

## ORIGINAL ARTICLE

# Frequency of Maternal Touch Predicts Resting Activity and Connectivity of the Developing Social Brain

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## Abstract

Previous behavioral research points to a positive relationship between maternal touch and early social development. Here, we explored the brain correlates of this relationship. The frequency of maternal touch was recorded for 43 five-year-old children during a 10 min standardized play session. Additionally, all children completed a resting-state functional magnetic resonance imaging session. Investigating the default mode network revealed a positive relation between the frequency of maternal touch and activity in the right posterior superior temporal sulcus (pSTS) extending into the temporo-parietal junction. Using this effect as a seed in a functional connectivity analysis identified a network including extended bilateral regions along the temporal lobe, bilateral frontal cortex, and left insula. Compared with children with low maternal touch, children with high maternal touch showed additional connectivity with the right dorso-medial prefrontal cortex. Together these results support the notion that childhood tactile experiences shape the developing “social brain” with a particular emphasis on a network involved in mentalizing.

**Key words:** affective touch, C-tactile afferents, resting-state fMRI, stroking, theory of mind

## Introduction

Touch powerfully communicates emotions and contributes to the formation of social bonds (Suvilehto et al. 2015). As such it plays an important role in parent–child interactions and early attachment formation. Here, we explored whether the touch parents direct at their children has effects beyond social bonding and shapes functional aspects of the developing brain. More specifically, we asked whether and how the frequency of parental touch predicts children’s engagement of brain structures known to contribute to the “social brain.”

The term “social brain” describes neuronal networks enabling our dealings with the social world. Specifically, our interest in others, our sensitivity to their emotions, thoughts, and intentions, and our ability to meaningfully interact with them are presumably supported by dedicated brain processes separate from those supporting our dealings with the inanimate world (Dunbar and Shultz 2007; Frith 2007; Adolphs 2009). Many structures, including posterior superior temporal cortex (pSTS), temporo-parietal junction (TPJ), and medial prefrontal cortex (mPFC), were identified as contributing to the “social brain” (Schirmer and Kotz 2006; Frith 2007; Van Overwalle 2009; Kennedy and Adolphs 2012;

Escoffier et al. 2013). In a recent review, these structures were organized into 4 networks referred to as 1) an amygdala network related to emotion, 2) a mentalizing network related to the attribution of mental states, 3) an empathy network related to feeling for others, and 4) a mirror network related to representing and mimicking others' actions (Kennedy and Adolphs 2012).

Although humans are born with a strong social interest and a capacity for forming social bonds, the complex social functioning of an adult requires many years of maturation and learning (Johnson et al. 2005; Happé and Frith 2014). Research into these processes identified a set of developmental periods progressing from birth to adolescence during which individuals achieve certain milestones such as the emergence of joint attention (~6 months) or basic morality (~3 years; Happé and Frith 2014). Of note, certain individual abilities such as the understanding of other's mental states that differ from one's own mental state evolve in a protracted manner spanning across developmental periods (for reviews, see Happé and Frith 2014; Lagattuta et al. 2015; Sprung et al. 2015).

The existence of developmental stages points to innate factors governing social development. Yet, environmental factors are also relevant. Parenting behaviors and, more specifically, the tactile care parents provide for their children have been highlighted in the literature. Research conducted primarily on infants points to a positive relationship between physical contact and general developmental markers such as body weight, motor control, or emotional management (Weiss 2005; Field et al. 2010). Additionally, some studies imply a positive relationship between physical contact and social development more specifically. For example, it was shown that touch promotes responsiveness to and engagement with a caregiver (Watt 1990; Peláez-Nogueras et al. 1996; Feldman et al. 2002; Jean et al. 2014) and that it furthers the formation of social attachments. Mothers who engaged in more frequent affectionate touch were more likely to have securely attached children than mothers who engaged in little affectionate touch (Ainsworth 1979; Egeland and Farber 1984; Grossmann et al. 1985; Anisfeld et al. 1990; Weiss et al. 2000).

