

Motherhood and theory of mind: increased activation in the posterior cingulate cortex and insulae

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Abstract

Despite growing evidence on effects of parenthood on social understanding, little is known about the influence of parenthood on theory of mind (ToM), the capacity to infer mental and affective states of others. It is also unclear whether any possible effects of parenthood on ToM would generalise to inferring states of adults or are specific to children. We investigated neural activation in mothers and women without children while they predicted action intentions from child and adult faces. Region-of-interest analyses showed stronger activation in mothers in the bilateral posterior cingulate cortex, precuneus (ToM-related areas) and insulae (emotion-related areas). Whole-brain analyses revealed that mothers compared to non-mothers more strongly activated areas including the left angular gyrus and the ventral prefrontal cortex but less strongly activated the right supramarginal gyrus and the dorsal prefrontal cortex. These differences were not specific to child stimuli but occurred in response to both adult and child stimuli and might indicate that mothers and non-mothers employ different strategies to infer action intentions from affective faces. Whether these general differences in affective ToM between mothers and non-mothers are due to biological or experience-related changes should be subject of further investigation.

Key words: fMRI; theory of mind; affective theory of mind; motherhood; children

Introduction

Becoming a parent is one of the most profound, life-changing experiences. Taking on the responsibility to care for a dependent life leads to dynamic and multilevel changes in parents (Pereira and Ferreira, 2016). The network of brain areas associated with parenting is often referred to as 'parental brain'. The human parental caregiving network according to Feldman (2015) consists of the amygdala and hypothalamus as well as areas associated with motivation-reward (nucleus accumbens and ventral tegmental area), empathy (anterior cingulate cortex, anterior insula, and supplementary motor area), embodied simulation (sensorimotor areas, inferior parietal lobule, and inferior frontal gyrus), mentalising (superior temporal gyrus, temporoparietal junction, temporal pole, precuneus, posterior cingulate cortex, and ventromedial prefrontal cortex) and emotion regulation (dorsolateral prefrontal cortex, medial orbitofrontal cortex, middle frontal gyrus, and frontopolar cortex) (Feldman, 2015). This 'parental brain' encompasses a myriad of neural structures that are also involved in cognitive and affective social understanding (Feldman, 2015).

This is unsurprising since successful parenting requires parents to feel with and understand their offspring (Camoirano, 2017). Social understanding of others is often conceptualised as involving both cognitive and affective processes (e.g. Shamay-Tsoory, 2011; Kanske, 2018). Cognitive processes focus on processing and inferring information, while affective processes like empathy focus on the emotional impact of others. One of the most vital cognitive processes of social understanding is theory of mind (ToM), the capacity to infer mental and affective states from others and predict behaviour based on these states (Schaafsma et al., 2015). When this capacity is used to infer affective states, it is referred to as affective ToM (aToM) as compared to cognitive ToM when inferring mental states like beliefs.

Differences between parents and non-parents in social understanding are found on the both behavioural and neural level. Parents compared to non-parents are more likely to ascribe mental states to infants (Shinohara and Moriguchi, 2017), express a stronger bias towards infant and child faces (Thompson-Booth et al., 2014a,b) and rate infant facial expressions as more extreme

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(Parsons et al., 2016). One study also indicates that mothers perform better in an affect recognition task with adult faces, although there was no difference between mothers and non-mothers with infant faces (Matsunaga et al., 2018). Differences between parents and non-parents also extend to the neural level. Hayashi et al. (2018) found larger Nogo-P3 amplitudes in mothers relative to non-mothers in response to emotional adult faces in a Go/Nogo task, which was interpreted as increased activation of emotion inhibition areas. In an affect recognition task, mothers vs non-parents showed larger N2 amplitudes in response to infant faces possibly indicating greater sensitivity to the intensity of the infants' emotional expression (Proverbio et al., 2006). This is in line with the results of Zhang et al. (2020) who found increased activation in mothers compared to non-mothers in a simple viewing task of emotional infant faces in several brain areas associated with facial recognition and social understanding, including bilateral inferior and middle frontal gyrus, lingual gyrus, fusiform gyrus as well as right middle temporal gyrus and cuneus. Using an affect recognition task, Nishitani et al. (2011) found differences in the neural activity of the prefrontal cortex between mothers and non-mothers in response to infant but not adult faces. Taken together, these studies show behavioural and neural differences between parents and non-parents in a variety of tasks involving social understanding.

Additionally to differences between parents and non-parents, adults in general treat infants and children preferentially compared to other adults, seeing them as more likeable and attractive, paying more attention to them and being more motivated by them (Lucion et al., 2017; Luo et al., 2015a, 2011; Thompson-Booth et al., 2014b). From an evolutionary perspective, this is an important feature to ensure that adults care for their and others' offspring (Luo et al., 2015b). This behavioural preferential treatment of children also extends to physiological and neural levels. Nulliparous women exhibit increased activation in the bilateral fusiform and right lingual gyrus in response to infant compared to adult emotional faces (Li et al., 2016). Leibenluft et al. (2004) investigated differences in mothers' brain responses to unfamiliar children and adults. They found increased activation in attention and face processing areas in response to children compared to adults. These studies indicate that adults generally and parents specifically react differently to child faces in a variety of tasks.

So far, the majority of the here presented studies have used face stimuli, for example, in affect recognition tasks (e.g. Nishitani et al., 2011). However, there have been no investigations of how this information is further used to infer mental states or make action predictions, vital aspects of ToM. The neural basis of ToM has been investigated extensively (Schurz et al., 2014; Molenberghs et al., 2016; Arora et al., 2017). aToM leads to strong activation in the bilateral posterior cingulate cortex and precuneus (Kogler et al., 2020). The precuneus is associated with the awareness of emotional state (Terasawa et al., 2013), the attribution of emotions (Ochsner et al., 2004) and ToM of emotional states (Atique et al., 2011). The posterior cingulate cortex is a highly connected area and the cingulate cortex is argued to be involved in action-outcome learning (Leech and Sharp, 2014; Rolls, 2019). Important areas for emotion processing are the bilateral amygdala and insulae. The amygdala is associated with affect recognition in general but with fear in particular (Adolphs, 2002). The bilateral insulae is implicated in empathy and a subjective feeling state as opposed to the cognitive nature of ToM (Singer et al., 2009). ToM processes elicited by affective face stimuli are likely to rely on both aToM and emotion processing areas as they connect processing of the emotional faces with the action prediction

based on them. Additionally, all of these areas have been associated with the 'parental brain' (Feldman, 2015). Therefore, neural differences between mothers and non-mothers are expected in these aToM and emotion processing areas.

