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The role of right supra-marginal gyrus and secondary somatosensory cortex in age-related differences in human emotional egocentricity

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Abstract

Emotional egocentric bias (EEB) occurs when, due to a partial failure in self-other distinction, empathy for another's emotion is influenced by our own emotional state. Recent studies have revealed a higher EEB in children, adolescents and older adults compared to young adults, but the neural correlates of this finding are largely unknown. We asked female participants (N = 95) from three different age groups (adolescents, young and older adults) to perform a well-validated EEB task in an MRI scanner. We assessed task-based changes in activity and effective connectivity as well as morphometric changes in regions of interest to pinpoint functional and structural age-related differences. Results revealed higher EEB in older compared to young adults and adolescents. Connectivity between right supramarginal gyrus (rSMG) and somatosensory cortices acted as a partial mediator between age and EEB. The findings suggest that an intact connectivity of rSMG, rather than its regional activity, with sensory-perceptual brain areas is crucial for overcoming egocentric biases of empathic judgments.

Keywords *(up to 5)*: adolescence, aging, connectivity, emotional egocentricity bias, fMRI

1. Introduction

Emotional egocentric biases (EEBs) occur when people's perceptions of others´ emotions are biased by their own, conflicting emotions – such as, e.g., when someone is not able to fully empathize with a friend's discomfort for his/her recent break up because he/she has just gotten married. EEB has been linked to a partial failure in self-other distinction (Riva et al., 2016; Silani et al., 2013; Steinbeis, 2016; Steinbeis et al., 2014; von Mohr et al., 2020, 2021), a fundamental component of empathy that allows the empathizer to keep track of the source of his/her own emotional experience and separate self-experienced emotions from the ones experienced by others (Lamm et al., 2016, for review). In a series of behavioral and neuroscientific studies, in which conflicting (vs. matching) transient emotional states were induced in pairs of participants while instructing them to empathize with the other's emotions, it has been shown that EEB may substantially vary with the age of the empathizer. For example, it has been observed that children below the age of 13 display higher EEB compared to young adults (around 20 to 30 years of age; Hayashi & Nishikawa, 2019; Hoffmann et al., 2015; Steinbeis et al., 2014). Similarly, adolescents and older adults are prone to a higher EEB compared to young and middle-aged (around 40-55 years old) adults (Riva et al., 2016). Neuroimaging studies of such age-related differences have been limited to children and young adulthood, leaving the neural underpinnings of EEB in adolescence and older age unexplored. Previous work with healthy young adults (Silani et al. 2013) indicates that EEB is associated with the activity of the right supramarginal gyrus (rSMG). This area is even causally involved in overcoming the bias, as shown by experiments temporarily disrupting its function by means of repetitive transcranial magnetic stimulation (rTMS) (Silani et al. 2013, see also Bukowski et al. 2020)). Increased connectivity of rSMG with right primary (rS1) and secondary (rS2) somatosensory cortices and bilateral visual cortex (Silani et al., 2013) have been advocated as a possible neural mechanism associated with overcoming such bias. It has thus been suggested that rSMG acts as a central node that helps to detect or even to integrate discrepancies between self-(i.e., S1, S2) and other-(i.e., V1) related sensory information, and thus to possibly resolve them (Lamm et al., 2016).

From a lifespan perspective, research on structural brain development has shown that parts of the parietal lobule (Giedd et al. 1999; Natu et al. 2019), including the SMG (Gogtay et al., 2004), reach full maturation only towards the end of adolescence. Moreover, a linear reduction of gray matter volume of the same area has been observed during adulthood, with a consistent drop after the seventh decade of life (Courchesne et al. 2000); (Sowell et al. 2003). The inverted U-shape trajectory of the structural development of SMG, together with the previous findings on its role in self-other distinction, point towards its possible involvement in the observed age-related change in EEB. Taken together with the previous neuroimaging findings in young adults, we hypothesized that rSMG could be linked to age-differences in EEB through changes in its functional activity and connectivity with sensory-perceptual cortices. The current study aimed at testing this prediction by investigating the neural underpinnings of EEB in three age groups of adolescent, young and older female participants, ranging from 14 to 76 years of age. 95 healthy volunteers were recruited and tested with the original EEB paradigm proposed by Silani et al. (2013) while lying in an MRI scanner. On the behavioral level, we predicted to replicate the previously found higher EEB in adolescents and older adults, compared to young adults. On the neural level, we expected this difference to be related to differences in functional activity as well as changes in connectivity of rSMG with somatosensory and visual cortices. In more details, based on (Silani et al. 2013), we expected rSMG activity to be lower in adolescents and older adults compared to young adults, while regarding the connectivity analysis, we expected age-related changes of rSMG connectivity with S1, S2 and visual cortex to be independent from each other, given the likely different functions subtended by each of these connections. Indeed, again based on Silani et al. (2013), connectivity between rSMG and visual cortex was hypothesized to underpin exteroceptive information processing about another person's sensations, while connectivity between rSMG and S1 to underpin sensory information accessible from a proprioceptive, first-person perspective, and lastly connectivity between rSMG and S2 to underpin both first-person sensory processing and empathic processing. Finally, we hypothesized the predicted differences in brain function to be subtended by differences in grey matter volume.