Recent discoveries concerning the human tactile sense revealed how tactile experiences might interface with the emerging "social brain." Specifically, research identified a special mechanoreceptor called the C-tactile (CT) afferent (Iggo 1960; Iggo and Muir 1969; Olausson et al. 2002; Vrontou et al. 2013). This receptor plays no role in discriminative touch as it is absent from the palms of our hands and the soles of our feet. Instead, it enables our appreciation of social touch. CT afferents are tuned to light pressure, moderate stroking at a rate of 1–10 cm/s (Olausson et al. 2002; Löken et al. 2009), and prefer stimulation at skin temperature (Ackerley et al. 2014). Moreover, CT firing rate correlates positively with the pleasure individuals derive from touch (Löken et al. 2009). Like other C-fibers, CT afferents send slow, unmyelinated projections to the thalamus. From there, CT input reaches insula and pSTS, bypassing primary sensory cortex. Thus, CT appropriate tactile stimulation is not merely processed as a sensory experience but, by traveling to the "social brain," creates a social experience and may shape social functioning (for review, see McGlone et al. 2014).

Taken together, the research reviewed here identified dedicated brain circuits that support social functioning. It also points to touch as an important environmental factor that could shape social development. To date, evidence for this comes from studies linking tactile care to children's social behavior as well as studies identifying a dedicated social touch system projecting to the social brain. Here we aimed at integrating these lines of work and to explore the relationship between tactile care and the emerging social brain.

To this end, we invited 5-year-old children and their mothers to participate in a behavioral and a neuroimaging session. The behavioral session comprised a 10-min observational period during which children played with their mothers and for which we recorded the frequency of maternal and child touch. During the neuroimaging session, we subjected children to functional magnetic resonance imaging (fMRI) as to measure their brain activity during wakeful rest. Here, our focus was on 2 variables referred to as regional homogeneity (ReHo) and resting-state functional connectivity (RSFC).

ReHo reflects local temporal synchronization in the spontaneous activity of nearest neighbor voxels in fMRI time series (for further details, see Materials and Methods). It sheds light on the so-called "default mode network" (DMN, Long et al. 2008)—a distributed set of brain regions that are active when participants are wakefully at rest but suppressed when they perform a task (Shulman et al. 1997; Gusnard and Raichle 2001; Raichle et al. 2001). Regions contributing to the DMN include medial structures such as mPFC, the medial temporal lobe, as well as the posterior cingulate cortex, but also more lateral areas such as the inferior parietal lobule (IPL), TPJ, and temporal poles. As such there is much anatomical overlap between the DMN and the "social brain" (Mars et al. 2012). Moreover, many studies have linked DMN activity to social functioning (for reviews, see Molnar-Szakacs and Uddin 2013; Li et al. 2014).

Apart from the DMN, resting-state research identified several other networks that mirror task-related activity and are referred to as task-positive. Using an RSFC approach, it was shown that certain regions supporting a particular motor or mental function slowly oscillate together when participants are without a task (Biswal et al. 1995; Deco and Corbetta 2011). For example, temporal regions identified by contrasting the visual encoding of people versus nonsocial objects were found to remain functionally connected after the task through slow oscillations in blood oxygenation (Simmons et al. 2010). Like DMN activity, RSFC was shown to predict performance in social paradigms (Zhu et al. 2011; Takeuchi et al. 2013, 2014).

Against the background of these findings, the present study tested the following hypotheses. First, we expected the frequency of maternal touch to predict resting-state activity in nodes overlapping with the "social brain." Moreover, of particular interest were insula and pSTS as their activity is directly modulated by tactile input. Second, we predicted that touch-dependent DMN effects have knock-on consequences for RSFC. Specifically, such consequences should emerge for regions implicated in social tasks like those that require mentalizing.

## Materials and Methods

### Participants

Fifty-five mother-child dyads were invited to participate in the study. Two of these children did not pass the mock scanner session and therefore did not enter the MR part of this study. Six children undergoing real MRI scanning failed to complete the scanning session resulting in incomplete data. Thus, only 47 data sets entered data processing and analysis. Out of these, 4 data sets had to be removed due to motion artifacts. The resulting data comprised 24 boys and 19 girls with a mean age of 5.5 years (range 5.0–5.9 years). Prior to participation, the children's parents gave written, informed consent, and children consented verbally to the study procedures. All children were right-handed with no history of neurological, medical, or psychological disorders. The study was approved by the Institutional Review Board of Leipzig University (Germany).