The aim of the present study was to investigate the effect of motherhood and protagonist (child vs adult stimuli) as well as their interaction on aToM. For this purpose, we combined the factors parenthood and protagonist by adapting a well-established aToM task (Mier et al., 2010). Participants were asked to make action intention predictions based on the facial affect of adult and child stimuli. We decided to use child instead of infant stimuli with protagonists between 7 and 10 years old to allow usage of the same action intentions in both protagonist groups. Furthermore, we focussed on mothers as they provide most of the primary care in Germany (Statistisches Bundesamt, 2018; BMFSFJ, 2019). Based on the previous literature, we hypothesised an enhanced brain response in mothers compared to non-mothers to both adult and child stimuli (main effect motherhood) and stronger brain activations in response to child relative to adult faces in mothers and non-mothers (main effect protagonist), in both emotion processing (bilateral insulae and amygdala; Gobbini and Haxby, 2007) and aToM areas (bilateral precuneus and posterior cingulate cortex; Kogler et al., 2020). Additionally, we expected an interaction of the factors protagonist and motherhood, with differences between mothers and non-mothers being more pronounced in response to child faces.

Methods

Preregistration, data and scripts of this study are available at: <https://osf.io/r7g9q/>. We preregistered our study design, including sample size, data collection procedures, measured variables and behavioural analyses, as well as our hypotheses prior to data collection. We did not specify the regions of interest or neuroimaging analysis in our preregistration.

Participants

We aimed for a sample of 54 women based on a priori estimation for a within-between interaction in a 2×2 mixed analysis of variance (ANOVA) in G*Power [$f = 0.25$, $\alpha = 0.05$, $(1 - \beta) = 0.95$, $\text{corr} = 0.5$; Faul et al., 2007]. We had to exclude three participants due to chance or worse performance in the task and two due to artefacts. We were not able to replace them due to the outbreak of Coronavirus disease 2019. The analysis includes 26 non-mothers (mean age 35.92 years, 25–50 years old) and 24 mothers (mean age 38.38 years, 33–46 years old). Mothers and non-mothers did not significantly differ in age, intelligence or socio-economic status (SES) (Table 1). Women were screened to ensure the following criteria: MRI compatibility, right-handedness, good health, cisgender woman, 25–50 years old and sufficient knowledge of German. Mothers had at least one biological child between 4 and 10 years of age of which they were the primary caretaker. Non-mothers were excluded if they interacted with children in a private or professional context on a regular basis. The Ethics committee of the Charité—Universitätsmedizin Berlin approved this study. It was conducted in accordance with the Declaration of Helsinki, and participants gave written informed consent before participation. All participants received monetary compensation for their time.

Materials

Our task was adapted from Mier et al. (2010). Participants saw pictures of angry, happy and afraid adult and child faces. There were 12 children (7–10 years old) and 12 adults (21–30 years old)

Table 1. Comparison of mothers and non-mothers using Bayesian Mann–Whitney U-tests and a Bayesian contingency table. Columns show averages, standard errors, corrected Bayes Factor and W for each test. All comparisons indicate no differences between groups

| Measurement | Mothers | Non-mothers | BF ₁₀ | W |
|-------------------------------------|-----------------------|-------------|------------------|--------|
| Age | 38.4 ± 0.8 | 35.9 ± 1.4 | 0.130 | 251.00 |
| Number of children | 2.04 ± 0.17 (max. 4) | – | – | – |
| Duration of motherhood | 9.63 ± 0.94 (max. 22) | – | – | – |
| ECR-rs | 25.1 ± 1.7 | 31.8 ± 1.7 | 0.770 | 446.00 |
| ERQ | 40.7 ± 1.3 | 42.9 ± 1.4 | 0.117 | 377.00 |
| Importance of having children (0–4) | 3.7 ± 0.1 | 2.7 ± 0.3 | 0.366 | 203.50 |
| IRI-emp | 44.6 ± 1.2 | 42.7 ± 1.4 | 0.130 | 269.50 |
| IRI-PT | 15.1 ± 0.4 | 15.0 ± 0.4 | 0.081 | 315.50 |
| KSE-G | 1.8 ± 0.1 | 2.0 ± 0.1 | 0.188 | 392.50 |
| minIQ | 28.2 ± 2.3 | 30.6 ± 2.2 | 0.089 | 334.00 |
| Mood state (0–4) | 3.0 ± 0.1 | 3.0 ± 0.1 | 0.081 | 311.00 |
| Single (proportion of group) | 25% | 73% | 108 | – |
| SES (3–21) | 14.1 ± 0.7 | 15.4 ± 0.8 | 0.141 | 187.50 |
| TAS | 38.7 ± 1.5 | 40.0 ± 1.9 | 0.081 | 329.00 |

IRI-emp = interpersonal reactivity index, empathy score; IRI-PT = interpersonal reactivity index, subscale perspective taking; KSE = Kurzskala Soziale Erwünschtheit (short-scale social desirability), positive and negative subscale.

resulting in 24 unique identities where the gender was balanced. Each participant saw each identity nine times. Stimuli were taken from the Dartmouth Database of Children's Faces (Dalrymple et al., 2013), the Developmental Emotional Faces Stimulus Set (Meuwissen et al., 2017) and the NimStim set of facial expressions (Tottenham et al., 2009). Faces were morphed to show emotions at 70% intensity to increase difficulty. All faces were greyscale and matched in luminance, contrast and colour composition.