2. Materials and Methods

2.1. Participants

Ninety-five female participants ranging from 14 to 76 years old took part in the study. Only female participants were recruited for two reasons, which were consistency with our previous studies using the same paradigm (Riva et al., 2016; Silani et al., 2013), and acknowledged gender differences in empathy and socio-affective skills, including EEB (Michalska et al., 2013; Schulte-Rüther et al., 2008; Tomova et al., 2014). Based on hormonal sexual maturation (i.e. puberty, full maturation, menopause) and societal role (pupil, university student/worker and retired), participants could be classified in three age cohorts: adolescents (AD, 14-17 years; N= 33), young adults (YA, 21-31 years; N=32), and older adults (OA, 56-76 years; N=30). Note that the same classification was adopted in our previous study (Riva et al. 2016). Differently from before, though, we did not assess middle-aged adults (33-55 years), since the extent of the EEB in young and middle-aged adults was not distinguishable (Riva et al. 2016) and since this age group seemed harder to recruit for participation in neuroimaging experiments. We note though that this is a limitation that we will be discussed further below. Three subjects had to be excluded from the analyses (two AD, one YA) for excessive movements (see fMRI analysis paragraph for exclusion criteria) during the scanning session. The final sample thus consisted of 31 AD (age range: 14-17 years old; M= 15.61; SD= 1.03), 31 YA (age range: 21-31 years old; M = 24.52; SD = 2.41) and 30 OA (age range: 56-76 years old; M = 63.42; SD = 4.6). All the participants were right-handed (Oldfield, 1971), had normal or corrected-to-normal vision, and reported no past or present neurological or psychiatric disorder. The German version of the Mini Mental State Examination (Kessler et al., 2000) was administered to older adults to avoid including participants at initial stages of neurodegenerative disorders. Only participants with a score higher than 27 (out of a maximum score of 30) were enrolled in the study, as this cut-off has been reported to be appropriate to screen for cognitive impairment (Kukull et al., 1994). Written consent was provided by participants, who received € 25 each for taking part in the study. The study received approval by the local ethics committee and was carried out in accordance with the Declaration of Helsinki (latest revision, 2013).

2.2 Task and Procedure

The experimental session begun with the participant being introduced to an alleged young female participant (the confederate of the study, from now on confederate) and the joint delivery of the instructions. During the instructions, the experimenter explained that the participant and the confederate were going to perform the same task, with the participant lying inside and the confederate seated outside the MR scanner. After the verbal instructions, the participant underwent a training where she was administered with few trials in order to get acquainted with the task. Following this initial phase, she was accompanied to the MR scanner room. Overall, the participants had to complete three tasks in the scanner: an empathy task, the EEB task, and an imitation-inhibition task (Brass et al., 2005). The order of the tasks was randomized across participants, but keeping the empathy task always before the EEB task (because it entailed crucial familiarization with the stimuli that were then used in the EEB task, and in accordance with our previous neuroimaging work on EEB (Silani et al., 2013)). The present paper focuses on the results of the EEB task, while the detailed results of the other tasks will be or have been reported elsewhere (Riva et al., 2018).

The EEB paradigm implemented in the current study closely followed the procedure of the second fMRI experiment described in Silani et al. (Silani et al., 2013). Each trial of the EEB task comprised a stimulation phase and a rating phase. In the stimulation phase, transient pleasant or unpleasant affective responses were induced, in both the participants and the confederate, by means of visuo-tactile stimulation. The affective responses elicited in the pairs of participants could be either congruent (both pleasant or both unpleasant, *congruent condition) or* incongruent (self pleasant and other unpleasant, or vice versa, *incongruent condition*). The visuo-tactile stimulation consisted of the participants seeing on the screen the picture of an object/animal (e.g., a rose, a snail, maggots) accompanied by the text “YOU” and simultaneously being stroked on their left palm by an experimenter using an object resembling the displayed object or animal. Next to the first picture, the picture of another object/animal accompanied by the text “OTHER” (Fig. 1) was displayed on the screen, indicating the object/animal with which the confederate’s palm was being stroked. The stimulation phase lasted for 3 s. The visual stimuli were presented and seen by means of a back-projection system installed on the scanner site. Afterwards, participants were asked to rate the pleasantness of the confederates' (*other*-judgment run) or their own (*self*-judgment run) feelings. Ratings were provided on a visual analogue scale ranging from -10 (very unpleasant) to +10 (very pleasant) by using an MR-compatible response box. Participants were instructed to respond as quickly and accurately as possible, with a response time limit of 5 s. Both the self- and the other-judgment runs contained 20 congruent and 20 incongruent trials (10 pleasant and 10 unpleasant). Trials and runs were counterbalanced between participants.

Computation of the EEB score

As in Silani et al. (2013) and Riva et al. (2016), EEB was computed, for each participant, by calculating the difference in ratings between *congruent* and *incongruent* trials of the *other*-judgment run ($\Delta_{\text{other-judgement}}$), and subtracting the same difference in ratings of the *self*-judgment run ($\Delta_{\text{self-judgement}}$), averaged across valences (pleasant-unpleasant). As in previous work, unpleasant ratings were multiplied by -1 to allow the joint analysis and averaging of the ratings across valences. EEB was calculated as $\text{EEB} = \Delta_{\text{other-judgement}} - \Delta_{\text{self-judgement}}$. Note that before testing our hypothesis on age-related differences of EEB, we computed two separate EEB scores, one for pleasant and one for unpleasant emotions, in order to explore whether emotional valence influences age-related differences in emotional egocentricity. These scores were subsequently correlated with age. Both correlations were significant (Pleasant: $r = .593$, $p<.001$; Unpleasant: $r = .543$, $p<.001$), but did not differ between each other. Thus, all the analyses were performed on the total EEB score (i.e., the average of EEB for pleasant and unpleasant emotions), as in previous studies (Riva et al., 2016; Silani et al., 2013).

