Motherhood and theory of mind: increased activation in affective theory of mind and emotion processing areas

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Abstract

There is growing evidence that parenthood changes how people face the specific needs and requests of infants and children, especially their own. However, little is known about the influence of parenthood on theory of mind, the capacity to infer mental and affective states of others and derive action predictions based on these states. It is also unclear whether the effects of parenthood generalise to inferring states of adults or are specific to children. In this study, we investigated neural activation in mothers and women without children during an affective theory of mind task that focuses on predicting action intentions from both child and adult faces. Region-of-interest analyses showed that both emotion and theory of mind areas were activated more strongly in mothers than women without children. These differences were not specific to child stimuli but occurred in response to both adult and child stimuli. Different neural recruitment of emotion and theory of mind related areas might indicate that mothers and non-mothers employ different strategies to infer action intentions from affective faces. Whether these general differences in affective theory of mind between mothers and non-mothers are due to biological or experience-related changes should be subject of further investigation.

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 multi-level changes in parents (Pereira & Ferreira, 2016). The network of brain areas associated with parenting is often referred to as “parental brain”. This “parental brain” encompasses a myriad of neural structures that are involved in cognitive and affective social understanding (Young et al., 2017). 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., Kanske, 2018; Shamay-Tsoory, 2011). 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 ToM is used to infer affective states, it is referred to as affective ToM (aToM) as compared to cognitive ToM (cToM) when inferring mental states like beliefs.

Differences between parents and non-parents in social understanding are found both on the behavioural and neural level. Parents compared to non-parents are more likely to ascribe mental states to infants (Shinohara & Moriguchi, 2017), express a stronger bias towards infant and child faces (Thompson-Booth et al., 2014b, 2014a) and rate infant facial expressions as more extreme (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 and colleagues (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 versus 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 and colleagues (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 and colleagues (2011) found differences in 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., 2011; Luo, Kendrick, et al., 2015; 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, Ma, et al., 2015). 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 and colleagues (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 (Arora et al., 2017; Molenberghs et al., 2016; Schurz et al., 2014). 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 theory of mind 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 & Sharp, 2014; Rolls, 2019). Important areas for emotion processing are the bilateral amygdala and insula. The amygdala is associated with affect recognition in general but with fear in particular (Adolphs, 2002). The insula 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. 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 versus 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 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 (BMFSFJ, 2019; Statistisches Bundesamt, 2018). Based on previous literature, we hypothesised stronger brain activations in response to child relative to adult faces in mothers and non-mothers (main effect protagonist) and generalised differences in brain responses between mothers and non-mothers (main effect motherhood), both in emotion processing (bilateral insula and amygdala; Gobbini & 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/>

Participants

We aimed for a sample of 54 women based on a priori estimation for a within-between interaction in a 2x2 mixed ANOVA in G*Power ($f = 0.25$, $\alpha = 0.05$, $(1-\beta) = 0.95$, $corr = 0.5$; 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 Covid-19 outbreak. The analysis includes 26 non-mothers (mean age 35.92 years) and 24 mothers (mean age 38.38 years). Post hoc power calculations for 50 participants indicate a power of 0.93 using the same settings as for the a priori estimation. Women were screened to ensure the following criteria: MRI compatibility, right-handedness, good health, cisgender woman, 25 to 50 years old and sufficient knowledge of German. Mothers had at least one biological child between 4 and 10 years of age. Non-mothers were excluded if they interacted with children in a private or professional context on a regular basis. Mothers and non-mothers did not significantly differ in age, intelligence or socio-economic status (see Table 1). 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.

Table 1: Comparison of mothers and non-mothers using Bayesian Mann-Whitney-U Tests. 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

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 to 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 to 4)	3.0 +- (0.1)	3.0 +- (0.1)	0.081	311.00
SES	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

ECR-RS = experiences in close relationships – relationship structures; ERQ = emotion regulation questionnaire;

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; SES = socio-economic status; TAS = Toronto alexithymia scale.

Materials

Our task was adapted from Mier and colleagues (2010). Participants saw pictures of angry, happy and afraid adult and child faces. There were 12 children (7 to 10 years old) and 12 adults (21 to 30 years old) 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 “adult” or “child” depending on the protagonist. Emotions were not analysed separately, resulting in 36 adult and 36 child stimuli in the aToM condition.

