuneus, right medial prefrontal cortex, right superior frontal gyrus, and left inferior orbital gyrus (see details in Table 2).

Second, the post-hoc paired t-test analyses revealed between which age groups the activation for self-perceptions, compared to the perception of others, were statistically different. For the MCC, discrimination of self-vs-other perception was true for all age groups, while not for the 7-10 y.o. group. For the right postcentral gyrus, self-vs-other perception differed for all age groups, while not for the 4-6.5 y.o. group (Table 3, Figure 2).

For the reverse contrast (i.e., higher activation while looking at others than oneself), developmental differences were also observed thanks to the paired t-tests. For the: right angular gyrus; left angular gyrus; right inferior temporal gyrus; right rectus; right precuneus; and right medial prefrontal cortex brain regions, discrimination between others and self increased with age starting at 7 y.o. (see details in Table 4). For the left middle temporal gyrus, neural activities significantly differed for all between others and self-presentations, except for the 7-10 y.o. group. Within the right superior frontal gyrus, neural activities significantly differed between self-vs-other perception from teenage years (i.e., > 11 y.o.). Finally, for the left inferior orbital gyrus, other versus self-discrimination was true for all, but not for the 11-19 y.o. group (see details in Table 4, Figure 3).

Table 2. Results of the ANOVA.

Localization	Coordinates (mm mm mm)			T	k _E	qFDR-corr
Self > Other						
Midcingulate cortex	00	12	32	5.28	273	0.001
Right postcentral gyrus	58	-22	32	4.60	414	0.001
Other > Self						
Right angular gyrus	42	-60	36	5.04	828	0.000
Left angular gyrus	-44	-68	48	4.96	504	0.000
Right inferior temporal gyrus	60	-10	-28	4.65	299	0.003
Left middle temporal gyrus	-62	-16	-24	4.77	452	0.000
Right rectus	04	38	-20	5.17	199	0.012
Right precuneus	04	-62	36	4.38	259	0.005
Right medial frontal gyrus	52	32	38	4.77	221	0.008
Right superior frontal gyrus	18	34	54	5.00	248	0.006
Left inferior orbital gyrus	-46	44	-10	5.11	136	0.046

Table 3. Higher activation for self-perceptions compared to others.

Brain region	4-6.5 y.o.	7-10 y.o.	11-19 y.o.	>20 y.o.
Midcingulate cortex	T(8) = 2.58, <i>p</i> = 0.016	T(9) = 0.775, <i>p</i> = 0.229	T(9) = 2.63, <i>p</i> = 0.014	T(9) = 3.40, <i>p</i> = 0.004
Right postcentral gyrus	T(8) = 0.22, <i>p</i> = 0.416	T(9) = 2.60, <i>p</i> = 0.014	T(9) = 2.18, <i>p</i> = 0.029	T(9) = 4.18, <i>p</i> = 0.001

Table 4. Higher activation for perceptions of other compared to self.