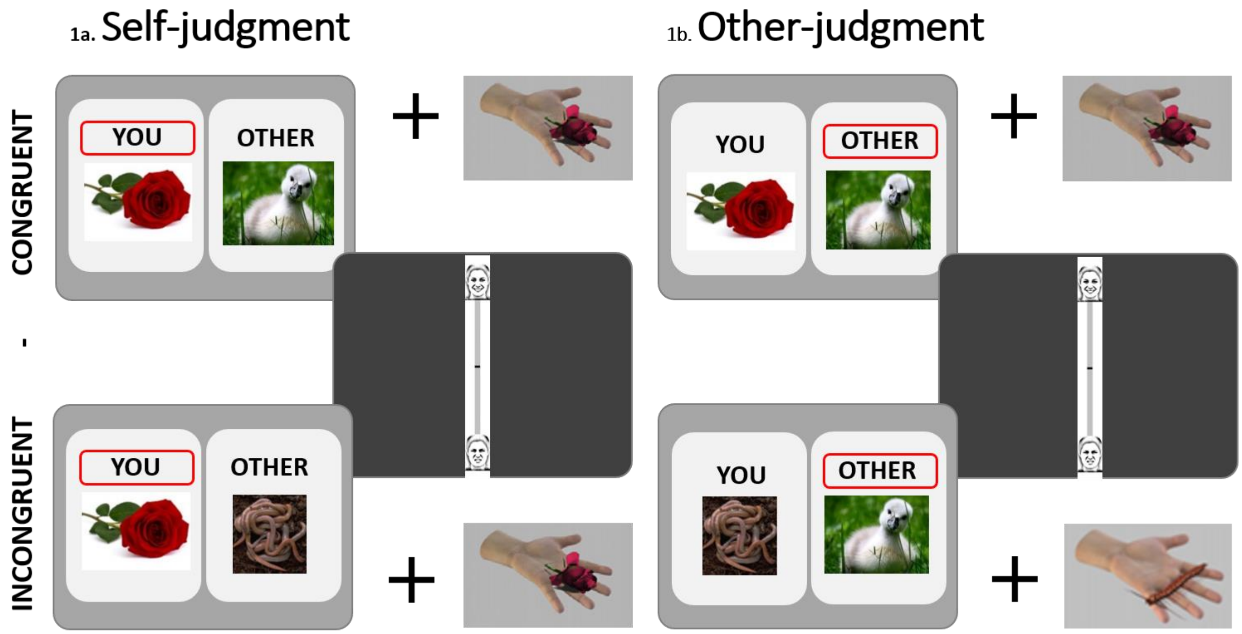


Fig 1. Overview of the experimental paradigm. **1a.** *Self*-judgment run: participants are touched on the palm of their left hand with an object and simultaneously see on the screen an object corresponding to the touch, as well as an object indicating the touch experienced by the other participant (in reality, a confederate). The affective responses elicited in the two participants could be either congruent (upper panel) or incongruent (bottom panel). Participants were asked to report their own affective state during the visuo-tactile stimulation, using a visual analogue scale. **1b**. *Other*-judgment run: Again, both participants are touched as in the self-judgment run, but now, participants are instructed to empathize with the other participant, and to provide ratings on the other´s affective state.

2.3 Additional measures

Self-report measures of depression, empathy, alexithymia, and social network were collected outside the scanner by means of questionnaires, in order to better characterize the three groups on different psychological and social dimensions. Depression was measured by means of the German version (Kühner et al., 2007) of the Beck Depression Inventory (BDI-II) (Beck et al., 1996), empathy (personal distress, empathic concern, perspective taking, and fantasy) by means of the German version of the Interpersonal Reactivity Index (IRI) (Paulus, 2014), and alexithymia by means of the Bermond Vorst Alexithymia Questionnaire (BVAQ) (Vorst and Bermond 2001). For the social network, three questions were administered: (1) number of friends; (2) number of close relatives; and (3) frequency of social contacts. Descriptive and group comparison results are reported in **Table 1**. Considered that none of the measures correlated with EEB, these measures were not considered further in the analyses (see Supplement for further details).

2.4 Behavioral Analysis

In order to determine our analysis strategy, we first performed two statistical tests on the age-related EEB score: a one-way ANOVA with Group (3 levels: AD, YA, OA) as a between-group factor on the one hand, and a regression analysis with age as a continuous predictor and EEB as the dependent variable on the other hand. The two models were then compared by means of the AIC index (Akaike's information criteria) calculated with R (R core Team, 2021), package *Stats*. Having the lower AIC index, the regression model resulted to be the better model (AIC model 1: 436.4577, AIC model 2: 429.531) to explain age-related differences in EEB. Thus, all the analyses performed and reported in the remainder of the paper were computed with age as a continuous predictor. To test our hypothesis of higher EEB in adolescents and older adults, both quadratic and linear relationships between age and EEB were tested for significance and compared by using the AIC calculate with the package S*tats* in R (R core Team, 2021). It is worth noticing that despite participants were not randomly sampled from the whole age range (missing middle-age adults' group), the regression approach is valid from a statistical point of view, since age is a continuous variable. However, the lack of sampling between the young and the older ages will be incorporated in the interpretation of the regression results, in the discussion section. Note also that in order to corroborate and interpret the regression findings, we performed complementary analyses and figures with age as a categorical factor (group) and reported them in the Supplemental Material.

2.5 Functional and structural MRI data acquisition, preprocessing, and analysis

Functional MRI scans were acquired using a 3T Siemens Magnetom Trio scanner equipped with a 32-channel head coil. For all participants, a high-resolution structural scan (sagittal T1-weighted MPRAGE sequence: TR: 2300 ms; TE: 2.91 ms; voxel size: 1 mm × 1 mm × 1.2 mm; slice thickness: 1.20 mm; FOV: 356 mm × 356 mm; 192 slices; flip angle: 9°), and field maps were obtained. Functional images were acquired in interleaved manner using a T2*-weighted echoplanar imaging (EPI) sequence with 33 transverse slices covering the whole brain with the following parameters: slice thickness = 3.0 mm; interslice gap = 0.3 mm; repetition time (TR) = 2060 ms, echo time (TE) = 30 ms; flip angle = 70°, field of view = 192 × 192 mm^2; matrix size = 64 × 64. Functional MRI data were preprocessed using SPM12 (Statistical Parametric Mapping, http://www.fil.ion.ucl.ac.uk/spm). Data pre-processing included realignment and un-warping for movement artefacts, correction for geometric distortions using the acquired fieldmap, slice-time correction, co-registration of the EPI scans to the skull-stripped T1-weighted structural scan, normalization to the standard stereotaxic anatomical Montreal Neurological Institute (MNI) space, smoothing with a 6 mm full-width at half-maximum (FWHM) Gaussian kernel, and resampling of voxel size to 3 mm isotropic. Participants who presented abrupt and sudden changes in the head´s position greater than 4 mm for translation or 4° for rotation were excluded.