Each trial started with a 2s presentation of a sentence followed by four faces presented for 2s each (see Figure 1). Faces were separated by a white fixation cross that was presented for on average 1.5s (based on a truncated exponential, $\lambda = 0.5565$, $min = 1$, $max = 3$). One block consisting of four faces lasted on average 16s. Blank grey screens were presented between blocks for 9.5s on average (based on a uniform distribution, $min = 8$, $max = 11$). Stimuli were presented in three runs of 18 blocks, each lasting around 8min. 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.

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

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 before they performed a short IQ screening (Baudson & Preckel, 2016) and filled out questionnaires targeting emotion regulation (ERQ; Abler & Kessler, 2009), relationship attachment (ECR-RS; Fraley et al., 2011), tendency to answer socially desirable (KSE-G; Kemper et al., 2012), alexithymia (TAS-20; Popp et al., 2008) and trait empathy (IRI; Paulus, 2009). The experiment lasted 90min with 60min spent in the scanner.

Sample characteristics and behavioural ratings

Analysis of the behavioural data were performed in JASP (JASP Team, 2020). Bayesian Mann-Whitney-U tests were computed with 10,000 random samples for age, socio-economic status (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 (de Jong, 2019; Westfall et al., 1997). Bayesian contingency tables were used to compare mothers' and non-mothers' relationship status. Response time and accuracy of aToM were combined to a linear integrated speed-accuracy score (LISAS; Vandierendonck, 2018) with lower scores indicating better performance. 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 3T 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 = 1mm³; TR = 2,539ms; FA = 7°; FOV = 256mm), followed by field maps (32 slices à 3mm; TR = 400ms; TE₁ = 5.19ms; TE₂ = 7.65ms; FA = 60°; FOV = 192mm). Six runs of functional images were acquired with T2*-weighted echo-planar imaging (EPI). Three runs per participant have been analysed for this article, each consisting of 244 scans acquired in 32 consecutive slices (voxel size = 3mm³; TR = 2,000s; TE = 30ms; FA = 78°; FOV = 192mm).

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., 2011). 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 6mm 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. 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 with a single mask containing all regions of interest: bilateral amygdala, insula, precuneus and posterior cingulate cortex. Masks for all regions were

taken from the Oxford atlas (Kennedy et al.). 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, socio-economic status, mood state, intelligence and importance of having children (for descriptive statistics and Bayes factor see Table 1). 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.

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% (see Table 2). To compare the performance of mothers and non-mothers, linear integrated speed-accuracy scores were computed out of the reaction times and the accuracies (see Figure 2). These were entered into a 2x2 Bayesian mixed ANOVA including factors motherhood (mothers versus non-mothers) and protagonist (children versus 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 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.

Table 2: Average and standard errors of reaction times and accuracies for mothers and non-mothers in the ToM task.

	Reaction times		Accuracies	
	Children	Adults	Children	Adults
Mothers	1125 ± 25	1106 ± 17	79.6% ± 1.6%	77.5% ± 1.6%
Non-mothers	1104 ± 22	1137 ± 20	80.1% ± 2.1%	76.0% ± 2.5%

Figure 2: Linear integrated speed-accuracy scores in the ToM task, separately for mothers and non-mothers and children and adult stimuli. Mothers' and non-mothers' performance were comparable for both protagonists.

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 insula) 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 (see Table 3). We found a strong 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 insula (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. This effect of motherhood was independent of the target stimuli characteristics (child or adult affective face stimuli).

Table 3: Results of the region-of-interest analysis. All clusters shown survive family-wise error correction with a threshold of $p < 0.05$ on the cluster level. There were no significant clusters in the comparison children versus 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

Figure 3: Results of the region-of-interest analysis of groups pooled over protagonists. Both contrasts are t-contrasts. Only clusters surviving family-wise error 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.

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 (see Table S2 and Figure S1 in the supplementary materials). Specifically, mothers relative to non-mothers more strongly activated areas in clusters centred around the calcarine fissure, in the bilateral middle and right superior temporal gyrus, the left

inferior frontal gyrus (triangular part) and insula, both anterior and posterior, as well as the medial superior frontal gyrus. Non-mothers, on the other hand, showed increased activation compared to mothers in occipital regions as well as the right inferior frontal gyrus (triangular part), the right supplementary motor area and supramarginal gyrus. 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 (see 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.

Figure 4: Results of the whole-brain analysis of protagonist pooled over groups. Both contrasts are t-contrasts. Only clusters surviving family-wise error correction with $p < 0.05$ on the cluster-level are shown. Children stimuli led to stronger activation in the occipital lobe, especially areas around the calcarine fissure. Adult stimuli led to increased activation in frontal areas, especially the medial superior frontal gyrus and the right middle frontal gyrus.