Brain region	4-6.5 y.o.	7-10 y.o.	11-19 y.o.	>20 y.o.
Right angular gyrus	T(8) = -0.58, <i>p</i> = 0.288	T(9) = -1.86, <i>p</i> = 0.021	T(9) = -2.36, <i>p</i> = 0.021	T(9) = -4.57, <i>p</i> < 0.001
Left angular gyrus	T(8) = -1.02, <i>p</i> = 0.169	T(9) = -1.84, <i>p</i> = 0.050	T(9) = -3.07, <i>p</i> = 0.007	T(9) = -4.90, <i>p</i> < 0.001
Right inferior temporal gyrus	T(8) = -1.31, <i>p</i> = 0.113	T(9) = -2.30, <i>p</i> = 0.024	T(9) = -4.05, <i>p</i> = 0.001	T(9) = -4.90, <i>p</i> < 0.001
Left middle temporal gyrus	T(8) = -1.97, <i>p</i> = 0.042	T(9) = -1.77, <i>p</i> = 0.055	T(9) = -3.00, <i>p</i> = 0.007	T(9) = -4.59, <i>p</i> < 0.001
Right rectus	T(8) = -1.46, <i>p</i> = 0.091	T(9) = -2.21, <i>p</i> = 0.027	T(9) = -4.45, <i>p</i> < 0.001	T(9) = -3.34, <i>p</i> = 0.004
Right precuneus	T(8) = -0.54, <i>p</i> = 0.301	T(9) = -2.14, <i>p</i> = 0.030	T(9) = -2.99, <i>p</i> = 0.008	T(9) = -2.74, <i>p</i> = 0.011
Right medial prefrontal cortex	T(8) = -1.33, <i>p</i> = 0.110	T(9) = -2.32, <i>p</i> = 0.023	T(9) = -2.04, <i>p</i> = 0.036	T(9) = -4.34, <i>p</i> < 0.001
Right superior frontal gyrus	T(8) = -0.17, <i>p</i> = 0.433	T(9) = -1.66, <i>p</i> = 0.065	T(9) = -2.02, <i>p</i> = 0.037	T(9) = -7.91, <i>p</i> < 0.001
Left inferior orbital gyrus	T(8) = -1.86, <i>p</i> = 0.050	T(9) = -2.23, <i>p</i> = 0.026	T(9) = -1.50, <i>p</i> = 0.084	T(9) = -4.93, <i>p</i> < 0.001

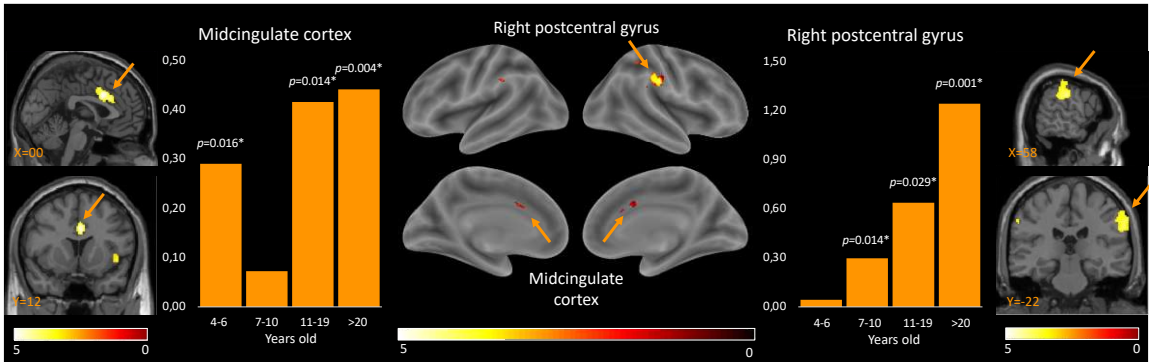


Figure 2. Results of the paired t-test analyses between the 4 different age groups, and the brain location for the self-perceptions.