2.5.1 Functional MRI analysis

Following the preprocessing, first-level analysis of the data of each participant was performed based on the General Linear Model framework as implemented in SPM12 (Friston et al. 1995). In the first-level model, eight regressors of interest convolved with SPM's canonical hemodynamic response function were included (one for each condition of the design, i.e., pleasant incongruent self-judgment, pleasant congruent self-judgment, unpleasant incongruent self-judgment, unpleasant congruent self-judgment, pleasant incongruent other-judgment, pleasant congruent other-judgment, unpleasant incongruent other-judgment, and unpleasant congruent other-judgment), along with the corresponding eight regressors of no interest modeling the rating phase. To account for residual motion artefacts, six nuisance regressors representing the realignment parameters were incorporated for each run in the first-level model as well. In line with our previous approach, which did not yield differences related to valence, both behavioral and neural data were collapsed across the two valence domains (see Note 1). Thus, following model estimation, the contrast of interest capturing the EEB was computed for each participant: $[(\text{pleasant incongruent - pleasant congruent}) + (\text{unpleasant incongruent - unpleasant congruent})]_{\text{other-judgment}} > [(\text{pleasant incongruent - pleasant congruent}) + (\text{unpleasant incongruent - unpleasant congruent})]_{\text{self-judgment}}$, and the resulting first-level contrast images were entered in the corresponding group-level (second level) analysis. All analyses were hypotheses driven. Therefore, we generated four ROIs using Marsbar (Brett et al., 2002) representing rSMG (740 mm^3), S1 (8590 mm^3), S2 (174 mm^3), and visual cortex (6680 mm^3) from the significant clusters reported in Silani et al. (2013). Note that these ROIs were thus fully independent from the data we analyzed. The ROIs were subsequently used for small volume corrections (SVC) and for region of interest analysis. All analyses used a family-wise error corrected threshold of $p<0.05$, at voxel-level. While the ROI-based analyses test activity/connectivity with higher sensitivity within predefined areas for which we had specific hypotheses, they are agnostic to potentially relevant activation/connectivity in other parts of the brain. Therefore, we complemented them with whole-brain analyses, thresholded at p<.05 FWE-corrected at voxel-level. Analysis details and results of the whole-brain analysis are included in the Supplemental Material.

2.5.1.1 Neural bases of EEB: replication in young adults

First, we were interested to test whether we could replicate our previous findings (Silani et al. (Silani et al. 2013), showing significant activity in the rSMG associated to the EEB contrast and increased connectivity of rSMG with rS1, rS2 and visual cortex (VC). To this aim, we performed two independent analyses: 1) a task-related functional activity analysis and 2) a task-related effective connectivity analysis, both focusing only on the young adults group.

1) To test rSMG activity associated to the EEB contrast, we performed a second-level random effects analysis on the first level contrast: [(pleasant incongruent - pleasant congruent) + (unpleasant incongruent - unpleasant congruent)]$_{\text{other-judgment}}$ > [(pleasant incongruent - pleasant congruent) + (unpleasant incongruent - unpleasant congruent)]$_{\text{self-judgment}}$. The analysis was small-volume corrected (SVC) within the rSMG ROI, at a threshold of p<0.05 at voxel-level.

2) In order to assess changes of rSMG connectivity, we performed psychophysiological interaction analyses (PPI, (Friston et al. 1997). Following the same procedure as in Silani et al. (Silani et al. 2013), we first extracted the deconvolved time course from the seed region rSMG (using the same ROI that was used for the univariate analysis). Second, a PPI regressor was obtained as product of the estimated (deconvolved) BOLD signal of the seed region and the vector representing the psychological variable of interest, namely the difference between incongruent and congruent conditions in the other-judgment run. Third, first-level analysis was performed by computing a multiple-regressor model with the estimated activity of the rSMG (Y), the experimental contrast (P) and the psychophysiological interaction (PPI) regressor. Contrast images

for the PPI regressor were estimated for each subject and used in a second-level random effect analysis. Three independent analyses were performed for the S1, S2 and VC ROIs, again using SVC with a threshold of $p<0.05$ (FWE) at voxel-level.

2.5.1.2 Age-related differences

Second, we tested age-related differences, both in task-related functional activity and effective connectivity. To this aim, we extracted mean activity for each of the ROIs defined in the previous section: namely, rSMG for the task-related activity analysis and rS1, rS2 and VC for the PPI analysis (both analyses performed in the same way as for the young adult participants), and with these values, we computed correlations with age and EEB scores as continuous predictors. Correction for number of ROIs was not applied because we tested three *a priori and distinct* hypotheses, one for each area. The relation between age, EEB and rSMG connectivity with sensory-perceptual cortices was further explored with a mediation analysis, in which connectivity values of rSMG - rS1 and rSMG - rS2 were considered and included in the analysis as parallel mediators. This analysis was conducted with the R package *boot* (Davison & Hinkley, 1997), we calculated bias-corrected and accelerated CIs (BCa_Cis) (Efron, 1987) using a bootstrapping procedure. BCa-CIs correct for bias and skewness of the bootstrap sample distribution. Statistical significance at $p < 0.05$ is indicated by the 95% confidence intervals not crossing zero.