Discussion

In the present study, we found that mothers activated areas associated with emotion processing and aToM more strongly than non-mothers regardless of the target (i.e., adult or child) of their social understanding. The aToM task was to infer the emotion from faces and make an action intention prediction based on the displayed emotion. Within our mask used for the region-of-interest analysis, mothers showed stronger activation than non-mothers in the bilateral insulae, an area associated

with emotion processing, and the bilateral posterior cingulate cortex extending into the precuneus, both areas implicated in aToM. The whole-brain analysis revealed differences in activation between mothers and non-mothers in further areas associated with social understanding, including the inferior frontal gyrus, superior temporal gyrus, supramarginal gyrus and the angular gyrus. This difference is generalised in that it not only occurs when mothers infer intentions from the emotional faces of children but also when they infer intentions from the emotional faces of adults. Thereby, this study extends existing results showing differences in social understanding in mothers and non-mothers to aToM. These differences in aToM generalise over protagonists, applying both to adult and child stimuli.

Mothers showed a stronger activation than non-mothers in the bilateral insula in response to both adult and child stimuli. The insula is associated with multimodal emotion processing. According to Schirmer and Adolphs (2017), the insula may integrate information from various sources and map it to a stored template or “emotional gestalt”. Similarly, Singer and colleagues (2009) propose that the insula is an integration hub that generates a subjective feeling state. The anterior insula is 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 insula finding indicates that mothers more strongly than non-mothers recruit regions associated with empathy and emotion processing even during an aToM task which does not explicitly require emotional involvement. This extends data showing increased activation in the bilateral insula 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 (Kogler et al., 2020; Leech & Sharp, 2014). 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 to both store and retrieve 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.

Mothers activated further areas associated with cognitive aspects of social understanding more strongly than non-mothers as found in our explorative whole-brain analysis. Among those were the bilateral middle temporal, the left superior temporal gyrus and the left angular gyrus (Mier et al., 2010; Schurz et al., 2020). Several studies have implicated the left angular gyrus with memory, more specifically autobiographical memory (Bonnici et al., 2018; Ramanan et al., 2018). Arioli & Canessa (2019) have associated the temporal cortex with a progression from processing individual actions to social interactions to mental states. They propose that the middle temporal cortex is more action oriented and areas closer to the temporo-parietal junction are more mental-state oriented. Interestingly, non-mothers activated areas in the right hemisphere associated with cToM more strongly than mothers, for example the right supramarginal gyrus (Schurz et al., 2020). This differential recruitment of social cognitive areas indicates that mothers and non-mothers may differ in their strategies, involving different ToM regions when performing the same aToM task. Together with the stronger activation in the bilateral posterior cingulate cortex, these results open the possibility that mothers rely more heavily on memory, learned connections and aToM while non-mothers more strongly used right-hemispheric areas associated with cToM to derive action intentions from affective faces.

The whole-brain analysis also revealed extensive differences in activation in prefrontal areas between mothers and non-mothers. Mothers activated ventral areas more strongly, while non-mothers showed stronger activation in medial dorsal areas but also in the bilateral inferior frontal gyrus. According to Philipps and colleagues (2003, 2008), ventral prefrontal areas are associated with

emotion identification and production, while dorsal areas are more strongly associated with emotion regulation. Binney and Ramsey (2020) also implicated the inferior frontal gyrus in social semantics and control. 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 sort of social control and emotion regulation (Etkin et al., 2015). Taken together with the stronger activation mothers show in the bilateral insula, one interpretation is that non-mothers regulated their emotions more strongly leading to less affective responsivity to the stimuli.

Notably, the differences in activation between mothers and non-mothers emerged despite of 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 low sensitivity of the specific task employed which was chosen to increase detection power for neural differences. 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).

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 occipital areas around the calcarine fissure in both mothers and non-mothers. This is in line with previous research showing increased activation in response to unfamiliar children compared to unfamiliar adults in both mothers (Leibenluft et al., 2004) and non-mothers (Li et al., 2016). 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. This is not in line with Li and colleagues (2016) who found higher activation in occipital but not frontal areas in response to adult compared to child stimuli. These differences might be due to task-related differences. The medial superior frontal cortex we found in our study is associated with reasoning and especially with ToM (Van Overwalle, 2011). This 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.