For each face, participants were asked to judge as fast and accurately as possible whether a sentence matches the face or not. Sentences required participants to either assess physical features, recognise the displayed emotion or recognise the emotion and infer an action intention (aToM). Only the aToM condition is subject of this paper. We used the same sentences as Mier et al. (2010) but replaced the subject with either 'person' or 'child' depending on the protagonist, for example: 'This child is going to run away' (fear), 'This person is going to complain' (anger) and 'This child is going to cry' (sadness). Similarly to previous studies by Mier and colleagues (Mier et al., 2010, 2013; Yan et al., 2020), emotions were not analysed separately as the paper focusses on aToM capacity irrespective of the specific emotion. This results in 36 adult and 36 child stimuli in the aToM condition.

Each trial started with a 2-s presentation of a sentence followed by four faces presented for 2 s each (see Figure 1). The order of matching and mismatching faces was randomised. Faces were separated by a white fixation cross that was presented for on average 1.5 s (based on a truncated exponential, $\lambda = 0.5565$, min. = 1, max. = 3). One block consisting of four faces lasted on average 16 s. Blank grey screens were presented between blocks for 9.5 s on average (based on a uniform distribution, min. = 8, max. = 11). Stimuli were presented in three runs of 18 blocks, each lasting around 8 min. Blocks were presented in pseudo-randomised order so that no more than two subsequent blocks had the same task or protagonist condition. Every block contained two pictures matching the sentence and two mismatching pictures presented in a randomised order.

Experimental procedure

First, participants were informed about the study and scanning procedure before signing the consent form. Then, an experimenter conducted a semi-structured interview on socio-demographics and family status with them. Their answers were used to calculate a socio-economic score ranging from 3 to 21

(SES; Lampert et al., 2013) and to ensure that non-mothers did not regularly interact with children. Then, they performed a short IQ screening (Baudson and Preckel, 2016) and filled out questionnaires targeting emotion regulation [emotion regulation questionnaire (ERQ); Abler and Kessler, 2009], relationship attachment [experiences in close relationships—relationship structures (ECR-RS); Fraley et al., 2011], tendency to answer socially desirable [Kurzskala Soziale Erwünschtheit (KSE-G); Kemper et al., 2012], alexithymia [Toronto alexithymia scale (TAS)-20; Popp et al., 2008] and trait empathy [interpersonal reactivity index (IRI); Paulus, 2009]. The experiment lasted 90 min, with 60 min spent in the scanner.

Sample characteristics and behavioural ratings

Analysis of the behavioural data was performed in JASP (JASP Team, 2020). Bayesian Mann–Whitney U-tests were computed with 10 000 random samples for age, SES (Lampert et al., 2013), intelligence, mood state (0–4), importance of having children (0–4) and all questionnaire scores. Mann–Whitney U-tests were corrected for multiple comparisons with Westfall's method (Westfall et al., 1997; de Jong, 2019). Bayesian contingency tables were used to compare mothers' and non-mothers' relationship status. The response time and accuracy of aToM were combined to a linear integrated speed-accuracy score (LISAS; Vandierendonck, 2017) with lower scores indicating better performance. LISAS have been shown to be a valid combination of speed and accuracy in tasks where both measures are related (Vandierendonck, 2017, 2018). To ensure this, participants were asked to respond as fast and accurately as possible. A Bayesian mixed ANOVA with factors motherhood and protagonist (child or adult) was performed to determine differences in LISAS. Variables where the Mann–Whitney U-test indicated group differences would have been added to the ANOVA as covariates; however, there were no group differences. All Bayes factors were labelled according to the adaptation of Jeffrey's scheme used in JASP (Goss-Sampson, 2020).

fMRI data acquisition

All scans were acquired at the Berlin Center for Advanced Neuroimaging using a 20-channel 3 T MRI (Siemens Magnetom Prisma, Siemens Medical Solutions, Erlangen, Germany). Structural images were acquired using a T1-weighted magnetically prepared rapid acquisition gradient echo (176 slices; voxel size = 1 mm³; repetition time (TE) = 2539 ms; echo time



Fig. 1. Schematic of block design. Each block starts with a 2-s presentation of the sentence followed by an ~ 1.5 -s presentation of a fixation cross. Then, four faces are presented for 2 s each and participants need to decide for each face whether it matches the sentence or not. Faces are separated by ~ 1.5 -s presentations of fixation crosses. Each block contains all emotions but only one task and one type of protagonist (children or adults).

(TE) = 4.94 ms; flip angle (FA) = 7°; field of view (FOV) = 256 mm), followed by field maps (32 slices each 3mm thick; TR = 400 ms; TE₁ = 5.19 ms; TE₂ = 7.65 ms; FA = 60°; FOV = 192 mm). Six runs of functional images were acquired with T2*-weighted echo-planar imaging. Three runs per participant have been analysed for this article, each consisting of 244 scans acquired in 32 consecutive slices (voxel size = 3 mm³; TR = 2,000 s; TE = 30 ms; FA = 78°; FOV = 192 mm).

fMRI data preprocessing

Preprocessing was performed using *fMRIPrep* 20.0.6 (Esteban et al., 2019) and is described in detail in an automatically generated boilerplate text included in the supplementary materials. Anatomical images were corrected for intensity non-uniformity, skull-stripped, segmented and used as T1-weighted references. Brain masks were refined and spatially normalised to the Montreal Neurological Institute space (MNI152Nlin2009cAsym, Fonov et al., 2009). Fieldmap correction, coregistration, realignment, slice time correction and normalisation were performed for each run. Only participants who moved less than one voxel over the course of each run were included in the analyses. Images were detrended based on a linear model of global signal (Macey et al., 2004), and 6 mm smoothing was applied in SPM12 (Wellcome Department of Imaging Neuroscience, University College London, UK, 2014).