2.5.2 Structural MRI analysis

Age-related differences in brain structure were investigated by means of voxel-based morphometry (VBM) analyses (Ashburner and Friston, 2000). VBM was implemented via the CAT12 toolbox (http://dbm.neuro.uni-jena.de/cat/) of SPM12. In short, preprocessing of the structural data included bias field correction, segmentation in gray matter, white matter and cerebrospinal fluid using a segmentation approach based on adaptive maximum a posterior segmentation and partial volume segmentation. The resulting segmentations were then normalized to the Montreal Neurological Institute (MNI) space using Diffeomorphic Anatomic Registration Through Exponentiated Lie algebra algorithm (DARTEL; Ashburner, 2007). Finally, the segmented images were scaled with the amount of volume changes due to spatial registration, so that the total amount of grey matter in the modulated image remained the same as it would be in the original image. The segmented, normalized and modulated images were finally smoothed with an 8 mm FWHM Gaussian kernel and used for subsequent statistical analyses. Average grey matter volume values were extracted from the rSMG ROI. Correlation analyses testing the relationship between i) age and rSMG volume, ii) EEB and rSMG volume and iii) EEB-related rSMG activity and rSMG volume were performed. To check whether EEB and rSMG gray matter volume correlate beyond age we also computed a partial correlation between these two variables controlling for age. Total Intracranial Volume (TIV) was included as covariate of no interest in the models. We also complemented the ROIs analyses with whole-brain analysis thresholded at $p<.05$ FWE-corrected at voxel-level. The analysis is reported in the Supplementary material.

3. Results

3.1 Behavioral results

Regression analysis revealed both a significant linear and a quadratic relationship between EEB and age (linear: $F(1,91) = 49.970$, $p < .001$, $R^2=.357$; AIC = 167.58; quadratic: $F(2,91) = 28.914$, $p < .001$, AIC = 178.75). Contrary to our hypothesis of higher EEB in both adolescence and at older age, compared to young adults, the comparison of the two models by means of the AIC index indicated that the linear model was 266.91 times more likely than the quadratic one (**Fig. 2**).

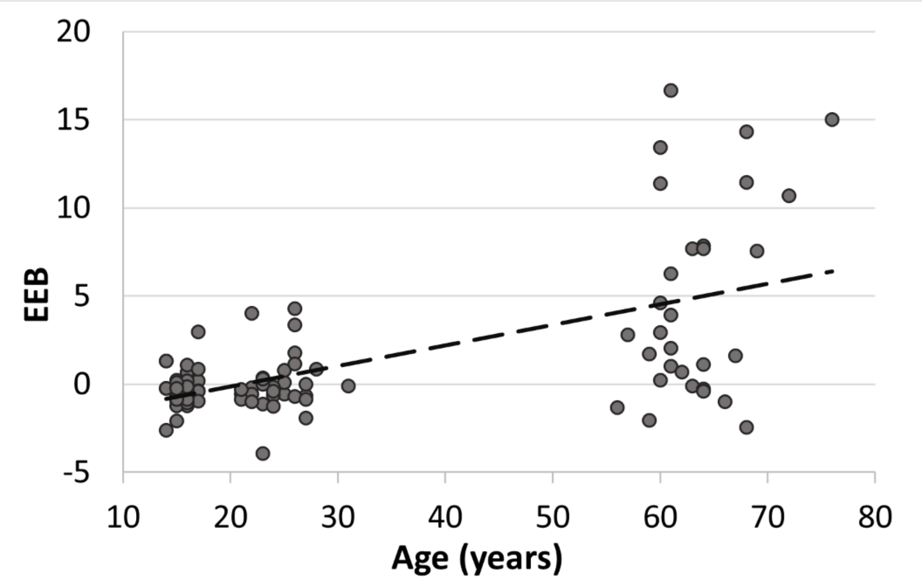


Fig. 2. Emotional egocentricity bias (EEB) (i.e., the influence of our own emotions when empathizing with others) at different ages. EEB scores are computed by calculating the difference in ratings between congruent and incongruent trials of the other-judgment run, and subtracting the same difference in ratings of the self-judgment run, averaged across valences. The graph represents the relationship between individual EEB scores (y-axis) and age (x- axis). The dashed line indicates the linear regression between age and EEB. See also supplementary Fig. S1 for data aggregated based on the three age groups.

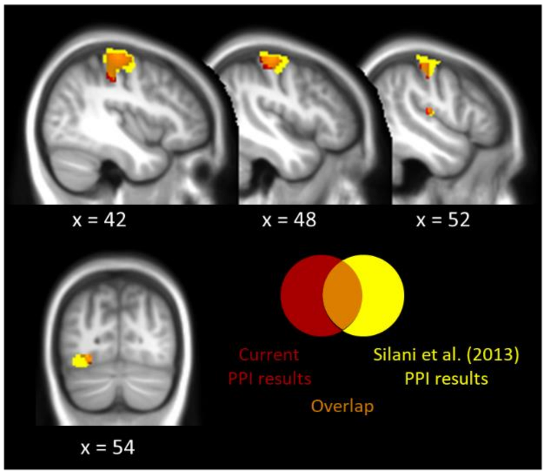
3.2 Functional MRI results

3.2.1 Neural bases of EEB: replication in young adults.

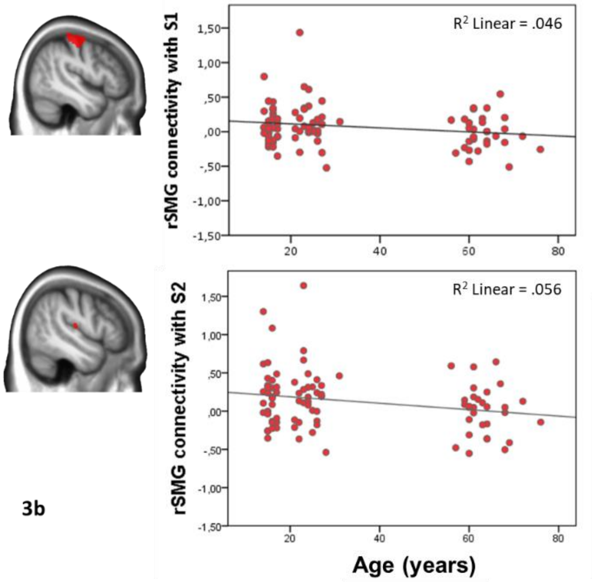
The task-related functional activity analysis revealed significant activity in the rSMG for the EEB-related contrast (peak voxel at MNI x/y/z= 60/-34/40), as well as significant increases in connectivity between rSMG and rS1 (45/-22/64), rS2 (48/-19/16) and visual cortex (fusiform visual cortex, -27/-76/-8) during other-judgments for incongruent vs. congruent trials (**Fig. 3a**).