Surprisingly, we found no interaction between motherhood and the protagonist. Studies on attention allocation (Thompson-Booth et al., 2014a) and affect recognition (Matsunaga et al., 2018; Nishitani et al., 2011) have found interaction effects both on the behavioural and the neural level. 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 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 three to 22 years giving enough time for generalisation to occur.

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 are still unclear with two main 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. The positive effect of empathy on romantic relationships has been well documented (Coutinho et al., 2014; Cramer & Jowett, 2010; Levenson & Gottman, 1985; Thomsen & Gilbert, 1998). However, some of the non-mothers in our sample may still end up having children based on their age and the importance they place on having children. It is impossible to disentangle the contributions of both based on this cross-sectional study and both might have influenced our results.

There are also several possibilities supporting the hypothesis that motherhood leads to neural differences. First, motherhood and the associated hormonal changes lead to structural differences in 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. Second, 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.

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. Therefore, relationship status may have influenced the results. 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 improved aToM for child stimuli while being in a romantic relationship improved aToM for 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 (Hayashi et al., 2018; Matsunaga et al., 2018; Nishitani et al., 2011; Parsons et al., 2016; Proverbio et al., 2006; Thompson-Booth et al., 2014b, 2014a; 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.

In conclusion, this study provides the first evidence for differences in ToM 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. All in all, the present findings suggest that motherhood is associated with differences in strategies for the derivation of action intention predictions, involving differences in emotion and ToM processing.

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Author contributions

IP, CH, ID and FB conceptualised and designed the study. IP took the lead on acquisition and analysis with contributions of CH. IP 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.

Competing interests

The authors declare no competing interests.

Supplementary Material

Table S1 Bayes Factors, posterior probability and error for all models of the 2x2 Bayesian mixed ANOVA investigating LISAS.

There is only anecdotal evidence for the second-best model which includes motherhood and protagonist as well as the interaction.

Models	$P(M data)$	BF_M	BF_{10}	error %
Null model (incl. subject)	0.240	1.260	1.000	
protagonist	0.296	1.684	1.237	2.499
protagonist + motherhood + protagonist * motherhood	0.238	1.249	0.993	2.687
protagonist + motherhood	0.123	0.560	0.513	2.412
motherhood	0.103	0.462	0.432	1.992
Analysis of effects			BF_{incl}	
protagonist			1.277	
motherhood			0.577	
protagonist * motherhood			1.249

Figure S1 Results of the whole-brain analysis of groups pooled over protagonists. Both contrasts are t-contracts. Only clusters surviving family-wise error correction with $p < 0.05$ on the cluster-level are shown.

Table S2 Results of the whole-brain analysis. All clusters shown survive family-wise error correction with $p < 0.05$ on the cluster level. There were no significant clusters in the interaction of protagonist and motherhood. 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							
Calcarine fissure	18	L	16431	22.84	-7	-97	12
	18			20.62	14	-95	18
	18			20.42	-29	-93	10
Middle temporal gyrus	21	L	497	12.88	-57	-49	6
	39			5.24	-63	-55	6
	39			5.12	-51	-53	20
Precentral gyrus	6	L	2146	12.69	-37	6	44
	1			10.23	-63	-15	30

	4			9.17	-53	-9	50
Superior temporal gyrus	22	R	674	11.61	62	-39	8
	22			8.98	50	-41	18
	40			7.25	52	-31	20
Middle frontal gyrus	9	R	621	11.50	34	32	40
	8			8.88	32	26	48
	9			8.02	36	38	26
Superior frontal gyrus	10	L	1606	11.06	-17	60	24
	10			10.69	10	54	10
	10			10.58	-3	60	8
Middle occipital gyrus	19	L	167	9.99	-41	-69	6
	19			6.10	-51	-77	-1
Inferior occipital gyrus	37	L	97	9.92	-49	-65	-15
	37			5.99	-51	-57	-15
Middle temporal gyrus	19	R	117	9.10	48	-63	12
	39			7.61	40	-59	14
Superior parietal gyrus	7	L	218	8.60	-25	-59	64
	7			7.39	-21	-57	56
	7			4.78	-31	-53	60
Inferior frontal gyrus	45	L	675	7.53	-43	36	2
	47			7.47	-51	28	-5
	46			7.09	-53	36	12
Insula	13	L	240	7.52	-33	-7	6
	13			4.20	-39	-11	12
Superior frontal gyrus	8	M	174	7.35	-11	42	52
	8			6.94	-17	42	46
	8			6.23	-7	38	46