fMRI analysis

Analysis of functional MRI data was performed using the general linear model (GLM) in SPM12. For each subject, one first-level GLM including all runs, conditions and tasks was specified and estimated. Each stimulus onset was modelled with the hemodynamic response function. Base contrasts for aToM stimuli were created for child and adult stimuli separately including both

matching and mismatching faces. On the second level, a flexible factorial model was specified including the factors subjects, group (mother or non-mother), protagonist (child or adult) and the interaction between group and protagonist. We performed a hypothesis-guided region-of-interest analysis by using a mask during the specification and estimation of the model, thereby applying small-volume correction. We used a single mask containing all ROIs: bilateral amygdala, insulae, precuneus and posterior cingulate cortex. Masks for all regions were taken from the Oxford atlas (Kennedy et al., n.d.). Additionally, whole-brain analyses were performed using a family-wise error (FWE) corrected $P < 0.05$ on the cluster level. A grey matter mask with a 10% probability was used on all whole-brain contrasts.

Results

Sample characteristics

Our groups of mothers and non-mothers were highly comparable. Bayesian Mann-Whitney U-tests did not reveal any significant differences between mothers and non-mothers in age, SES, mood state, intelligence and importance of having children (for descriptive statistics and Bayes factor, see Table 1). Both mothers and non-mothers had on average upper middle to high socioeconomic scores (Lampert et al., 2013). Additionally, groups did not differ significantly in the questionnaires measuring emotion regulation (ERQ), social desirability (KSE-G), alexithymia (TAS), relationship attachment (ECR-RS), trait empathy and perspective taking (both IRI). However, there is decisive evidence that more mothers were in a relationship than non-mothers as evidenced by a Bayesian Contingency table (indep. multinomial, $BF_{10} = 108$). In fact, 73% of non-mothers but only 25% of mothers in this sample were single. Thus, despite being similar in many relevant aspects, mothers and non-mothers differed in their relationship status.

Table 2. Average and standard errors of reaction times and accuracies for mothers and non-mothers in the aToM task. For the LISAS, lower scores correspond to a better performance. Performance in the task was not significantly associated with the predictors protagonist and motherhood or the interaction of both predictors

| | Reaction times (ms) | | Accuracies (%) | | LISAS | |
|-------------|---------------------|-----------|----------------|------------|-----------|-----------|
| | Children | Adults | Children | Adults | Children | Adults |
| Mothers | 1125 ± 25 | 1106 ± 17 | 79.6 ± 1.6 | 77.5 ± 1.6 | 1278 ± 29 | 1276 ± 22 |
| Non-mothers | 1104 ± 22 | 1137 ± 20 | 80.1 ± 2.1 | 76.0 ± 2.5 | 1260 ± 29 | 1319 ± 29 |

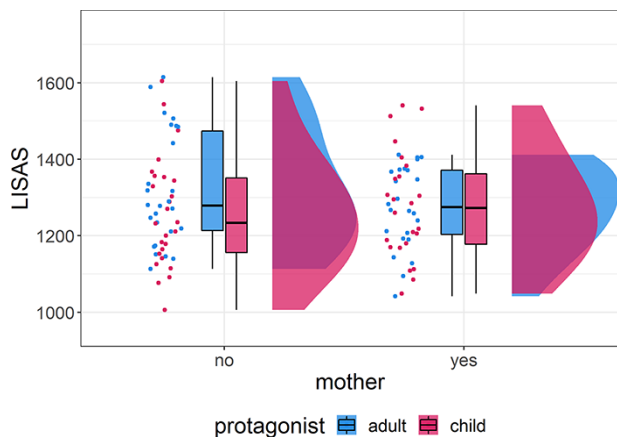


Fig. 2. LISASs in the aToM task, separately for mothers and non-mothers and children and adult stimuli. The dots represent average scores for each participant and the box plots show median and variation, with the boxes signifying values within the middle two quartiles. Additionally, the distribution of the average values of the participants is plotted per group and protagonist. For LISAS, lower scores indicate a better performance. Mothers' and non-mothers' performances were comparable for both protagonists.

Performance and LISAS

Participants performed an aToM task where they had to infer action intentions from affective adult and child faces. Generally, both groups showed a good performance with average accuracies above 75% (Table 2). To compare the performance of mothers and non-mothers, LISASs were computed out of the reaction times and the accuracies (see Figure 2). These were entered into a 2 × 2 Bayesian mixed ANOVA including factors motherhood

(mothers vs non-mothers) and protagonist (children vs adults). The Bayesian mixed ANOVA did not provide clear evidence in support of any alternative nor the null model (range BF_{10} 0.43–1.24; see Supplementary Table S1 in the supplementary materials). The inclusion Bayes factor shows anecdotal evidence against the factor motherhood ($BF_{incl} = 0.58$). This indicates that mothers' and non-mothers' performances were overall comparable. To ensure that the LISAS accurately captured the performance, we also performed Bayesian mixed ANOVAs for reaction times and accuracies which led to the same results (see Tables S1 in the supplementary materials).

fMRI results

We expected stronger brain activations in response to child relative to adult faces and generalised differences in brain responses between mothers and non-mothers as well as an interaction between both factors. To test our hypotheses, we used a flexible factorial model with one mask containing brain areas associated with emotion processing (bilateral amygdala and insulae) and aToM (bilateral precuneus and posterior cingulate cortex). The model included the factors subjects, motherhood (mother or non-mother) and protagonist (child or adult) as well as the interaction between motherhood and protagonist (Table 3). We found a significant effect of motherhood: mothers exhibited stronger activation than non-mothers in several regions of interest, notably in the bilateral posterior cingulate cortex extending into the precuneus and in the bilateral insulae (see Figure 3). No regions of interest were more strongly activated in non-mothers. We also found no differences due to the protagonists or the interaction between motherhood and protagonist. This indicates that mothers activated both emotion processing and aToM regions more strongly than non-mothers regardless of the protagonist of the stimulus.