3.2.2 Age-related differences

The analysis of age-related differences in task-related activity within rSMG revealed no significant correlation, neither linear nor quadratic, between EEB-related rSMG activity and age (all *p* > .244) (see supplementary Fig. S2). A negative correlation was found between age and connectivity of rSMG with rS1 and rS2 during the other-judgment run (S1: *r* = -.213, *p* = .041, S2: *r* = -.226, *p* = .030) (**Fig. 3b**).



3a



3b

Fig. 3. Results from the PPI analysis. **3a.** Brain regions showing increased effective connectivity (PPI analysis) with the rSMG in young adults: S1, S2 (sagittal view) and VC (coronal view). For display purposes, the results are shown at p = .001 uncorrected (in red), and without restriction on whether they fall within the area of the analogous PPI findings reported in Silani et al. 2013 (shown in yellow). The orange area thus indicates the overlap between the present and the previous study. **3b.** Strength of effective connectivity between rSMG and S1, S2 (y-axis) plotted against age (x- axis). Solid lines indicate the linear regressions between age and connectivity strengths. The left panel shows the location and the extent of the ROI masks for S1 and S2, built from the corresponding results in Silani et al. (2013). See also supplementary Fig. S3 for data aggregated based on the three age groups.

Furthermore, significant correlations were found between EEB scores and connectivity of rSMG with S1 (*r* = .223, *p* = .034), S2 (*r* = -.301, *p* = .004) and a trend with VC (*r* = -.202, *p* = .055). The mediation analysis revealed that connectivity between rSMG and rS1 did not significantly mediate the effect of age on the EEB (*indirect effect* = 0.0003656487, 95% BCa CI=[-.0081, .0124]); however, the connectivity between rSMG and rS2 partially mediated the relation between age and EEB (*indirect effect*=0.0071811085, 95% CI=[.0008, .0227]). Indeed, as shown in Figure 4, the direct effect of age on EEB is smaller compared to the total effect of age on EEB, as the connectivity rSMG-SII partly captured this effect (**Fig. 4**).

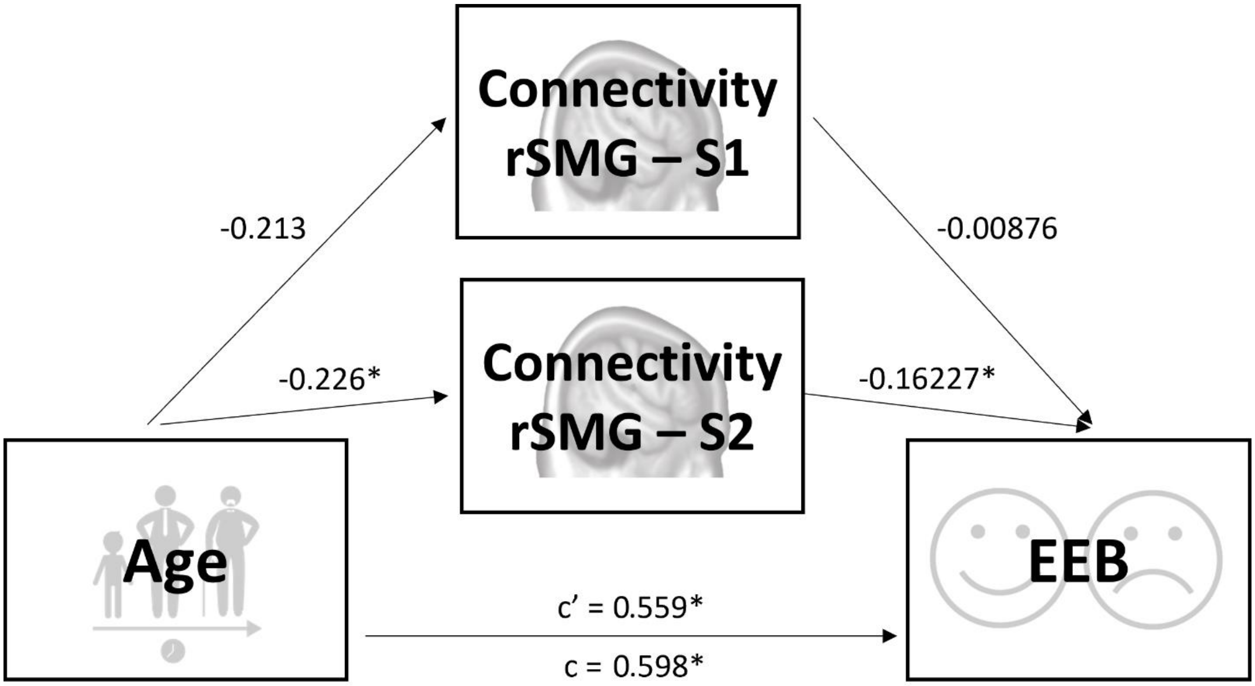


Fig. 4. Mediation analysis computed with age as independent variable, EEB as dependent variable, and with rSMG-S1 and rSMG-S2 connectivity as mediators. The rSMG-S1 did not result to be a mediator, while the connectivity rSMG-S2 partially mediated the effect of age on EEB. Numbers represent the standardized regression coefficients for the relationship between age and the connectivity with S1 and S2, and between the connectivity with S1 and S2 and EEB; c’ = direct effect of age on EEB, and c = total effect of age on EEB. *p < .05

3.3 Structural MRI results

A significant negative correlation emerged between age and rSMG gray matter volume (r = -.672, p < .001). Moreover, rSMG gray matter volume negatively correlated with EEB (r = -.409, p < .001), while no significant correlation emerged between rSMG gray matter volume and rSMG activity related to EEB (*p* = .560). Results from the partial correlation showed a not-significant correlation between EEB and rSMG grey matter volume when controlling for age (*r* = -.012, *p* = .909).

