

Neural representation of the parent–child attachment from infancy to adulthood

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Abstract

Attachment theory is built on the assumption of consistency; the mother–infant bond is thought to underpin the life-long representations individuals construct of attachment relationships. Still, consistency in the individual's neural response to attachment-related stimuli representing his or her entire relational history has not been investigated. Mothers and children were followed across two decades and videotaped in infancy (3–6 months), childhood (9–12 years) and young adulthood (18–24 years). In adulthood, participants underwent functional magnetic resonance imaging while exposed to videos of own mother–child interactions (Self) vs unfamiliar interactions (Other). Self-stimuli elicited greater activations across preregistered nodes of the human attachment network, including thalamus-to-brainstem, amygdala, hippocampus, anterior cingulate cortex (ACC), insula and temporal cortex. Critically, self-stimuli were age-invariant in most regions of interest despite large variability in social behavior, and Bayesian analysis showed strong evidence for lack of age-related differences. Psycho–physiological interaction analysis indicated that self-stimuli elicited tighter connectivity between ACC and anterior insula, consolidating an interface associating information from exteroceptive and interoceptive sources to sustain attachment representations. Child social engagement behavior was individually stable from infancy to adulthood and linked with greater ACC and insula response to self-stimuli. Findings demonstrate overlap in circuits sustaining parental and child attachment and accord with perspectives on the continuity of attachment across human development.

Key words: attachment; longitudinal studies; mother–child relationship; ACC

Introduction

Since the discovery of social bonding by Lorenz (1935), the ensuing research of the ethologists (Tinbergen, 1963) and Bowlby's (1969) adaptation of these findings into a comprehensive theory of human development, the mother–child attachment has been a key lens for understanding human nature, generating extant research across ages, cultures and pathological conditions (Bretherton, 2010; Dykas and Cassidy, 2011; Zimmermann and Iwanski, 2015; Keller, 2016). Among the central propositions of attachment theory is the consistency of attachment across development; the nature of the bond formed between mother and infant defines the trajectory of their relationship and predicts a host of child social, emotional, cognitive and physiological outcomes (Sroufe et al., 1999; Waters et al., 2000; Valadez et al., 2020). In parallel, disruptions to the mother–infant attachment carry long-term negative consequences that are moderated, at least in part, by the consistency of attachment over time (Sroufe, 2005). The consistency hypothesis has

been described not only throughout development but also across attachment relationships. Conceptual models (Mikulincer and Shaver, 2005, 2012) and empirical studies demonstrate continuity from the parent–infant to romantic attachment (Selcuk et al., 2010; Göbel et al., 2019) and friendship quality (Freeman and Brown, 2001; Feldman et al., 2013), indicating that the mother–infant bond shapes the individual's later attachments throughout life (Verhage et al., 2016). Consistency has also been found across measures. Behavioral markers of attachment in infancy (i.e. the 'strange situation') have been associated with narrative quality of the parent–adolescent attachment (Hamilton, 2000; Chae et al., 2018) and the adult child's romantic attachment (Weinfeld et al., 2004; Pascuzzo et al., 2013), and the parent's attachment-related narrative during pregnancy was found to predict the infant's behavior-based attachment classification (Fonagy et al., 1991) despite a significant difference in measure. The long-term impact of the mother–infant attachment on the adult human appears to draw from its substantial consistency—across

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the individual's developmental history, across attachment relationships and across modes of dialogue between partners and measurements of attachment.