Table 3. Results of the region-of-interest analysis. All clusters shown survive FWE correction with a threshold of $P < 0.05$ on the cluster level. There were no significant clusters in the comparison children vs adult stimuli and none in the interaction. Coordinates are in MNI space. H = hemisphere; L = left; R = right; M = medial; BA = Brodmann area

| Region | BA | H | Cluster size | t-value | x | y | z |
|----------------------------|----------------------------------|---|--------------|---------|-----|-----|----|
| Mothers > non-mothers | | | | | | | |
| Posterior cingulate cortex | 23 | L | 744 | 11.32 | -5 | -47 | 36 |
| | 7 | | | 8.81 | 6 | -49 | 52 |
| | 23 | | | 7.65 | 6 | -51 | 22 |
| Posterior cingulate cortex | 24 | R | 145 | 7.82 | 8 | -21 | 42 |
| | 31 | | | 7.04 | -3 | -25 | 46 |
| Insula | 13 | L | 134 | 7.24 | -39 | -5 | 2 |
| | 13 | | | 4.89 | -35 | -9 | 8 |
| Insula | 13 | R | 54 | 4.97 | 38 | -11 | 8 |
| | 13 | | | 3.92 | 44 | 2 | 4 |
| Insula | 13 | | | 3.56 | 42 | -11 | -3 |
| Non-mothers > mothers | No clusters reached significance | | | | | | |
| Adults > children | No clusters reached significance | | | | | | |
| Children > adults | No clusters reached significance | | | | | | |
| Interaction | No clusters reached significance | | | | | | |

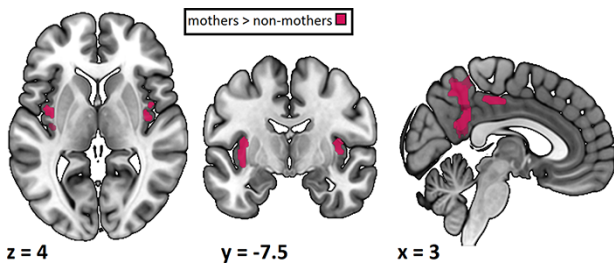


Fig. 3. Results of the region-of-interest analysis of groups pooled over protagonists. Both contrasts are t-contracts. Only clusters surviving FWE correction with $P < 0.05$ on the cluster level are shown. Mothers showed stronger activation than non-mothers in the bilateral posterior cingulate cortex and insula. There were no clusters more strongly activated in non-mothers than mothers.

This effect of motherhood was independent of the target stimuli characteristics (child or adult affective face stimuli).

To further explore differences outside of our predefined regions of interest, the same model was computed using a whole-brain analysis. We found differences between mothers and non-mothers when protagonist was pooled (Figure 4 and Supplementary Table S2 in the supplementary materials). Specifically, mothers relative to non-mothers more strongly activated areas in temporal and temporoparietal areas (bilateral middle

temporal gyrus, right superior temporal gyrus, left angular gyrus), frontal areas (bilateral middle frontal gyrus, left inferior frontal gyrus, dorsal part of medial superior frontal gyrus) and medial and superior occipital areas (around the calcarine fissure and in the fusiform gyrus). Non-mothers, on the other hand, showed increased activation compared to mothers in posterior temporal areas, the right supramarginal gyrus and supplementary motor area, frontal areas (right middle frontal gyrus, right inferior frontal gyrus, ventral part of medial superior frontal gyrus) as well as lateral and posterior occipital areas. We also observed a main effect of protagonist: for mothers and non-mothers, adult stimuli elicited higher activation of the right middle frontal and the medial superior frontal gyrus (Supplementary Table S2 in the supplementary materials and Figure 4). Child stimuli, in contrast, led to a higher activation in areas around the calcarine fissure. No regions were significantly associated with the interaction of motherhood and protagonist.

Discussion

In the present study, we found that mothers activated several areas associated with social understanding more strongly than non-mothers regardless of the target (i.e. adult or child) of their social understanding. The hypotheses-guided region-of-interest analysis revealed stronger activation in mothers than non-mothers in the bilateral insulae, an area associated with