4. Discussion

We used a multi-modal neuroimaging approach, combining morphometry, task-related functional activity and connectivity analyses, to shed light on the neural bases of age-related differences in emotional egocentricity bias. While we hypothesized based on previous findings that EEB in adolescence and at older age should be higher compared to EEB in young adults, results showed a linear increase of EEB with age. This trajectory is best explained by age-related differences in rSMG´s effective connectivity with the secondary somatosensory cortex, which mediated differences in EEB across the ages investigated.

More specifically, in a sample of young healthy female participants, we observed increased activity of rSMG during EEB-related tasks and increased effective connectivity of the same region with rS1, rS2, and visual cortex, thus replicating the original findings (Silani et al., 2013). Notably, in spite of a lack of association of age with task-related rSMG activity, significantly lower connectivity between rSMG and rS1 and a trend towards significant connectivity with rS2 was associated with older age. Mediation analysis revealed that connectivity of rSMG with rS2 is a partial mediator of the relationship between age and EEB, indicating that preserved connectivity is fundamental in overcoming the EEB. Reduced gray matter volume in rSMG in older compared to young adults was also detected. However, its correlation with EEB was not significant when controlled for age, suggesting that the gray matter volume reduction of rSMG alone is not sufficient to influence emotional egocentricity. It is worth noticing that although EEB was correlated with chronological age, EEB scores in the older adults showed higher variability than in the other two groups. This implies that some of the older adults show an EEB similar to younger participants, while others do show much higher values. Higher variability associated to increasing age is a common finding in gerontology research, present in many different domains (Anne Nelson & Dannefer, 1992; Stone et al., 2017), such as for example cognitive functions (Hultsch et al., 2002; Sylvain-Roy & Belleville, 2015), brain activity (Jockwitz et al., 2017), physical well-being (Chmelo et al., 2015), or orosensation (Song et al., 2016). Thus, it has been suggested that while aging is the main cause of the declines observed in the different domains, chronological age alone might not be sufficient to explain interindividual differences. Additional factors, such as genetics and life experiences/habits, are likely to play significant part the way we age and need to be considered for future studies. In the current study, self-reported measures of depression, empathy, alexithymia, and social network were collected in order to better characterize the three groups on different psychological and social dimensions, possibly associated with EEB. In spite of some group differences on various scales (see Table 1), no significant correlations between them and EEB emerged, suggesting that EEB is probably an independent psychological construct (see Table S1 in the Supplement). On the other hand, results of the current study fit well with data coming from previous studies showing age-related worsening of abilities within the domain of social cognition. Compared to young adults, older adults show deficit in recognizing emotional facial expressions (Cortes et al., 2021; Ruffman et al., 2008), in processing others' mental states when making moral judgments, in false beliefs' tasks (Moran et al., 2012), in self-other processing on level two perspective-taking (Martin et al., 2021), in theory of mind abilities (ToM) (Sullivan and Ruffman 2004; Wang and Su 2013), and in visual perspective taking (Martin et al., 2019).

Differently from our initial hypothesis, adolescents did not show more egocentrism than young adults. Various reasons may account for the lack of replication of our previous behavioral findings (Riva et al., 2016). First, in the previous study, participants´ ratings were collected using a response device (a touch screen) that enabled faster and more automatic responses. In the MR scanner, it was not possible to use a touch screen and responses were collected by moving a cursor on the response scale. The possibility to adjust the cursor position while entering the response might have resulted in additional time and reflection to overcome and control for initial bias. Note that the discrepancy between response modalities (touch screen vs. slider) has also been observed in our previous work (Silani et al., 2013). Another reason might be a difference in the two adolescent samples, which, amongst general sampling issues (i.e., self-selection to participate in an fMRI study, see Charpentier et al., 2021), might be due to the different countries (Italy and Austria) where the two studies were performed. At the brain level, adolescents showed greater gray matter volume in rSMG compared to young adults, which is likely to indicate ongoing development processes, such as pruning and myelination, as proposed by various researchers (Ducharme et al., 2015; Tamnes et al., 2017). Notably, such structural difference was not associated to differences in task-related rSMG activity or connectivity between adolescents and young adults.

Considering data from both adolescents and older adults, age-related changes in rSMG connectivity with somatosensory cortices and visual cortex seems to play a central role in changes of emotional egocentricity across different ages. When considering the whole sample, increasing age was found to negatively correlate with connectivity between rSMG and somatosensory cortices, and in particular the coupling between rSMG and rS2 partially mediates the relationship between age and EEB. S2 is a brain area involved in a variety of processes, from the perception of touch intensity (Case et al., 2017) to emotional processing (Adolphs et al., 2000) and attentional modulation of somatosensory stimuli (Chen et al. 2008). Importantly, in addition to being activated by first-person touch stimulation, S2 has been associated with observation of vicarious touch and to empathy for touch (Jackson et al., 2006; Keysers et al., 2004; but see Hartmann et al., 2021; for review see Keysers et al., 2010; Riečanský & Lamm, 2019). Thus, a possible, though speculative, interpretation might be that both self- and other-related emotional experiences are represented in S2 and transferred to rSMG. In young adults, when the two representations are incongruent, the coupling between S2 and rSMG increases, possibly because of the higher complexity or the greater quantity of information exchanged with rSMG. Being a central area for self-other distinction in the emotional domain (Silani et al., 2013; Steinbeis et al., 2014), rSMG keeps separated and weights information related to one's own and to the other's emotional states, providing the basis of the empathic judgment. However, since the increase in the rSMG-rS2 coupling is not observed in older adults, this might suggest that the complexity associated to simultaneous incongruent emotional states between self and other is not or less effectively transferred to the rSMG. Thus, participants in this group may use the more salient representation (i.e., the self) to inform their empathic judgment, thus resulting in a higher egocentric bias.