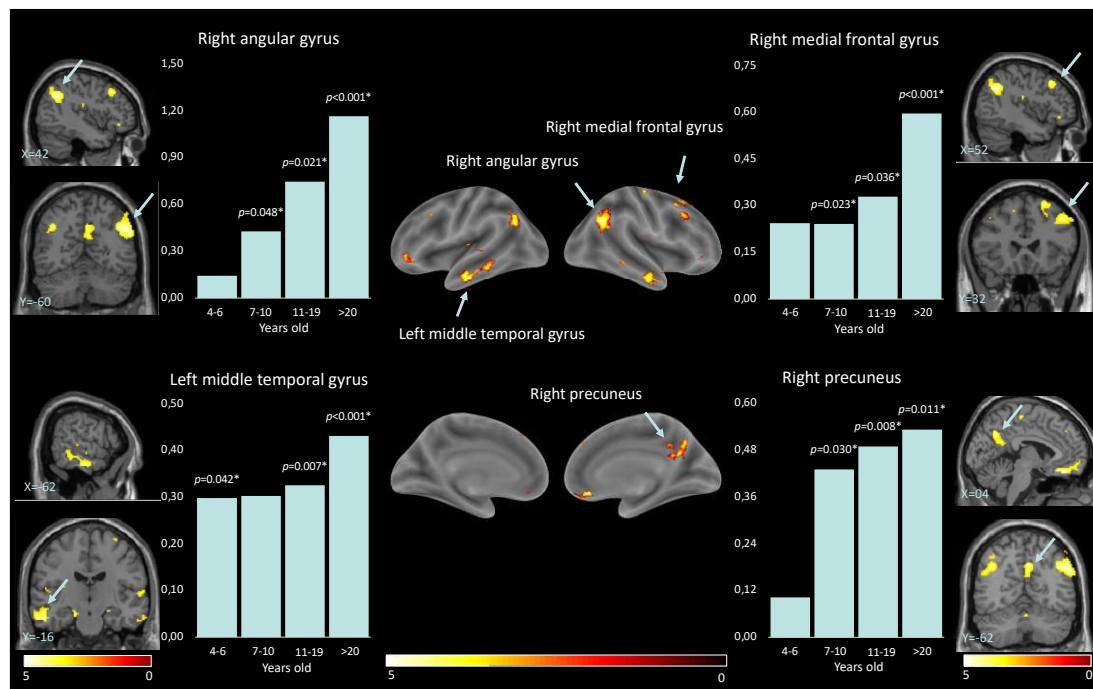


Figure 3. Results of the paired t-test analyses between the 4 different age groups, and the brain location for the perception of others.

Discussion

Human beings are inherently social and cooperation is essential for good life conditions. Consequently, we constantly read others' actions, gestures, and faces, relying on the core capacity to discriminate self-vs-others. Unveiling the emergence of self-vs-others' discrimination at the neural level across the development could reveal differences in social needs and help adapt learning environments, for example. To this end, we compared brain activity during self-vs-other stimuli, revealing a total of 11 brain regions whose activation maps significantly differ as a function of age groups.

First, two brain regions showed higher activation for the self than for the other across development; the MCC and the right postcentral gyrus. According to past work, the MCC is involved in a wide range of social cognitive processes (Lou et al., 2004), including self-referential processing (Denny et al., 2012) and empathy (Fan et al., 2011). Moreover, the MCC is a key node in both the salience network and the social brain, two networks closely interconnected and working together to support social cognition and behavior (Menon & Uddin, 2010). The MCC showed higher activity for oneself than others across development, except in middle age children (i.e., 7-10 yo.). This pattern could reflect a transient developmental shift, leading the MCC to be permeable to peers' information in 7-10 y.o.; self-vs-other perceptions are less distinct allowing children to learn through peer-to-peer interactions and consequently improve their social skills. In line with this idea, a recent neuroimaging study revealed how 7-12 y.o. children activate specifically their salience network when watching peers but not adults performing unexpected actions (Chiron*, Notter", et al., *in prep.*).

Activity within the right postcentral gyrus was increasingly higher for self-vs-others' stimuli from 7 years old on, highlighting a gradual gain in discriminative abilities across development. The postcentral gyrus is involved in the processing of sensory information from the body and may play a role in the formation of body image and self-awareness (Salvato et al., 2020). However, the lack of significant activation in the 4-6.5-year-old group suggests that the ability to distinguish between self and others at the sensorimotor level may not be fully developed at this age.

Second, nine brain regions showed significantly higher activation for the other than for the self across development. Except for the left inferior orbital gyrus, which showed a non-linear developmental pattern, increasing neural activities for others were observed in participants from 7