## Materials and Procedure

We conducted a behavioral observation session and a neuroimaging session separated by about 2 weeks (mean 13.4 days, SD 11.5). During the behavioral observation session, children and mothers interacted with each other in a standardized setting in a quiet, child-friendly room. They were seated on a sofa next to each other with a table in front of them. Initially, child, mother, and experimenter played a short warm-up game (memory game). Subsequently, the experimenter provided mother and child with toy blocks (Playmobil® Farm) and asked them to play for 10 min as they would at home, while remaining on the sofa and keeping toy blocks on the table. Mothers were told that this part of the procedures was recorded on video tape, but no information about our interest in touch was provided. Following this, the experimenter left the room. The interaction was recorded on video by 2 cameras (AXIS Q1755), 1 positioned in front, and 1 above the sofa.

Prior to the neuroimaging session, children were familiarized with the scanner environment in a mock MR scanner on a separate day. During this familiarization, children practiced to rest without movement in the scanner. Children who were able to do so were invited to participate in the actual neuroimaging session within 1 week. During the neuroimaging session, children rested in a 3T magnetic resonance scanner (Siemens Tim Trio, Erlangen, Germany) with a 12-channel head coil. They were instructed to lie as still as possible, while watching a calm screen-saver showing a lava lamp. Resting-state functional MRI (rs-fMRI) whole-brain volumes were acquired by a  $T_2^*$ -weighted gradient-echo echo-planar imaging (EPI) sequence, TR 2000 ms, TE 30 ms, flip angle 90°, slice thickness 3 mm, gap 1 mm, FOV 19.2 cm, matrix 64 × 64, 28 slices, 100 volumes, and duration 3.3 min. High-resolution 3D structural images were acquired with a  $T_1$ -weighted, magnetization prepared rapid gradient-echo (MPRAGE) sequence, TR 1480 ms, TE 3.46 ms, flip angle 10°; slice thickness 1.5 mm, gap 0 mm; matrix 250 × 250; spatial resolution 1 × 1 × 1.5 mm, and duration of 6 min. This protocol had been used successfully in previous studies (Xiao et al. 2016a, 2016b).

## Data Preprocessing and Analysis

After the behavioral session, maternal touch was coded independently by 2 coders using the ELAN software (Lausberg and Sloetjes 2009), which allowed synchronizing the 2 videos for each dyad. For each instance of touch within the 10-min session, the coders recorded the video time stamp and classified the touch as being initiated by the mother (experimental variable) or the child (control variable).

The coding of touch in social interactions is challenging. Touch is an inconspicuous social cue (Fisher et al. 1976) that, in our study, was embedded in a rich visual scene and, thus, occasionally missed. To maximize coding accuracy, we, therefore, developed a master list containing the video time stamps from both coders and highlighted time stamps coded by 1 but not the other. Coders were then given the highlighted time stamps only and asked to determine whether they had missed a tactile incident or wrongly inferred one. If they had missed a tactile incident, they were to add this to their original coding sheet. If they had wrongly inferred touch, they were to remove the corresponding entry. Coding reliability was calculated using a 2-way consistency intraclass correlation (ICC). The resulting score was 0.873.

For the analysis of neuroimaging data, we discarded the first 3 fMRI time points to allow for signal equilibration. The remaining images were preprocessed using DPARSF (Chao-Gan and Yu-Feng 2010; <http://www.restfmri.net>). Preprocessing steps included the