The relation between age and task-free functional connectivity (such as measured during resting state scans) have been fairly extensively investigated (Damoiseaux, 2017; Geerligs et al., 2015; Hughes et al., 2020; McCormick et al., 2018) and showed associations between age-related differences in social/cognitive abilities and age-related changes in task-free functional networks (e.g.: default mode network). For example, in a study by Hughes et al., (2019), researchers found that (weaker) task-free connectivity between the right temporoparietal junction and the right temporal pole mediated age differences in theory of mind. However, the relation between age-related changes in socio-cognitive processes and differences occurring with development and aging in task-related effective connectivity has been given less attention so far. The current study provides a case on how differences in regional functional activity might not always be able to account for age-related differences in (socio)cognitive processes, whereas task-related functional connectivity might play a key role in identifying these differences. Thus, a more systematic and regular analysis of task-related effective connectivity may open new venues for understanding age-related changes in brain functionality.

Apart from what we propose to be robust findings based on solid experimentation and analysis strategies, our study also includes some limitations that need specific consideration. First, the confederate playing the “other” in the task was a young adult for all the three groups and this might have influenced the degree to which the participants were able to empathize with them. However, it is important to note that our previous study (Riva et al., 2016), where confederate’s age matched participant’s age, yielded similar results as the current one, thus suggesting that the confederate’s age might not be critical for the EEB. Second, for practical reasons and because our previous study showed no behavioral differences between young and middle-aged adults (Riva et al., 2016), the latter group was not included in the current study. This leaves an age gap between young and older adults that could not be investigated. Even if previous findings do not report an abrupt change in trajectory for this age group (linear or quadratic), we nevertheless cannot rule out that this was not the case. Future studies are then needed to extend our findings to this age range. Third, considered that this is a cross-sectional study, factors associated to cohorts rather than age might have played a role in the way participants empathized. The adolescents in this study grew up in a time when expressing emotions and empathy was (relatively more) encouraged, while older adults' upbringing was likely more focused on practical matters and less involved in emotional education (Gruehn et al. 2008). Fourth, overcoming emotional egocentricity likely involves cognitive abilities, such as conflict control or inhibition, that decline with aging. Thus, we cannot rule out that higher EEB in older adults might be due to a decline of these underlying cognitive skills. Unfortunately, apart from the MMSE which excludes initial stages of dementia, we did not collect other cognitive measures, so in order to deeply understand the involvement of different cognitive abilities in higher EEB in aging future studies are needed. Fifth, despite our paradigm has been already employed in different studies/experiments (Riva et al., 2016; Silani et al., 2013; Tomova et al., 2014), the validation of the present results by means of similar paradigms investigating the same processes (Steinbeis et al., 2014; Trilla et al., 2021; von Mohr et al., 2020, 2021) is required. Finally, further research is needed to extend the present results to the aging male population, as we only report findings from female participants here.

Conclusions

The current study replicates previous behavioral findings that older age is associated with higher EEB, but produced inconsistent results on the question whether EEB is also higher in adolescence. At the neural level, our findings indicate that rSMG is a central area for efficient self-other distinction in the emotional domain and that an intact effective connectivity of this area, rather than its regional activity, is crucial for overcoming emotionally biases of empathic judgments. Together, the present and previous findings suggest that rSMG works in interaction with other, predominately sensory-perceptual brain areas to integrate as well as to differentiate affective information pertaining to self and other.

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6. Conflict of interest

Declarations of interest: none.

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8. Tables

Table 1. Psychological and personality characteristics of the three groups.

Self-reported measures	Adolescents Mean (SD)	Young adults Mean (SD)	Older adults Mean (SD)	Results
BDI	8.82 (5.63)	8.83 (6.98)	7 (5.004)	=
IRI				
Empathic concern	14.75 (2.27)	16.17 (5.48)	15.77 (2.67)	YA > AD*
Personal distress	11.14 (3.44)	15.17 (3.09)	13.42 (2.28)	=
Fantasy scale	16.07 (2.61)	12.00 (2.49)	11.04 (2.85)	YA, AD > OA *
Perspective taking	12.79 (2.91)	14.90 (2.44)	15.42 (3.26)	YA, OA > AD*
BVAQ				
Emotionalizing scale	8.00 (2.67)	7.80 (2.76)	8.07 (2.68)	=
Verbalizing scale	11.48 (3.50)	9.40 (3.39)	8.89 (2.94)	AD > OA*
Fantasizing scale	9.50 (3.64)	10.00 (3.40)	12.46 (4.24)	OA > YA, AD*
Identifying scale	9.54 (3.11)	9.43 (3.12)	6.73 (2.41)	YA, AD > OA*
Analyzing scale	7.96 (2.30)	7.77 (2.10)	7.86 (2.55)	=
Social network size				
N. of friends	6.35 (2.70)	6.8 (3.67)	7.43 (4.85)	=
N. of close relatives	6.55 (5.48)	6.1 (4.44)	7.50 (4.84)	=
Frequency of social contacts	2.32 (0.75)	2.30 (0.95)	2.80 (0.66)	=

Table 1. One-way ANOVAs were computed for the BDI (Kühner et al., 2007) and for each of the social network questions. In case of significance, Bonferroni-corrected pairwise comparisons were calculated to compare groups. Two multivariate ANOVAs were computed for the IRI (Paulus, 2014) and the BVAQ (Vorst & Bermond, 2001) including scales as a within-group factor (4 levels for IRI, 5 levels for BVAQ) and group as a between-group factor (3 levels), to correct for multiple comparisons of the sub-scales of each questionnaire. In case the interaction *questionnaire * group* was significant, Bonferroni-corrected post-hoc pairwise comparisons were computed for each subscale comparing the groups. Analyses were computed using SPSS v.25 (Statistical Package for the Social Sciences, IBM SPSS Inc., Chicago, IL, USA). *p-value <.05, Bonferroni post-hoc test p<.05.