More recent studies tapped the brain basis of attachment to describe the neural networks that underpin the parent–infant bond. This line of research typically examined parents' neural response to own-infant stimuli as compared with unfamiliar infant. To target the attachment context, numerous studies across several labs exposed parents to naturalistic video vignettes of their own parent–child interaction as compared with unfamiliar interaction (Noriuchi *et al.*, 2008; Atzil *et al.*, 2011; Abraham *et al.*, 2014, 2016a; Elmadih *et al.*, 2016). This experimental paradigm is based on two conceptual tenets in ethology and attachment theory. First, that humans form exclusive attachment with their infants, hence their brain reacts distinctly to one's own child, and second, that in order to study bonding one must go to the natural habitat and observe bonding-related features in the natural ecology (Feldman, 2016). Cumulative evidence from this research has delineated the neural structures that underpin human attachment (Swain *et al.*, 2014; Feldman, 2015b, 2017). The amygdala, ventral tegmental area (VTA) along other subcortical regions of the dopamine network (Strathearn *et al.*, 2009) and hippocampus, areas rich in oxytocin receptors (Boccia *et al.*, 2013; Raam *et al.*, 2017), play a key role in mammalian mothering and are causally involved in bond formation (Insel and Harbaugh, 1989; Oxley and Fleming, 2000; Numan, 2020). In humans, these subcortical regions are similarly implicated in maternal attachment (Strathearn *et al.*, 2009) and are connected via multiple ascending and descending projections with several cortical regions into an integrated caregiving network that sustains human attachment. Among the key cortical structures that underpin attachment are the anterior insula (AI), which supports interoception (Craig, 2003; Zaki *et al.*, 2012; Salomon *et al.*, 2016) and empathy (Singer *et al.*, 2009; Weisz and Zaki, 2018; Lamm *et al.*, 2019), the anterior cingulate cortex (ACC), a higher-order limbic interface of social, affective and representational functions (Bush *et al.*, 2000; Fan *et al.*, 2011), and temporal regions implicated in social understanding, embodiment and mentalization (Frith and Frith, 2003; Mar, 2011; Qin *et al.*, 2020). In anterior temporal regions, dissociable patterns of activation were found in response to one's parent stimuli, compared to other attachment figures (Laurita *et al.*, 2017). Importantly, while these circuits are not specific to attachment and support multiple affective processes of both social and non-social nature (Eslinger *et al.*, 2021), research has repeatedly implicated these regions in the formation and maintenance of the parent-to-child attachment (Swain *et al.*, 2004, 2007), and, consistent with prior work, we cautiously term it in the following as an 'attachment network'.

Studies on the neural basis of human attachment lend further support to the consistency hypothesis by showing that other attachments throughout life, including romantic love and friendship, are underpinned by the same neural circuits (Feldman, 2017). The same neural structures that activate in parents in response to attachment reminders also activate when individuals observe their romantic partner, co-parent or close friend (Bartels and Zeki, 2004; Acevedo *et al.*, 2012; Abraham *et al.*, 2017; Laurita *et al.*, 2017), suggesting continuity from parental to romantic to filial attachment. Similar to the parent–infant attachment, the neural basis of other attachments has been linked with oxytocin levels and sensitive inter-partner behavior (Abraham *et al.*, 2017; Scatliffe *et al.*, 2019). Still, very little research assessed the neural underpinnings of the child's attachment to the parent. For instance, a magnetoencephalography study showed that

adolescents exhibited increased activations in a wide cortical cluster of the attachment network, including the insula, cingulate cortex and superior temporal sulcus (STS)/superior temporal gyrus (STG), in response to own mother–child interaction compared to unfamiliar interactions (Pratt *et al.*, 2018). These activations were predicted by mother–child behavioral synchrony in early childhood and decreased in cases of maternal postpartum depression (Pratt *et al.*, 2019), supporting the consistency hypothesis. Similar findings emerged from a study of 10-year-olds' neural response to own mother's picture compared with a stranger's picture in a sample receiving attachment-based intervention in infancy. Findings showed that mother's picture activated nodes of the attachment network and following attachment intervention children displayed increased activation in the cingulate cortex and hippocampus (Valadez *et al.*, 2020). Similarly, stimuli involving narrative measures of attachment elicited activations in nodes of the attachment network (Buchheim *et al.*, 2006). Yet, despite the reported consistency in the neural network sustaining human attachments, consistency in the adult child's neural response to cues representing his or her relational history from infancy to adulthood has not been examined.

In this study, we utilized a longitudinal cohort followed for over two decades from infancy to young adulthood. Employing the same paradigm used to test the neural basis of parental attachment (Swain *et al.*, 2007), naturalistic mother–child interactions were videotaped in the home ecology at three age groups: infancy (3–6 months), childhood (10–12 years) and young adulthood (18–24 years). In young adulthood, participants were scanned in functional magnetic resonance imaging (fMRI) while observing these ecological videos spanning three stages in their development in addition to three vignettes of unfamiliar gender- and age-matched dyads. Such longitudinal stimuli spanning their entire attachment history were thought to tap the consistent representations adults construct of their attachment relationship (Goossens *et al.*, 1986; Lewis *et al.*, 2000; Fraley, 2002). Notably, while mothers were not scanned in the current study, we expected that the same regions previously found to underpin the parent's attachment to the child would also underlie the adult child's neural response to attachment-related stimuli, including the amygdala, hippocampus, VTA, temporal cortex, insula and ACC (Feldman, 2017), and that these regions would show higher blood oxygen level dependent (BOLD) activity when viewing Self-stimuli across the ages as compared with similar videos of unfamiliar dyads (hypothesis 1). We also examined whether these regions would show consistent, age-invariant responses to attachment-related stimuli from the three age groups presented in adulthood, as compared with unfamiliar interactions (Other) from infancy, childhood and adulthood (hypothesis 2).