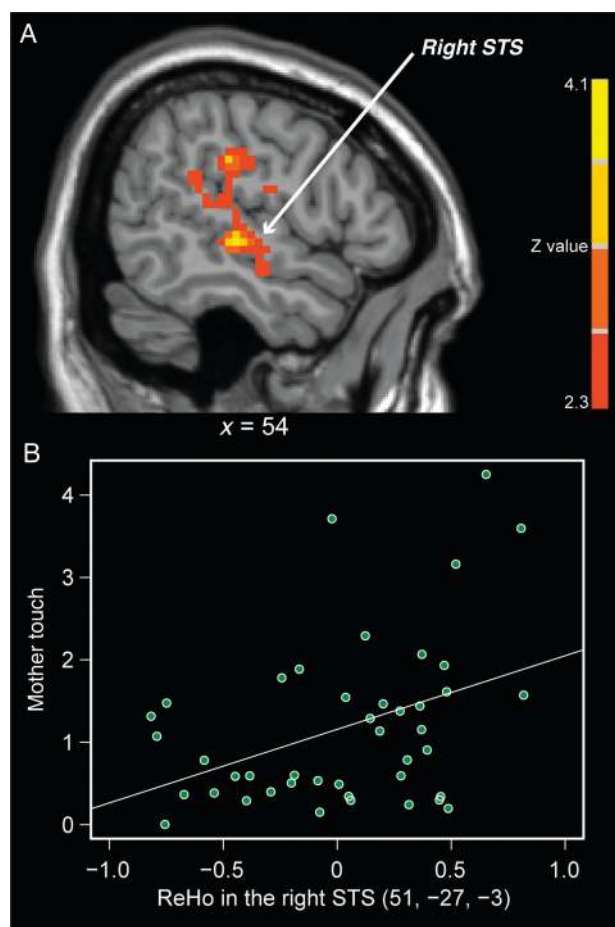
following: 1) slice timing by shifting the signal time points measured for each slice to match the signal time points of the slice at the midpoint of each TR; 2) 3D motion correction using a least squares approach and a 6-parameter (rigid body) spatial transformation; 3) reorienting both functional and MPRAGE images and then co-registering MPRAGE images to the mean functional image of each subject; 4) segmenting MPRAGE images into gray matter, white matter (WM), and cerebrospinal fluid (CSF) based on the NIH pediatric atlas (Fonov et al. 2011; <http://www.bic.mni.mcgill.ca/ServicesAtlases/NIHPD-obj1>) using its asymmetric,  $T_1$  version and a 4.5–8.5 years age range (prepuberty, based on 82 subjects); 5) spatially normalizing images by using the parameters from the segmentation procedure in each subject and resampling voxel size to 3 × 3 × 3 mm<sup>3</sup>; 6) spatially smoothing images with a 6-mm full-width-at-half-maximum (FWHM) Gaussian kernel (for RSFC only); 7) nuisance regression, including principal components (PC) extracted from subject-specific WM and CSF masks (5 PC parameters) using a component-based noise correction method (CompCor; Behzadi et al. 2007), as well as Friston's 24-parameter model including 6 head motion parameters for the current time point, 6 head motion parameters for the preceding time point, and their 12 corresponding values squared (Friston et al. 1996); the CompCor procedure comprised detrending, variance (i.e., WM and CSF) normalization, and PC analysis; and 8) band-pass temporal filtering (0.01–0.1 Hz).

Given recent concerns regarding the confounding influence of micromovements on intrinsic functional connectivity analyses (Power et al. 2012, 2014; Satterthwaite et al. 2012; Van Dijk et al. 2012), the frame-wise displacement (FD) of time series was computed (Jenkinson et al. 2002). As mentioned previously, 4 participants were excluded for whom the mean FD values were >2 SDs above the group mean (i.e., >0.476 mm) (Yan et al. 2013). For the remaining 43 datasets, the group mean FD was 0.138 mm (SD = 0.09 mm, range = 0.047–0.45 mm). Because boys showed stronger head motion than girls ( $t(41) = 2.97$ ,  $P = 0.005$ ), individual FD means were included as a covariate of no interest in the group-level statistical analyses.

## ReHo Analysis

Regional homogeneity (ReHo) analysis uses Kendall's coefficient of concordance (KCC) to measure the temporal synchronization of fMRI time series from nearest neighbor voxels. Although its physiological underpinnings are still incompletely understood, ReHo shows some convergence with other analysis methods for fMRI time series (Zang et al. 2004). A key advantage of the ReHo approach is that it is data-driven and as such independent of a prior seed or model. It has, therefore, become a popular index of baseline brain activity and a tool in the exploration of resting-state fMRI data. Among others, the ReHo approach has been successfully applied to the investigation of individual differences in a variety of domains including cognitive control (Tian et al. 2012), personality (Wei et al. 2011), psychological resilience (Kong et al. 2015), unwanted thoughts (Kühn et al. 2014), and intelligence (Wang et al. 2011).