Fusiform gyrus	37	R	101	7.10	24	-45	-19
Angular gyrus	39	L	145	7.05	-41	-59	42
	39			5.04	-45	-75	42
	39			4.78	-43	-57	34
Middle frontal gyrus	9	L	105	6.77	-37	28	38
	9			5.57	-31	36	32
Middle frontal gyrus	8	L	241	6.51	-29	26	52
	9			5.76	-25	26	40
	6			5.71	-25	16	48
Caudate		R	105	6.49	2	6	6
				4.35	-5	12	6
non-mothers > mothers							
Middle occipital gyrus	18	R	5878	28.06	42	-87	2
	18			24.27	34	-81	6
	18			22.00	28	-87	4
Inferior occipital gyrus	18	L	2298	24.13	-31	-89	-5
	18			16.26	-21	-91	-13
	19			15.03	-37	-77	-19
Inferior parietal gyrus	7	L	793	14.23	-27	-73	42
	7			10.59	-31	-69	58
	7			8.49	-27	-53	40
Inferior frontal gyrus	9	R	1394	13.18	42	30	28
	10			10.11	42	50	18
	8			9.64	38	8	50
Supplementary motor area	6	R	1299	11.71	2	10	58
	8			9.43	8	30	40
	8			8.58	-1	26	40

Middle temporal gyrus	19	L	101	9.87	-55	-69	10
Middle frontal gyrus	9	R	242	9.45	34	46	36
	9			6.38	26	38	40
Supramarginal gyrus	40	R	266	9.35	64	-41	34
	40			7.13	60	-27	30
Inferior frontal gyrus	46	L	114	8.03	-47	48	2
Inferior parietal gyrus	40	L	152	7.99	-51	-49	56
	39			6.60	-49	-55	50
	40			6.23	-55	-41	52
Precuneus	7	L	218	7.23	-9	-67	50
	7			6.86	-11	-65	40
	31			6.31	-13	-57	42
Inferior frontal gyrus	44	R	211	7.13	44	16	4
	45			7.11	32	34	4
	45			5.59	40	20	12
Precentral gyrus	6	L	125	6.30	-55	6	26
	44			4.91	-33	10	26
	44			3.97	-43	12	26
Inferior frontal gyrus	45	L	131	5.20	-45	16	2
	44			4.81	-39	16	10
	45			4.14	-31	20	8
adults > children							
Middle frontal gyrus	8	R	337	6.70	46	20	48
	6			5.09	28	18	58
	8			4.52	28	26	56
Superior frontal gyrus	8	M	235	5.49	2	34	54
	8			4.28	4	38	42

	8			3.93	-1	22	48
children > adults							
Calcarine fissure	18	L	1251	9.43	-13	-91	-5
	18			7.00	16	-87	-5
	18			6.90	18	-95	8
Interaction	No clusters reached significance						

fMRIPrep Boilerplate Text

Results included in this manuscript come from preprocessing performed using fMRIPrep 20.0.6 (Esteban, Markiewicz, et al. (2018); Esteban, Blair, et al. (2018); RRID:SCR_016216), which is based on Nipype 1.4.2 (Gorgolewski et al. (2011); Gorgolewski et al. (2018); RRID:SCR_002502).

Anatomical data preprocessing

The T1-weighted (T1w) image was corrected for intensity non-uniformity (INU) with N4BiasFieldCorrection (Tustison et al. 2010), distributed with ANTs 2.2.0 (Avants et al. 2008, RRID:SCR_004757), and used as T1w-reference throughout the workflow. The T1w-reference was then skull-stripped with a Nipype implementation of the antsBrainExtraction.sh workflow (from ANTs), using OASIS30ANTs as target template. Brain tissue segmentation of cerebrospinal fluid (CSF), white-matter (WM) and gray-matter (GM) was performed on the brain-extracted T1w using fast (FSL 5.0.9, RRID:SCR_002823, Zhang, Brady, and Smith 2001). Brain surfaces were reconstructed using recon-all (FreeSurfer 6.0.1, RRID:SCR_001847, Dale, Fischl, and Sereno 1999), and the brain mask estimated previously was refined with a custom variation of the method to reconcile ANTs-derived and FreeSurfer-derived segmentations of the cortical gray-matter of Mindboggle (RRID:SCR_002438, Klein et al. 2017). Volume-based spatial normalization to one standard space (MNI152NLin2009cAsym) was performed through nonlinear registration with antsRegistration (ANTs 2.2.0), using brain-extracted versions of both T1w reference and the T1w template. The following

template was selected for spatial normalization: ICBM 152 Nonlinear Asymmetrical template version 2009c [Fonov et al. (2009), RRID:SCR_008796; TemplateFlow ID: MNI152NLin2009cAsym],