Our third hypothesis considered functional connectivity. Studies showed increased connectivity in the parent's brain in response to attachment stimuli (Leibenluft *et al.*, 2004), and we explored whether Self-stimuli would elicit increased connectivity among nodes that sustain the parent–child attachment. We were particularly interested in the coupling of the ACC with other regions of the attachment network. The ACC is an integrative interface of sensation, cognition, emotion, arousal and neuro-modulation (Peterson *et al.*, 1999; Bush *et al.*, 2000; Rolls, 2019; Vassena *et al.*, 2020) and is among the most interconnected hubs in the brain (Margulies *et al.*, 2007), with both upstream and downstream connections (Rushworth *et al.*, 2007; Pavlovlić *et al.*, 2009). The ACC contains evolutionary-conserved reciprocal projections with all subcortical regions of the attachment network, including amygdala, hippocampus, ventral striatum and VTA, which enable

the regulation of emotion and motivation within attachment contexts (Beauregard et al., 2001; Burgos-Robles et al., 2019). We hypothesized that the coupling between the ACC and other regions that underpin the parent–child attachment may contribute to consolidation of the long-term representation of attachment relationships (hypothesis 3).

Finally, we tested whether the strength of neural activations in response to Self-stimuli would correlate with the degree of observed maternal sensitivity and child social engagement in the presented interactions. Maternal sensitivity and child social engagement are two key behavioral markers of the mother–child attachment that have shown individual stability from infancy to adolescence (Feldman, 2010) and support child resilience, well-being and adaptation (Ulmer-Yaniv et al., 2017; Feldman, 2020). Since the inception of attachment theory (Ainsworth et al., 1978), maternal sensitivity has been consistently shown to predict attachment security (Meins et al., 2001; Belsky and Fearon, 2002), and activation of nodes in the parental brain has been linked with both maternal sensitivity (Atzil et al., 2011; Kim et al., 2011) and child social engagement (Shimon-Raz et al., 2021). We thus expected that these behavioral markers would correlate with the participants' neural response to attachment cues and focused on correlations with the ACC and insula (hypothesis 4). Activation of the ACC and insula in the maternal brain was found to correlate with sensitive caregiving (Atzil et al., 2014), and insular activations in the child's brain were predicted by engaged and synchronous mother–child interactions across development (Pratt et al., 2019; Ulmer Yaniv et al., 2021), suggesting that greater activation of the ACC and insula may correlate with more sensitive and engaged interactions.

Materials and methods

Participants

Participants included 65 young adults (mean age = 20.03 years, s.d. = 2.0, 33 males) who were followed from infancy and participated in two visits at the adult stage, a home visit and a brain imaging session. All participants were healthy, without chronic medical or psychiatric conditions, and completed at least 12 years of education. All children were born to middle-class, two-parent families, and their parents completed high-school education, were above 21 years at the child's birth, were above poverty line and were screened for psychiatric or psychosocial conditions. All participants were of Israeli–Jewish ethnicity.

Longitudinal study design

Families were recruited in infancy to participate in a longitudinal study on mother–infant attachment and its developmental consequences. Home visits were conducted at three timepoints: infancy (3–6 months), childhood (9–12 years) and young adulthood (18–25 years). Visits were scheduled for the afternoon or evening hours. We were specifically interested in observing naturalistic interactions between mother and child that reflect, as much as possible, their habitual daily interactions. For all interactions, mother and child were videotaped in a face-to-face position. The cameras were placed at 1.2 m from the interacting dyad, and filming tried to capture participants' faces as much as possible.

At the adult stage, two visits were conducted within a ~6 week period, including a home visit conducted in the evening hours that lasted ~3.5 h and a magnetic resonance imaging (MRI) scan session. The study was approved by the Bar-Ilan University's Institutional Review Board (IRB). Both mother and young adult signed

an informed consent and received a gift card of 250 NIS (~60 USD) for their participation.

Our pre-registered study included two cohorts. Cohort 1 was used for region-of-interest (ROI) definition and included 15 participants who were randomly assigned to this cohort 1. Cohort 2, our main study, included 50 participants with a full dataset. Results reported here are based on data from these 50 participants.

Overall, 81 participants had data from all three stages of the study, including the MRI scan. Ten subjects were discarded due to misplacement in scanner, one for no visual activity and one for bad scan. Four additional subjects were discarded due to problems with the video stream during the scan (video stuck or mistakenly doubled), leaving the final cohort of 65 participants. No differences on demographic information emerged between participants with and without valid data.