We analyzed ReHo using REST (Song et al. 2011; <http://www.restfmri.net>) following the procedures from previous studies (Zang et al. 2004; Zuo et al. 2013). Briefly, from the preprocessed data, we computed KCC (Kendall and Gibbons 1990) for the time series of each gray matter voxel and that of its nearest neighbors. This produced a KCC map for each subject, which was Z-transformed by subtracting the subject's mean ReHo value of all voxels within the brain mask from the score of individual voxels and then dividing the result by the subject's standard deviation (Zuo et al. 2010). This was done to increase



**Figure 1.** A significant correlation between regional homogeneity in resting-state fMRI time series and mother touch was observed in a cluster with peak in the right STS (A). The scatter plot (B) illustrates individual data points for ReHo in the right STS cluster and mother touch ( $r = 0.40$ ,  $P < 0.01$ ). Multiple comparison correction was applied at the cluster level using Gaussian random field theory ( $Z > 2.3$ , cluster-wise  $P < 0.05$ , GRF corrected). STS, superior temporal sulcus.

normality of the KCC distribution. All Z-transformed data were spatially smoothed with a Gaussian kernel of 6 mm FWHM. Subsequently, these ReHo values were entered into a correlation model to calculate the partial correlation coefficients with mother touch, controlling for age, sex, mean FD, and child touch. The correlation map ( $r$ -map) was then transformed into a Z-map via the “rest\_TFRtoZ” function in the REST toolbox (Song et al. 2011; <http://www.restfmri.net>) and further corrected for multiple comparisons using Gaussian Random Field (GRF) theory ( $Z > 2.3$ , cluster-wise  $P < 0.05$ , GRF corrected) with a minimum cluster size of 130 voxels.

### RSFC Analysis

The results of the ReHo analysis informed seed selection for a subsequent RSFC analysis. This analysis was performed separately for each participant using the REST toolbox. First, an average time series of all voxels in the seed (6-mm sphere centered on ReHo peak coordinate) was computed. Then, an RSFC correlation map ( $r$ -map) was produced for the whole brain and converted into a z-map with application of Fisher’s  $r$ -to- $z$  transformation as to increase normality of the data. The resulting participant maps were divided into 2 groups based on a median split of the maternal touch score. Then, the low- and the high-touch

**Table 1** Local maxima within the cluster showing a significant correlation between ReHo and mother touch while controlling for child touch

Region	Peak MNI coordinates			Peak Z value
	x	y	z	
R Superior temporal sulcus	51	-27	-3	4.1
R Supramarginal gyrus	48	-18	24	3.65
R Insula	33	-22	12	2.51

R, right hemisphere.

maps were subjected to unpaired voxel-wise  $t$ -tests controlling for age, sex, mean FD, and child touch.

## Results

### Behavioral Results

The average frequency of touch per minute was 1.18 (SD 1.01) for maternal touch and 2.03 (SD 1.30) for the children’s touch. Correlations with age and sex were nonsignificant in both cases. However, maternal touch positively predicted the children’s touch ( $r = 0.76$ ,  $P < 0.001$ ). Because of this, child touch was included as a control variable in the analyses reported below.