Functional data preprocessing

For each of the 6 BOLD runs found per subject (across all tasks and sessions), the following preprocessing was performed. First, a reference volume and its skull-stripped version were generated using a custom methodology of fMRIPrep. A B0-nonuniformity map (or fieldmap) was estimated based on a phase-difference map calculated with a dual-echo GRE (gradient-recall echo) sequence, processed with a custom workflow of SDCFlows inspired by the `epidewarp.fsl` script and further improvements in HCP Pipelines (Glasser et al. 2013). The fieldmap was then co-registered to the target EPI (echo-planar imaging) reference run and converted to a displacements field map (amenable to registration tools such as ANTs) with FSL's `fugue` and other SDCflows tools. Based on the estimated susceptibility distortion, a corrected EPI (echo-planar imaging) reference was calculated for a more accurate co-registration with the anatomical reference. The BOLD reference was then co-registered to the T1w reference using `bbregister` (FreeSurfer) which implements boundary-based registration (Greve and Fischl 2009). Co-registration was configured with six degrees of freedom. Head-motion parameters with respect to the BOLD reference (transformation matrices, and six corresponding rotation and translation parameters) are estimated before any spatiotemporal filtering using `mcflirt` (FSL 5.0.9, Jenkinson et al. 2002). BOLD runs were slice-time corrected using `3dTshift` from AFNI 20160207 (Cox and Hyde 1997, RRID:SCR_005927). The BOLD time-series (including slice-timing correction when applied) were resampled onto their original, native space by applying a single, composite transform to correct for head-motion and susceptibility distortions. These resampled BOLD time-series will be referred to as preprocessed BOLD in original space, or just preprocessed BOLD. The BOLD time-series were resampled into standard space, generating a preprocessed BOLD run in MNI152NLin2009cAsym space. First, a reference volume and its skull-stripped version were generated using a custom methodology of fMRIPrep. Several confounding time-series were calculated based on the preprocessed BOLD: framewise displacement

(FD), DVARS and three region-wise global signals. FD and DVARS are calculated for each functional run, both using their implementations in Nipype (following the definitions by Power et al. 2014). The three global signals are extracted within the CSF, the WM, and the whole-brain masks. Additionally, a set of physiological regressors were extracted to allow for component-based noise correction (CompCor, Behzadi et al. 2007). Principal components are estimated after high-pass filtering the preprocessed BOLD time-series (using a discrete cosine filter with 128s cut-off) for the two CompCor variants: temporal (tCompCor) and anatomical (aCompCor). tCompCor components are then calculated from the top 5% variable voxels within a mask covering the subcortical regions. This subcortical mask is obtained by heavily eroding the brain mask, which ensures it does not include cortical GM regions. For aCompCor, components are calculated within the intersection of the aforementioned mask and the union of CSF and WM masks calculated in T1w space, after their projection to the native space of each functional run (using the inverse BOLD-to-T1w transformation). Components are also calculated separately within the WM and CSF masks. For each CompCor decomposition, the k components with the largest singular values are retained, such that the retained components' time series are sufficient to explain 50 percent of variance across the nuisance mask (CSF, WM, combined, or temporal). The remaining components are dropped from consideration. The head-motion estimates calculated in the correction step were also placed within the corresponding confounds file. The confound time series derived from head motion estimates and global signals were expanded with the inclusion of temporal derivatives and quadratic terms for each (Satterthwaite et al. 2013). Frames that exceeded a threshold of 0.5 mm FD or 1.5 standardised DVARS were annotated as motion outliers. All resamplings can be performed with a single interpolation step by composing all the pertinent transformations (i.e. head-motion transform matrices, susceptibility distortion correction when available, and co-registrations to anatomical and output spaces). Gridded (volumetric) resamplings were performed using `antsApplyTransforms` (ANTs), configured with Lanczos interpolation to minimize the smoothing effects of other kernels (Lanczos 1964). Non-gridded (surface) resamplings were performed using `mri_vol2surf` (FreeSurfer).

Many internal operations of fMRIPrep use Nilearn 0.6.2 (Abraham et al. 2014, RRID:SCR_001362), mostly within the functional processing workflow. For more details of the pipeline, see the section corresponding to workflows in fMRIPrep's documentation.

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