Home observation of mother–child interactions

In infancy (mean age = 4.8 months, s.d. = 1.1), mother and infant were videotaped at home, and instructions were 'play with your infant as you normally do' for 5 min. In childhood (mean age = 10.9 years, s.d. = 1.2) and young adulthood (mean age = 20.03 years, s.d. = 2), mother and child engaged in a validated conversation-based positive interaction for 7 min (Feldman et al., 2014; Ulmer-Yaniv et al., 2017, 2018). Interactions were used for offline coding and as fMRI stimuli. For the fMRI task, 2 min from the middle of the interaction was selected.

Coding of social behavior

Videos of mother–child interactions were coded with the Coding Interactive Behavior (CIB) manual (Feldman, 1998). The CIB is a global rating system for social interactions with multiple codes for parent, child and dyadic behavior and several manuals for coding social behavior from newborns to adults that are based, whenever possible, on the same codes and similar conceptual principles. The CIB has been validated in hundreds of studies with infants, children, adolescents and adults across multiple cultures and high-risk conditions. The system has good psychometric properties, including construct validity, test–retest reliability and predictive validity (Feldman, 2012, 2021).

In the current study we used the following two constructs:

Maternal sensitivity—was the averaged codes of mother's acknowledgment of child communication, constant gaze, warm positive affect, warm vocalization, appropriate range of affective expression and consistent style from the three age groups ($\alpha = 0.92$).

Child positive engagement—was the averaged of codes related to social engagement, affection and trust toward parent, positive affect and involvement from the three stages ($\alpha = 0.86$). The construct includes only child, not adult behaviors. In infancy, codes included child positive affect and child social alertness. In late childhood and young adulthood, in addition to these codes, the construct also includes the following codes: child affection to parent, child trust and openness to parent, child involvement in the conversation and child warmth.

Coding was conducted by two coders blind to other information and trained to 90% reliability. Inter-rater reliability, computed for 20% of the videos averaged 94% ($k = 0.87$).

MRI data acquisition

MRI data were collected using a 3T scanner (SIEMENS MAGNETOM Prisma syngo MR D13D, Erlangen, Germany) located at the Tel Aviv Sourasky Medical Center. Scanning was conducted with a 20-channel head coil for parallel imaging. Head motion was

minimized by padding the head with cushions, and participants were asked to lie still during the scan. High-resolution anatomical T1 images were acquired using magnetization prepared rapid gradient echo sequence: repetition time (TR)=1860 ms, echo time (TE)=2.74 ms, field of view (FoV)=256 mm, voxel size = $1 \times 1 \times 1$ mm, flip angle = 8° . Following, functional images were acquired using echo-planar imaging (EPI) gradient echo sequence. TR=3000 ms, TE=35 ms, 44 slices, slice thickness = 3 mm, FoV=220 mm, voxel size = $2.3 \times 2.3 \times 3$ mm, flip angle = 90° . In total, 300 volumes were acquired during the functional scan, and the first three functional volumes, before signal stabilization, were automatically discarded by the scanner to allow for T1 equilibrium (resulting in 277 volumes). Videos were displayed to subjects inside the scanner, using a projector (Epson PowerLite 74C, resolution = 1024×768), and were back-projected onto a screen mounted above subjects' heads and seen by the subjects via an angled mirror. The stimuli were delivered using windows media player software (Microsoft Corporation). The study was approved by the Bar-Ilan University's IRB and by the Helsinki committee of the Sourasky medical center, Tel Aviv (ethical approval no. 0161-14-TLV). Before participating, participants signed an informed consent according to protocols approved by the ethics committee of the Tel-Aviv Sourasky Medical Center. Participants received a gift certificate of 300 NIS (~85 USD) for their participation in the scan session.

Attachment paradigm

Consistent with research in parents, the attachment fMRI paradigm presented subjects with a series of video vignettes while lying in the scanner that included two types of matched stimuli 'Self' and 'Other'. The 'Self' Stimuli included a 2 min

movie of the subject–mother interactions from each age: infancy, childhood and young adulthood. In the 'Other' condition, participants viewed an unfamiliar mother–child dyad matched for gender and age in a similar interaction. Before the first video, participants were presented with a fixation cross for 30 s. Between videos, fixation cross was presented for periods of alternately 15 or 18 s. Total time of the paradigm was 13:51 min. Stimuli were tailor-made for each subject in the home setting. The order of presentation was counterbalanced so that half the subjects viewed themselves first, and half watched the unfamiliar dyad first (see Figure 1 for details); however, the order of age conditions presentation was not randomized in order to present a coherent narrative on the maturation of the mother–child attachment from infancy to adulthood. The paradigm has been validated in several previous studies of the parental brain (Atzil *et al.*, 2011; Abraham *et al.*, 2014).