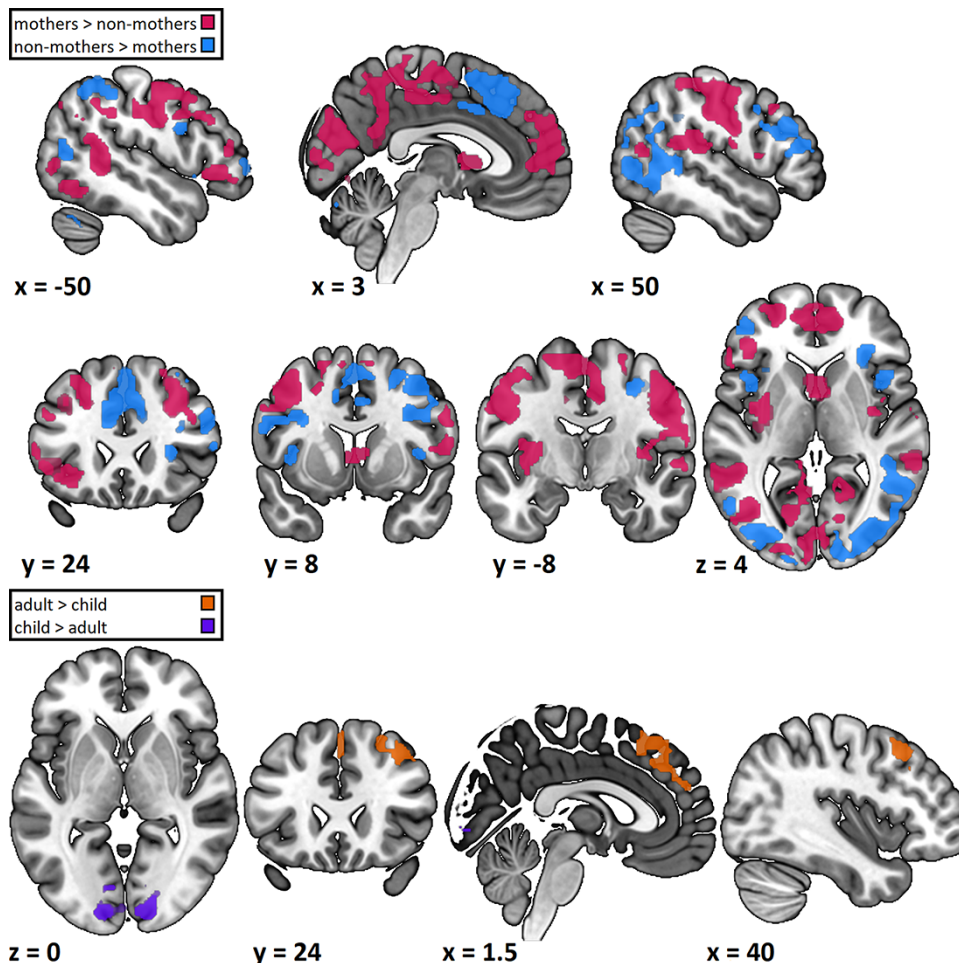


Fig. 4. Results of the whole-brain analysis. All contrasts are t-contracts. Only clusters surviving FWE correction with $P < 0.05$ on the cluster level are shown.

emotion processing, and the bilateral posterior cingulate cortex extending into the precuneus, both areas implicated in aToM. The explorative whole-brain analysis revealed differences in activation between mothers and non-mothers in further areas associated with social understanding, including the medial superior frontal gyrus, inferior frontal gyrus, middle and superior temporal gyrus, supramarginal gyrus and the angular gyrus. These differences are generalised and do not only occur when mothers infer intentions from the emotional faces of unfamiliar children but also when they infer intentions from the emotional faces of unfamiliar adults. The observed differences were independent of differences in behavioural performance, which was comparable in mothers and non-mothers. This could either indicate different strategies leading to comparable performance or be due to the low sensitivity of the task or power issues. The present study extends existing results showing differences in social understanding in mothers and non-mothers to aToM. These differences in aToM generalise over protagonists, applying to both adult and child stimuli.

Mothers showed a stronger activation than non-mothers in the bilateral insulae in response to both adult and child stimuli. The insulae are associated with multimodal emotion processing. According to Schirmer and Adolphs (2017), the insulae may integrate information from various sources and map it to a stored template or 'emotional gestalt'. Similarly, Singer et al. (2009) propose that the insulae are an integration hub that generates a subjective feeling state. The anterior insulae are also a core region in empathy, an important aspect of affective social understanding where a person feels with a target (Preckel et al., 2018). Our insulae finding indicates that mothers more strongly than non-mothers recruit regions associated with empathy and emotion processing even during an aToM task that does not explicitly require emotional involvement. This extends data showing increased activation in the bilateral insulae in mothers compared to non-mothers in response to others in pain in an empathy task (Plank et al., 2021).

In our aToM task, mothers relative to non-mothers more strongly activated the bilateral posterior cingulate cortex extending into the precuneus. The posterior cingulate cortex has been consistently associated with aToM although its specific role is still unclear (Leech and Sharp, 2014; Kogler et al., 2020). According to Rolls (2019), it is possible that the cingulate cortex performs action-outcome learning. The posterior cingulate cortex has outputs to the memory system, which might indicate that it allows both storing and retrieving the learned link of action and outcome. In the context of our task, where participants had to link an emotion to an action intention, the posterior cingulate cortex may have enabled them to rely on learned connections to derive predictions. A stronger activation in mothers compared to non-mothers may indicate that they rely more heavily on these memories to derive an action intention from affective faces.

Contrary to our expectations, there were no differences in the amygdala in any of our contrasts. The amygdala has been consistently associated with emotion processing (Baas et al., 2004). Although it is predominantly associated with fear processing, the amygdala has also been implicated in processing social stimuli (Bzdok et al., 2011). Most importantly, the amygdala is a key component of the parental brain (Feldman, 2015). However, this association is based on studies that compare own vs unfamiliar children (Luo et al., 2015b). Therefore, the missing effect in the amygdala could indicate that this area is associated with responses to the own child and is not generally affected by motherhood.

In summary, the explorative whole-brain analysis revealed a clear pattern of activation where mothers show increased activity in areas associated with autobiographical memories and the experience of emotions while non-mothers more strongly activated areas associated with attention reorienting, emotion regulation and social control. In the following paragraphs, we will discuss selected areas and their functions in more detail.

Mothers activated several temporal and temporoparietal regions especially in the left hemisphere more strongly than non-mothers. Among those were the bilateral middle temporal gyrus, the left superior temporal gyrus and the left angular gyrus. However, they activated more posterior subareas of the left middle temporal gyrus as well as temporoparietal regions in the right hemisphere including the supramarginal gyrus less strongly than non-mothers. Arioli and Canessa (2019) have associated the temporal cortex with a progression from processing individual actions to social interactions to ToM. In our study, mothers activated areas that Arioli and Canessa associated with ToM more strongly, while activating areas associated with action observation and social interaction less strongly. Additionally, the more superior regions around the temporoparietal junction showed a lateralised difference between mothers and non-mothers with increased activation in the left hemisphere in mothers and increased activation in the right hemisphere in non-mothers. Several studies have implicated the left angular gyrus with memory, more specifically autobiographical memory (Bonnici et al., 2018; Ramanan et al., 2018). The increased activation in this region could indicate that mothers more strongly rely on their previous experiences to make their aToM judgements than non-mothers. On the other hand, mothers activated the right supramarginal gyrus less strongly than non-mothers. The right supramarginal gyrus is associated with attention reorienting and spatially close to the temporoparietal junction (Schurz et al., 2017). The differential recruitment of areas implicated in cognitive social understanding indicates that mothers and non-mothers may differ in their strategies, involving different ToM regions when performing the same aToM task. These results open the possibility that mothers rely more heavily on memory and learned connections as reflected by their increased activation of the angular gyrus while non-mothers more strongly used right-hemispheric areas associated with attention reorienting as reflected by the supramarginal gyrus to derive action intentions from affective faces. Together with the stronger activation in the bilateral posterior cingulate cortex and the stronger activation in areas Arioli and Canessa associated with ToM, indicating a stronger reliance on classical aToM areas, this might indicate a stronger focus on affective and mental states in mothers than non-mothers.