### Maternal Touch Predicts Activity in the DMN

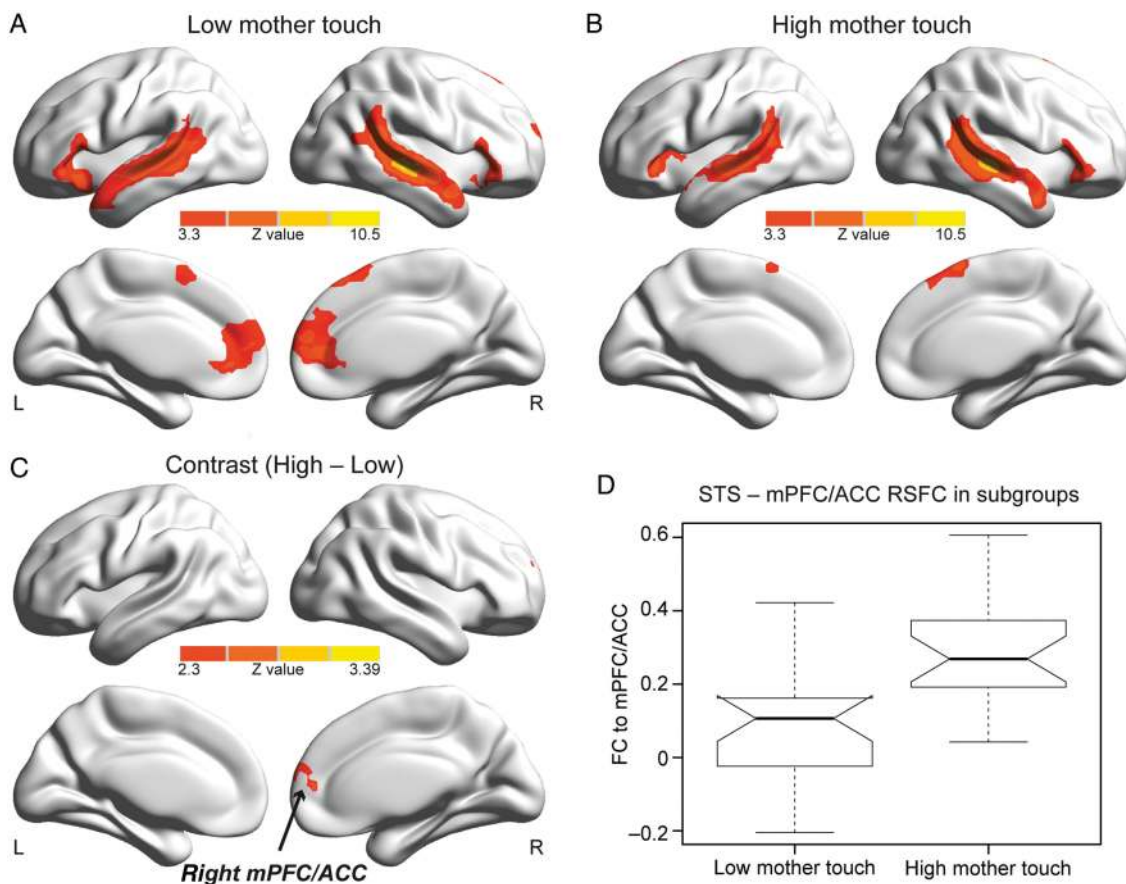
As expected, we found a significantly positive correlation between ReHo and mother touch in regions of the DMN, specifically in the right STS stretching into the TPJ. This effect was maximal at 51, -27, -3 (MNI coordinates) and extended over 353 voxels (Fig. 1) with 2 further local maxima in the supramarginal gyrus and the insula (Table 1).

### Maternal Touch Predicts Connectivity of the Resting Brain

We conducted an RSFC analysis with seed in the right STS centered at the ReHo peak coordinates (51, -27, -3). The results were subjected to 2 one-sample  $t$ -tests (against 0) for children with high and low maternal touch, respectively. Test results were thresholded at  $Z > 3.3$  ( $P < 0.001$ , GRF corrected) with a minimum cluster size of 100 voxels. As shown in Figure 2A,B, both groups of children engaged a wide range of correlated regions including bilateral superior and middle temporal cortex, bilateral inferior frontal cortex, right supplementary motor cortex, and left insula (see also Tables 2 and 3). However, children with high maternal touch additionally involved right insula, left putamen, left caudate, and dorsal mPFC/anterior cingulate cortex (ACC). A comparison between the 2 groups using a 2-sample  $t$ -test, thresholded at  $Z > 2.3$  ( $P < .05$ , GRF corrected) with a minimum cluster size of 140 voxels, revealed stronger RSFC between the right STS seed and dorsal mPFC/ACC (158 voxels; peak MNI coordinates: 9, 66, 18; peak  $Z = 3.39$ ) in children with high compared with low maternal touch (Fig. 2C,D). All maps are displayed with the BrainNet Viewer (Xia et al. 2013, <http://www.nitrc.org/projects/bnv/>).

## Discussion

This study explored the relationship between maternal touch and resting activity in the developing “social brain.” As expected, the frequency of maternal touch positively predicted activity in an area extending from mid STS to TPJ and insula in the right hemisphere, partially overlapping with the DMN. Moreover, RSFC between the peak area of this activity in the pSTS and the dorsal



**Figure 2.** Functional connectivity maps based on the right STS seed in high and low mother touch subgroups (A and B) as well as their comparison (C). The notched boxplot (D) depicts the connectivity strength between the right STS seed and mPFC/ACC in both low and high mother touch groups. Functional connectivity maps for both groups were thresholded at  $Z > 3.3$  ( $P < 0.001$ , GRF corrected); for the comparison, the threshold was set at  $Z > 2.3$  ( $P < 0.05$ , GRF corrected). mPFC/ACC, medial prefrontal cortex/anterior cingulate cortex.