Data analysis

Data preprocessing

Data preprocessing and data analysis were conducted using BrainVoyager QX software package 20.6 (Brain Innovation, Maastricht, The Netherlands). Preprocessing of functional scans included three-dimensional (3D) motion correction, slice scan time correction, drift removal using a temporal high pass filter and spatial smoothing by a full width at half maximum 6 mm Gaussian kernel. The functional images were then superimposed on two-dimensional anatomical images and incorporated into the 3D dataset trilinear interpolation. The complete dataset was normalized into Montreal Neurological Institute (MNI) space, using ICBM-452 template.

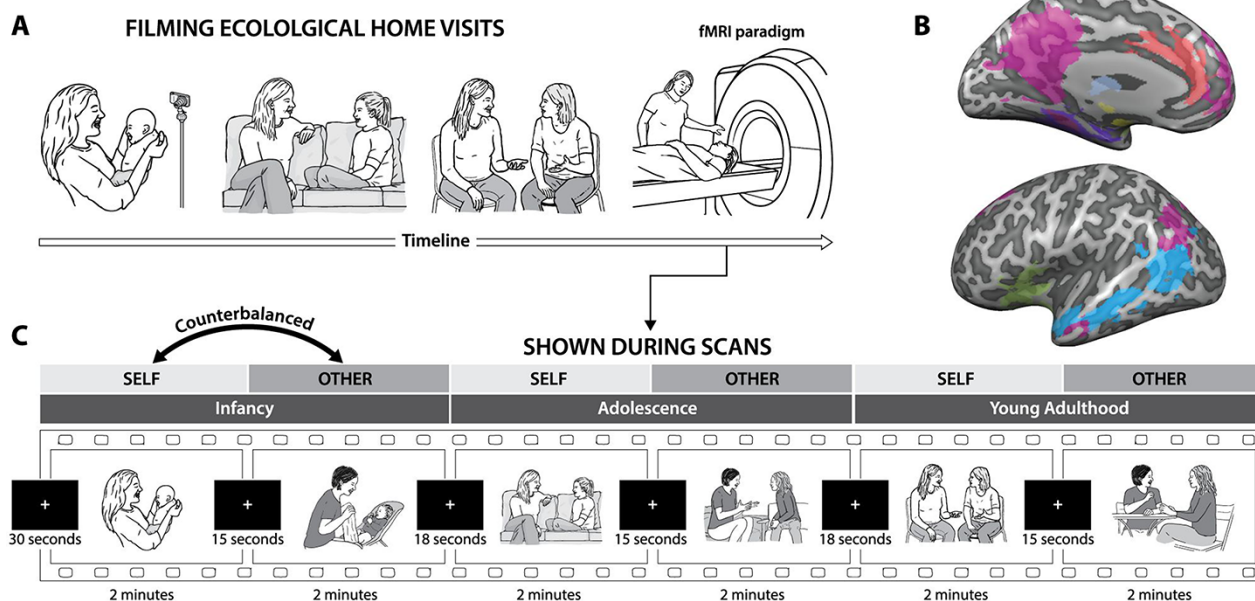


Fig. 1. Longitudinal research plan and fMRI paradigm. (A) Experimental procedure. Participants were initially recruited as infants, around 3 months of age, participated again as children and later in young adulthood (current study phase). All sessions included a home visit in which a videotaped interaction of participants and their mothers took place. Video vignettes of interactions were used as fMRI stimuli. (B) Experimental paradigm. Participants were presented with six video vignettes of self and other dyadic interactions. Each age (infancy, childhood and young adulthood) was presented as an interaction of the participant and his mother (or a gender-matched stranger). Clips lasted 2 min each and were previewed by a fixation cross for 30 s. Between videos, fixation cross was presented for periods of alternately 15–18 s. Order of self–other was counterbalanced between participants. (C). Pre-registered regions of interest: ACC (red), insula (green), PHG (purple), amygdala (yellow), temporal cortex (light blue) and DMN (fuchsia).

Whole-brain analysis

Multi-subject general linear model (GLM) was computed with random effects, with separate subject predictors, in which the different conditions (videos or fixation) were defined as predictors and convoluted with a standard hemodynamic response predictor. Following, a whole brain, two factors (Attachment (Self/Other) \times Age (Infancy/Childhood/Young Adulthood)) repeated measures analysis of variance (ANOVA) was performed. Whole-brain maps were created and voxelwise corrected for false discovery rate (FDR) of $q < 0.050$ (Benjamini and Hochberg, 1995). For visualization of results, the group contrasts were overlaid on a MNI-transformed anatomical brain scan of a single participant.