The whole-brain analysis also revealed extensive differences in activation in prefrontal areas between mothers and non-mothers. Mothers activated medial ventral areas more strongly, while non-mothers showed stronger activation in medial dorsal areas. According to Phillips et al. (2003, 2008), ventral prefrontal areas are associated with emotion identification and production, while dorsal areas are more strongly associated with emotion regulation possibly indicating that mothers may have focused more on emotion identification and non-mothers on regulation. Another area differentially activated in mothers and non-mothers was the inferior frontal gyrus. The inferior frontal gyrus specifically has been implicated in both social semantics and control as well as emotion regulation (Morawetz et al., 2017; Binney and Ramsey, 2020). Mothers activated mainly subareas of the inferior frontal gyrus in the left hemisphere more strongly but in the right hemisphere less strongly than non-mothers. The same holds for the middle

frontal gyrus with mothers activating the left more strongly and the most subareas of the right less strongly than non-mothers. According to Ochsner et al. (2012), the right prefrontal cortex is more strongly associated with specifically the downregulation of emotion (Ochsner et al., 2012). Therefore, many of the regions that non-mothers activated more strongly than mothers (frontal areas but also the supplementary motor area) have been associated with some social control and emotion regulation (Etkin et al., 2015). One possible interpretation is that non-mothers downregulated their emotions more strongly than mothers did, while mothers focused more strongly on emotion identification and production as reflected by the increased activation in the insulae.

Some of the areas differentially activated by mothers and non-mothers have been implicated in grey matter volume reductions due to motherhood. This includes already discussed areas in the middle temporal gyrus, medial frontal gyrus, inferior frontal gyrus and the precuneus but also areas in the fusiform gyrus (Hoekzema et al., 2017). The fusiform gyrus is most commonly associated with face processing (Kanwisher et al., 1997). In our sample, mothers activated the left fusiform gyrus more strongly but the right less strongly as compared to non-mothers. According to Meng et al. (2012), it is possible that the left hemisphere is responsible for 'low-level' facial features while the right is performing a deeper analysis (Meng et al., 2012). Another area that changes when women become mothers is the ventral striatum (Lisofsky et al., 2016; Hoekzema et al., 2020). Although we did not find any differences in the ventral striatum itself, mothers activated an adjacent area in the caudate nucleus more strongly. In mothers, the reduction in the ventral striatal volume was associated with neural activation in response to offspring cues, indicating that this reduction may have led to increased responsiveness in the maternal reward system (Hoekzema et al., 2020). These differences might indicate that at least some functional differences are due to structural changes during pregnancy.

Notably, the differences in activation between mothers and non-mothers emerged despite no evidence for differences in performance. Generally, both groups showed a good performance with average accuracies above 75%. The fact that there was no clear evidence for performance differences due to motherhood and protagonist may be due to the low sensitivity of the specific task employed, which was chosen to increase the detection power for neural differences. Additionally to a lack of power due to the task, the lack of differences may also be caused by a lack of power due to the sample size. Therefore, it cannot be ruled out that more sensitive behavioural measures might detect differences similarly to those observed for affect recognition (Matsunaga et al., 2018). The differences on the neural level observed in this study may be a precursor of subtle differences on the behavioural level as well.

We found no differences between adult and child stimuli within the regions of interest but significant clusters outside of the regions of interest in the whole-brain analysis. Child stimuli led to a higher activation in visual processing areas around the calcarine fissure including the lingual gyrus, cuneus and the fusiform gyrus in both mothers and non-mothers. This is in line with previous research showing increased activation in these areas in response to unfamiliar infants or children compared to unfamiliar adults in both mothers (Leibenluft et al., 2004) and non-mothers (Glocker et al., 2009; Caria et al., 2012; Li et al., 2016). It has been argued that increased activation of visual processing areas in response to infant faces may be evolutionarily beneficial as it increases caregiving (Kringelbach et al., 2017). This is corroborated by the findings of increased activation in the fusiform gyrus in response to the own as compared to an unfamiliar child

(Stoeckel et al., 2014). Although we used child and not infant faces, a similar effect may be the reason for this increased activation in visual processing areas. In turn, adult stimuli led to a stronger activation of frontal areas, more specifically the right middle frontal gyrus and the medial superior frontal gyrus. The area in the medial superior frontal cortex overlaps partially with a cluster associated with cognitive social understanding in the meta-analysis by Kogler et al. (2020). According to them, this area is associated with perspective-taking and self-other distinction. It is possible that the higher similarity between our participants and the adult stimuli has led to a higher need for self-other distinction, which is reflected in this increased activity in the medial superior frontal gyrus. The right middle frontal gyrus has been implicated in reorienting attention (Japee et al., 2015). Overall, the differential pattern of activation observed in the present study might indicate that while child stimuli led to a stronger engagement of visual processing, there are some aspects of aToM processing that were more strongly activated in response to adult stimuli possibly due to the higher similarity.