**Table 2** Significant clusters resulting from the functional connectivity analysis with seed in the right STS in children with low mother touch

Region	Peak MNI coordinates			Peak Z value
	x	y	z	
R Superior temporal gyrus/sulcus	51	-27	-3	10.45
L Superior temporal gyrus/sulcus	-54	-27	0	6.29
R Supplementary motor area	3	12	63	5.94
L Inferior frontal gyrus	-42	30	0	5.56
R Inferior frontal gyrus	51	12	-15	5.5
L Insula	-31	18	-11	3.85

L, left hemisphere; R, right hemisphere.

mPFC was enhanced in children receiving more compared with less tactile attention from their mothers. The following sections describe these findings in more detail and integrate them with the literature on social touch and resting brain activity.

Social touch excites a dedicated tactile system to which CT afferents provide input. To date, little is known about the ontogeny of this system. Connectivity of the pSTS—a CT afferent target—appears to develop until individuals reach adolescence (Alaerts et al. 2015). Yet, rudimentary CT processing is probably already available in infancy. First, there is much evidence indicating that infants find physical contact with their caregiver rewarding (Stack and

**Table 3** Significant clusters resulting from the functional connectivity analysis with seed in the right STS in children with high mother touch

Region	Peak MNI coordinates			Peak Z value
	x	y	z	
R Superior temporal gyrus/sulcus	51	-27	-3	10.5
L Superior temporal gyrus/sulcus	-66	-42	6	6.34
R Medial prefrontal cortex/anterior cingulate	9	54	18	5.62
L Inferior frontal gyrus	-42	21	-9	5.61
R Inferior frontal gyrus	48	30	0	5.48
R Supplementary motor area	6	36	54	5.36
L Insula	-30	17	-5	4.48
L Caudate	-13	14	7	3.79
L Putamen	-21	5	7	3.67

L, left hemisphere; R, right hemisphere.

Muir 1992). Second, other aspects of the somatosensory system appear largely intact at birth (Rees et al. 2010; Nevalainen et al. 2014). Last, a study in children aged 5 and above found adult-like brain responses when comparing CT with non-CT touch (Björnsdotter et al. 2014). Our results align with this literature by showing, in children aged 5, a relation between social touch and resting activity in right pSTS and insula—regions previously associated with CT processing.

Apart from establishing CT compatible effects in childhood, our study suggests that CT stimulation may help shape the developing “social brain.” The association between the frequency of maternal touch and resting activity also overlapped with areas previously implicated in theory of mind and in representing others’ mental states (Mars et al. 2012). Moreover, the previous research has found that activity in STS and TPJ during a mentalizing task and during rest is positively associated (Hyatt et al. 2015). Linking this evidence with the present results, one may speculate that children with more touch more readily engage the mentalizing component of the “social brain” and that, perhaps, their interest in others’ mental states is greater than that of children with less touch.

To further explore the present resting-state effects, we conducted an RSFC analysis using peak coordinates in the right pSTS as the seed. In both children with high and low maternal touch, this revealed connectivity with areas along the bilateral superior and middle temporal cortex, the bilateral inferior frontal gyrus, right supplementary motor cortex, and left insula. In children with high maternal touch, we additionally observed connectivity with right insula, left putamen, left caudate, and dorsal mPFC/ACC. Moreover, a group comparison indicated that connectivity within the latter region was significantly greater in high- compared with low-touch children.

Together, these results show that enhanced right pSTS activity, possibly a consequence of touch, feeds into systems related to social and emotional processing. With respect to social processing, we identified areas implicated in the mentalizing (STS/dorsal mPFC), empathy (insula), and mirroring (IFG, motor) networks of the social brain (Kennedy and Adolphs 2012). With respect to emotional processing, right pSTS activity oscillated with nuclei in the basal ganglia known for their role in the appreciation of rewards (Fisher et al. 2005; Muranishi et al. 2011). Thus, one can speculate that engagement of the right pSTS benefits processing in these social and emotional circuits. Moreover, enhanced right pSTS activity in high-touch children seems to translate into additional mentalizing benefits via connectivity with the dorsal mPFC. In line with this possibility, the present study identified a positive relation between the frequency of maternal touch and how actively children touched their mothers. Additionally, a related behavioral study using a similar observation protocol found a relation between the frequency of maternal touch and the children’s bias toward social relative to nonsocial stimuli (Reece C et al. in press).