ROI definition and preregistration

Based on cohort 1 and a priori theory-based selection, eight ROIs were selected and pre-registered at Open Science Framework: hippocampus and parahippocampal gyrus (PHG), amygdala, VTA, ACC, insula, a temporal cluster encompassing the superior temporal sulcus and gyrus, from the occipito-parietal border to the temporal pole, and the default mode network (DMN) as a network. Pre-registration was made following the completion of data collection and is available at https://osf.io/2ndxr/?view_only=ba738b07cad249e0b1f08c2f458ddb35.

Cohort 1 included a group of 15 subjects (mean age 18.93 years old (s.d. = 0.88), 46.7% males, 86.7% right-handed). Fixed effects multi-subject GLM activation maps were used for ROI definition of the amygdala and thalamus. The DMN was defined based on individual functional connectivity maps with seed in the precuneus, which were superimposed to create a 70% mutual probability map. The temporal cortex region was defined based on the pilot map combined with STS region from the Glasser atlas (Glasser et al., 2016). The insula, ACC and hippocampus-PHG were also taken from the Glasser atlas. VTA was defined by three 5 mm spheres based on coordinates from the literature (Murty et al., 2014). Figure 1 shows the ROIs and Supplementary Figure S1 shows cohort 1 Self > Other map.

Psycho-physiological interaction analysis

Classical psycho-physiological interaction (PPI) analysis (Friston et al., 1997) was done using PPI plugin for BrainVoyager (V1.30) to assess PPI predictors and confounds as follows: pre-registered ACC was defined as the seed region, and psychological conditions were defined as Self > Other, for all timepoints. For each condition, weight was assigned in such a way that the resulting time course will be zero centered (self adult +1, self child +1, self infant +1, other adult -1, other child -1, other infant -1). Fixation weight was set to zero.

For each subject, the time course of the ACC ROI was extracted, Z-transformed and then convolved with the hemodynamic response function. Then, it was multiplied TR by TR with the task time course (task time course was based on the protocol associated with the data) to create the ACC PPI predictor. Additionally, for each subject, a psychological regressor, based on the associated protocol, an ACC predictor, based on the ACC time course correlation, and a complementary regressor were created. Additional motion correction predictors were added and Z-transformed. The resulting set of four PPI predictors for each subject were used in a multi-subject GLM analysis. The PPI ACC predictor allows to create a group map of voxels that increase their interaction with the ACC for the self conditions compared to other conditions, over and above what is

explained by the task itself (Self > Other contrast; psychological component) and by the global functional connectivity of the ACC (physiological component). Multi-subject GLM analysis was restricted to our pre-registered ROIs, using a mask. Then, the ACC-PPI maps were corrected using Monte Carlo cluster level statistical threshold estimator, with 1000 simulations to estimate cluster-level probabilities (Forman et al., 1995).

Statistical analysis

Statistical analysis was conducted using JASP (Version 0.12.1 for windows, JASP Team, 2020), SPSS (SPSS statistics V25, IBM Corp.) and R version 4.0.0 (R Core Team, 2020) with Tidyverse package (Wickham et al., 2019). Null effects were assessed using Bayesian statistics (Keysers et al., 2020). Greenhouse-Geiser correction was used for sphericity violations. Repeated measures Bayesian ANOVA was used to evaluate the evidence for the null effect found using the standard repeated measures (RM) ANOVA analysis. Of note, throughout the analysis, we used the exclusion Bayes factor (BF). As such, a low value for BF signifies support for the inclusion of the effect (i.e. evidence for the effect): BF < 0.33 denotes moderate evidence, BF < 0.1 denotes strong evidence and BF < 0.03 denotes very strong evidence for the inclusion of the model (Kelter, 2020).

Results

As a first step, we examined the overall brain response to attachment stimuli of naturalistic mother-child interactions vs the baseline fixation condition. A whole-brain map comparing the epochs of audio-visual stimulation to fixation of the analysis dataset (50 subjects; Figure 2), is parallel to the map of cohort 1 dataset (15 subjects; Supplementary Figure S2A). As expected, both maps show wide activations in the visual cortex, spreading to the temporal cortex. Additional activations were observed in the DMN, and in limbic regions such as the PHG, and amygdala. Note that the two maps were highly similar despite differences in the number of subjects.