years old within the right and left angular gyrus, the right precuneus, the right inferior temporal gyrus (ITG), the right rectus, and the right medial frontal gyrus (MFG), and beyond 10 years old within the left middle temporal gyrus and the right superior frontal gyrus. These findings suggest a developmental trajectory of a gradual gain in discriminative abilities for others-versus-self. These brain regions are all associated with different fundamental aspects of social cognition. In fact, social cognition relies on multisensory skills, such as audiovisual speech or face-voice integrations (the angular gyrus and the left middle temporal gyrus; Bernstein et al., 2008; Joassin et al., 2011; Seghier, 2013; Pourtois et al., 2005), somatosensory abilities (the MFG; Amodio & Frith, 2006), or perception and processing of complex visual stimuli, including facial expressions and emotional states or body language (the ITG, Haxby et al., 2001, 2000). Furthermore, social cognition relies on self-processing (Cavanna & Trimble, 2006), perspective-taking, empathy (the MFG), and theory of mind (the precuneus; Schilbach et al., 2006; Schurz et al., 2014). Additionally, social cognition relies on the ability to understand and respond to social cues, emotions, and the intentions of others (the right rectus; Hiser & Koenigs, 2018; Ruby & Decety, 2004). Finally, social cognition implies working memory and spatial processing (the right superior frontal gyrus; Boissgueheneuc et al., 2006; El-Baba & Schury, 2022; Job et al., 2021; Shelton et al., 2011); integrating social spatial cues to build a social network.

Both the angular gyrus and the precuneus are considered key nodes of the default mode network (DMN), a network of interconnected brain regions active during rest and self-referential mental activity (Li et al., 2014). It is also involved in social cognition and theory of mind, the ability to understand the mental states of others (Xie et al., 2016). It has been demonstrated that during childhood and adolescence, there is a functional reconfiguration of the DMN, which coincides with the period of social and cognitive development (Fan et al., 2021). There may be a link between the DMN and the representation of others in that they are both involved in processing self-referential information and constructing senses of self-related to others (i.e., tailoring perceptions). Therefore, the increase in other-perception activation in these regions may reflect the growing ability to engage in perspective-taking, empathy, and theory of mind. Our results further highlighted a particularly significant increase in the level of MFG activation for the > 20-year-old group when looking at others. One possible explanation is that older adults have greater social knowledge, which may enable them to process information about others in a more nuanced and sophisticated way. Therefore, these results could be linked to changes in the social environment or the types of social information that individuals are exposed to as they age. Alternatively, it could reflect changes in the way that older adults process social information, such as a greater focus on evaluating the emotional significance of social stimuli or a greater ability to integrate information from multiple sources.

Finally, the left inferior orbital gyrus showed a non-linear pattern, with a null difference between others- and self-perception in the 11-19 y.o. group. This brain region is known for being involved in reward value as well as emotion (Rolls et al., 2020). Emotional understanding is crucial for children's successful social adjustment. In addition to developing appropriate social skills and prosocial responses to peers, children who are more successful at understanding emotions have a greater chance of forming positive interpersonal relationships that facilitate social adaptation (Martins et al., 2014; Rosnay et al., 2013). As the processing of emotions changes across the development, and during adolescence especially, it may become increasingly unstable, and more intense (Bailen et al., 2018).

Together, these results are consistent with previous research showing that self-referential processing is a fundamental aspect of human cognition and occurs early in development, continuing throughout life (Northoff et al., 2006). It happens concomitantly to the ability to discriminate others from oneself. However, we show that it is a complex and dynamic process.

A few limitations refrain from a clear generalization of our results. First, each age group had a limited sample size. As it is a clear challenge to have young children enrolled for an MRI study, it is even more complicated to address movement in a task-based fMRI experiment with 4- to 7-year-olds. However, future work should creatively find a way to overcome this aspect to replicate this work with a larger population, or at least use a longer task. Furthermore, here we tested same-gender, same-ethnicity social partners for the 'other' condition. However, this does not reflect real life where

more diversity exists. We could invent stimuli to test variations in age, gender, or ethnicity to explore how social enrichment stimulates the social brain at best across development.

We show that while 4-6-y.o.-children have little discriminative skills, for both self and other perceptions, a developmental shift seems to operate from 6 years on, with transient periods in specific neural activities up to adulthood. However, all share a fundamental capacity for introspection and self-reflection that is essential to our understanding of the human mind and behavior, even very young children. These findings are important to better understand how social processing develops, and consequently when, why, and which social context can support learning processes across childhood and teen years.

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Ethics: This study was approved by the local ethics commission (CER-VD 2018-00244).

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