Of note is the right lateralization of the present pSTS effect. It agrees well with the extant literature. For one, studies exploring the processing of CT appropriate, gentle touch typically report pSTS activation in the right rather than the left hemisphere (Gordon et al. 2013; Voos et al. 2013; Bennett et al. 2014). Additionally, research on other nonverbal channels established a similar pattern. Studies comparing the processing of faces with nonface objects found stronger activation in right relative to left hemisphere regions. Moreover, the right pSTS, in particular, has been identified as supporting the analysis of changeable facial information (i.e., expressions) (Hoffman and Haxby 2000; Watson et al. 2014; De Winter et al. 2015). Likewise, voice perception preferentially engages the right pSTS especially in the context of nonverbal (e.g., emotional) analysis (Belin et al. 2000; Schirmer and Kotz 2006; Watson et al. 2014; but see Schirmer et al. 2012) as does the integration of dynamic social signals across the different nonverbal channels (Watson et al. 2014).

The importance of right pSTS in the context of tactile and nontactile social perception aligns with insights from autism. Looking at tactile perception, Kaiser et al. (2015) found

that autism reduces the strength with which CT-appropriate touch activates the right pSTS, among other areas, but enhances responses to non-CT touch in parietal somatosensory areas. Looking at nontactile social processing, there are reports of hypoactivity in the right pSTS of autistic individuals to stimuli involving irony (Wang et al. 2007), gaze-object incongruity (Pelphrey et al. 2005), awkward social scenarios (Pantelis et al. 2015), or the recognition of emotions from point-light displays (Alaerts et al. 2014). Interestingly, the latter finding could be linked to altered RSFC of the right pSTS and impaired emotion recognition performance (Alaerts et al. 2014). Taken together then, the present and past studies point to a special role of the pSTS in interpersonal touch complementing and/or shaping more general social computations of this region. Moreover, like nontouch social processing, tactile effects appear lateralized to the right hemisphere. Although speculative, one possible explanation for this is that parents being predominantly right-handed bestow more touch on the left half of their children’s body, which in turn may emphasize right hemisphere development. Future research would have to test this possibility.

Before coming to a close, we would like to acknowledge that, like most developmental studies in humans, the present study affords correlational rather than causal evidence. Because we could not assign children to touch exposure randomly, we cannot be certain that the observed relationship between touch and neuroimaging data is indeed due to touch or caused by a third variable that happens to co-vary with touch. For example, touching mothers may simply be more caring and provide nontactile input (e.g., speech) that benefits the developing “social brain.”

Yet, what is impossible in humans has been done in research with nonhuman animals. In a series of studies, Meaney and colleagues placed rodent pups with adoptive dams for whom they measured licking and grooming or isolated pups and provided standard care that included varying amounts of tactile stimulation from a brush (for review, see Cameron et al. 2005). Such manipulations revealed that frequency of licking and grooming regulates brain development in the offspring. Tactile input was found to increase cortisol receptors in the hippocampus and to make the offspring’s stress response more efficient (Liu et al. 1997; Weaver et al. 2004; for corresponding human work, see McGowan et al. 2009). Additionally, it was shown to up-regulate the number of oxytocin receptors in numerous brain regions such that, as adults, individuals are more caring towards own pups (Champagne et al. 2001). Specifically, rodents exposed to much licking and grooming show a greater frequency of licking and grooming their offspring, thus, mirroring their mothers’ behavior. Interestingly, the present study yielded similar results whereby children of high-touch mothers touched more than children of low-touch mothers. On the backdrop of this work then, it is not unreasonable to suspect a potential causal role of touch for human development.

To conclude, this study presents a first attempt to link early tactile experiences to the developing human brain. We show that the frequency of maternal touch, as measured in a 10-min play session, positively predicts children’s resting-state activity in brain regions associated with social functioning. Compared with children receiving less maternal touch, children receiving more maternal touch display greater resting activity and connectivity in the right pSTS. Thus, the present data raise the possibility that, as was shown in the nonhuman brain, tactile care supports emerging social networks in the human brain.

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## Notes

*Conflict of Interest:* None declared.

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