Next, we examined the experimental factors using two-factorial ANOVA analysis of Attachment (Self/Other) \times Age (Infancy/Childhood/Young Adulthood) on whole-brain activity ($N = 50$). The ANOVA map of the Attachment main effect (Figure 3A) revealed that the main regions showing differential BOLD responses between the Self and Other conditions include the ACC, thalamus and midbrain. Investigation of Self > Other contrast map indicated stronger activity for the Self condition in the middle ACC (Brodmann area (BA) 32), posterior ACC (BA 24), and a large activation cluster extending from the thalamus ventrally to the brain stem. Additional bilateral activations were found in the visual association regions—peristriate cortex (BA 19), supplementary motor area (SMA) (BA 6) and cerebellum. In addition, a bilateral deactivation was found in the hypothalamus (Supplementary Figure S2, Table 1).

The main effect of Age was associated with activation across occipito-temporal regions, mainly in the visual association regions (BA 18) as well as limbic regions (PHG and amygdala) and a parietal cluster (Figure 3B). Random effects GLM maps of the Age contrasts (infancy > childhood, infancy > young adulthood, Supplementary Figure S3) show that visual association regions are activated across all contrasts. There was considerable resemblance between the Adulthood > Infancy and Childhood > Infancy contrast maps, while in the Childhood > Adulthood contrast map, the activations were weaker and sparse. Critically, there was no significant interaction between Attachment and

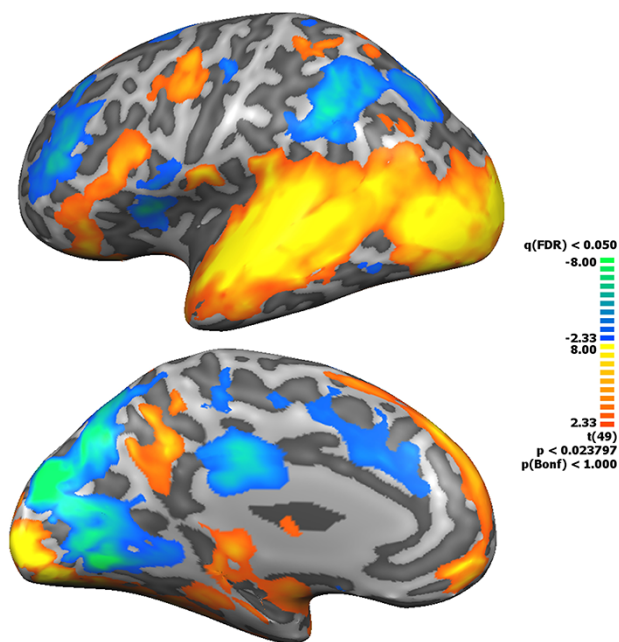


Fig. 2. Whole-brain multi-subject GLM map of the analysis dataset ($N = 50$). random effects GLM, whole-brain visual stimuli map, corrected for multiple comparisons at $q(\text{FDR}) < 0.05$.

Age at the whole-brain level (Figure 2), lending support to the consistency hypothesis of attachment.

Next, we examined the pre-registered ROIs to test our hypothesis of a network responding to self-related attachment stimuli. Beta weights were extracted from ROIs and analyzed with a 2×3 Attachment (Self/Other) \times Age (Infancy/Childhood/Young Adulthood) repeated measures ANOVA. We examined the hypothesis that the ROIs would show higher BOLD activity when viewing own attachment videos than when viewing similar videos of others. Indeed, results revealed that across all ROIs, self-related attachment videos elicited stronger BOLD activity, and this difference was significant in all regions except for the DMN. Significant self-related attachment effects were found in the insula ($F(1,49) = 4.56$, $P = 0.03$, $\eta^2 = 0.08$, $\text{BF} = 0.86$), PHG ($F(1,49) = 5.34$, $P = 0.02$, $\eta^2 = 0.09$, $\text{BF} = 0.971$), temporal cortex ($F(1,49) = 5.18$, $P = 0.027$, $\eta^2 = 0.096$, $\text{BF} = 0.489$), ACC ($F(1,49) = 9.46$, $P = 0.003$, $\eta^2 = 0.16$, $\text{BF} = 0.273$) and amygdala

($F(1,49) = 9.87$, $P = 0.003$, $\eta^2 = 0.16$, $\text{BF} = 0.093$). The extremely low BF in the VTA ($F(1,49) = 18.34$, $P < 0.001$, $\eta^2 = 0.27$, $\text{BF} = 0.003$) and thalamus ($F(1,49) = 19.81$, $P < 0.001$, $\eta^2 = 0.28$, $\text{BF} = 3.42 \times 10^{-5}$) suggests very strong evidence for the inclusion of the attachment model, whereas in the temporal cortex and insula, the evidence is moderate, and in the PHG, BF is relatively high, suggesting very weak evidence for own attachment model inclusion. As predicted, our pre-registered ROIs showed increased activation for the Self condition compared to the Other condition (Figure 4). Contrary to our hypothesis, the DMN did not show significant differential activation for the Self compared to the Other stimuli, and BF suggested inconclusive evidence for the Attachment model ($F(1,49) = 2.69$, $P = 0.107$, $\text{BF} = 2.054$).