Surprisingly, we found no interaction between motherhood and the protagonist. Studies on attention allocation (Thompson-Booth et al., 2014a) and affect recognition (Nishitani et al., 2011; Matsunaga et al., 2018) have found interaction effects both on the behavioural and the neural level using unfamiliar faces. However, most of the studies used infant and not child stimuli. As children age, their faces become increasingly similar to adult faces. Differences between mothers and non-mothers that might exist when comparing the processing of infant and adult faces could decrease when comparing child and adult faces. Additionally, none of the studies have investigated aToM. Higher cognitive functions like aToM may be less influenced by the protagonist because salience differences in emotion expression are less important than they are in basic emotion processing and recognition. Therefore, an interaction possibly only applies to some subprocesses of social understanding or affects only infants.

The missing interaction in our data indicates that differences in aToM between mothers and non-mothers are not confined to unfamiliar children but generalise to other adults as well. aToM involves additional inferential processing of the information compared with affect recognition. This leads to a higher level of abstraction, which might be the reason for this generalisation. However, another reason for the generalisation in our study could be the duration of motherhood and not the type of task. The above-mentioned studies all used infant stimuli and therefore mothers of infants. In our study, the duration of motherhood ranged from 3 to 22 years giving enough time for generalisation to occur. It is also worth mentioning that the here presented study used unfamiliar faces and does not rule out increased responses to mothers' own children (see, for example, Kluczniok et al., 2017).

This study shows differences in neural activity in mothers compared to non-mothers when performing an aToM task. The causal relationship between the neural differences and motherhood cannot be determined by this cross-sectional study; however, there are two options, which may also be working together: either differences in neural processing lead to an increased likelihood to become a mother or motherhood leads to the neural differences. Supporting an influence of differences in neural processing on the likelihood to become a mother are studies reporting a positive effect of empathy on romantic relationships (Levenson and Gottman, 1985; Thomsen and Gilbert, 1998; Cramer and Jowett, 2010; Coutinho et al., 2014). Additionally, some of the non-mothers are potentially not childless by choice. The reasons

for this potentially unintended childlessness of some of the non-mothers may include biological reasons but also factors that may be connected to social understanding. Specifically, increased neural response to social understanding tasks may increase the likelihood to be in a relationship and also to become a mother.

There are also several possibilities supporting the hypothesis that motherhood leads to neural differences. First, motherhood is associated with hormonal changes, which in turn have been shown to impact emotion processing (Graham *et al.*, 2017; Osório *et al.*, 2018; Wu *et al.*, 2014a,b). As female hormonal levels vary across the cycle and lifetime with, for example, levels of oestradiol declining in menopause (Galea *et al.*, 2018; Dubol *et al.*, 2021; Rehbein *et al.*, 2021), follow-up studies should include hormonal levels to investigate whether the neural changes we found in the present study are connected with hormones. Second, motherhood leads to structural changes in brain areas strongly associated with social understanding (Hoekzema *et al.*, 2017, 2020). Many of these structures also showed increased activation in mothers compared to non-mothers in the present study, including the superior temporal sulcus and fusiform gyrus. Structural changes could also explain why the effect generalises to adult stimuli and is not confined to children. Third, studies have also shown that social understanding can be trained and shaped by experience (Hildebrandt *et al.*, 2019; Trautwein *et al.*, 2020). Parenting involves high frequency of social understanding combined with high importance of correctly interpreting social cues and therefore might serve as a training for social understanding. Studies comparing biological mothers with foster and adoptive mothers have found remarkable similarities in attention allocation (Grasso *et al.*, 2009) and cortical synchronisation as measured with electroencephalography (Pérez-Hernández *et al.*, 2017). This indicates that even without genetic relation, motherhood still leads to differences in social understanding lending further support for the possibility of training effects of motherhood. However, it is impossible to disentangle the direction of the here presented effect of motherhood based on this cross-sectional study and both directions might have influenced our results.

Despite mothers and non-mothers being comparable in many aspects in this sample, there was one factor in which they differed: relationship status. While most mothers were in a relationship, most non-mothers were single. For women who want to have children, being in a relationship may increase the likelihood of them having a child. Therefore, relationship status may have influenced the results in either direction: increased neural response when performing aToM may increase the likelihood to be in a relationship or being in a relationship may affect neural processing. Romantic relationships require increased levels of aToM and other aspects of social understanding, similarly to parenting. Specifically, the non-existent interaction effect may have been due to relationship status. Being a mother might have increased neural response in our regions of interest in response to child stimuli while being in a romantic relationship led to the same effect in response to adults. Apart from Parsons *et al.* (2017) who also reported that mothers were more likely to be in a relationship, most other studies comparing mothers and non-mothers have not reported relationship status (Proverbio *et al.*, 2006; Nishitani *et al.*, 2011; Thompson-Booth *et al.*, 2014a,b; Parsons *et al.*, 2016; Hayashi *et al.*, 2018; Matsunaga *et al.*, 2018; Zhang *et al.*, 2020). Therefore, it is necessary to conduct further research to disentangle parenthood and relationship status and shed further light on the influences of parenthood on social understanding separated from possible influences of relationship status.

In conclusion, this study provides evidence for differences in aToM processing between mothers and non-mothers in response to adult and child stimuli. Mothers more strongly recruited areas associated with emotion processing and aToM, whereas non-mothers relied more heavily on areas associated with emotion regulation and social control. This difference in activation might reflect differences in strategies when solving the same task with a comparable level of performance with mothers possibly processing the emotions more strongly while non-mothers regulate them. Interestingly, there was no interaction between motherhood and the protagonist of the stimuli on the neural level, suggesting that the effect of motherhood is not specific to children but generalises to other adults as well. Overall, the present findings suggest that motherhood is associated with differences in strategies for the derivation of action intention predictions, involving differences in emotion and aToM processing.

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Conflict of interest

The authors declare no competing interests.

Supplementary data

Supplementary data are available at SCAN online.

Author contributions

I.S.P., C.H.A., I.D. and F.B. conceptualised and designed the study. I.S.P. took the lead on acquisition and analysis with contributions of C.H.A. I.S.P. wrote the draft. All authors contributed to the interpretation of the data and the revision of the manuscript. All authors provided critical feedback and helped shape the research, analysis and manuscript.

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