To ensure that the Self–Other effect is not due to a spurious effect related to the random selection of participants to either the ROI definition cohort (cohort 1) or the analysis cohort (cohort 2), we employed a permutation test. Results indicated that the effect is robust and stable across 10 000 different permutations of the subject pool (see Supplementary Materials for the full analysis).

Then, we investigated the consistency of attachment across ages by testing whether these regions would show differential responses to stimuli from the three age groups (Infancy/Childhood/Young Adulthood). The temporal cortex was the only region to show a significant main effect for Age ($F(1.5,76) = 6.85$, $P = 0.004$, $\eta^2 = 0.12$, $\text{BF} = 0.003$). Other regions showed strong evidence for exclusion of the age model: insula ($\text{BF} = 21.71$), ACC ($\text{BF} = 25.57$), PHG ($\text{BF} = 15.48$), thalamus ($\text{BF} = 23.47$), VTA ($\text{BF} = 18.38$) and DMN ($\text{BF} = 12.09$); in the amygdala, no such strong evidence was found ($\text{BF} = 2.22$). It thus appears that most nodes of the attachment network were time-invariant, and only one ROI showed sensitivity to age.

Next, we examined interaction effect of Attachment \times Age. In the RM ANOVA, there was no significant interaction effect in the whole-brain analysis, as well as in any of the eight pre-registered ROIs (Supplementary Figure S4). This finding suggests that our ROIs did not show differential Self–Other responses for different ages. However, since a lack of significant interaction effect does not provide sufficient evidence for its absence, we employed a repeated measures Bayesian ANOVA to quantify evidence for lack of such interaction (Bayes exclusion factor > 10 indicates strong evidence against an interaction between Attachment and Age conditions). BFs in the insula ($\text{BF} = 11.50$), ACC ($\text{BF} = 81.69$), PHG ($\text{BF} = 12.09$), amygdala ($\text{BF} = 11.39$), thalamus ($\text{BF} = 14.12$), temporal cortex ($\text{BF} = 14.28$) and DMN ($\text{BF} = 9.81$) all

Table 1. Clusters activated in Self $>$ Other contrast, analysis dataset

Region	BA	Hemisphere	Peak cluster voxel			Cluster size	t	P
			X	Y	Z			
Cerebellum		R	36	−61	−26	641	4.60	0.000031
Extrastriate cortex	19	R	39	−76	7	496	4.99	0.000008
White matter (WM)		R	33	−64	−5	516	4.52	0.00004
Thalamus to midbrain tegmentum		R, L	6	−22	−5	10 490	5.80	0
SMA	6	R	6	17	61	579	4.93	0.00001
Hypothalamus		R, L	0	2	−15	267	−4.18	0.000118
Ventral/medial ACC	24, 32	L	−3	−1	34	1963	5.21	0.000004
Cortex–cerebellum border		R	0	−82	−23	374	4.31	0.000079
Medial ACC	32	R	3	29	25	321	4.02	0.000198
Cerebellum			−3	−58	−20	295	4.52	0.00004
Cerebellum			−18	−61	−38	523	4.41	0.000056
Fusiform gyrus to Extrastriate cortex	19, 37	L	−39	−58	−5	3083	4.68	0.000023
Cerebellum		L	−30	−85	−26	336	4.77	0.000017

L=left; R=right.

showed strong evidence for exclusion of the interaction model. In the VTA ($BF = 5.96$), the evidence was moderate. These findings indicate that in all of our pre-registered regions (apart from the DMN), a significant main effect for own attachment was found, manifested as stronger neural responses to self-within-attachment relationship. However, age-related effects (i.e. age differences in neural response to stimuli) emerged only in the temporal cortex ROI. Critically, there was strong evidence against interaction model across all but one of our ROIs, indicating age invariant brain activity for attachment stimuli.

To capture the ongoing exchange of information between our ROIs during the task, we utilized PPI analysis. Briefly, PPI examines task-specific changes in the correlated activity across different brain regions by identifying voxels that show increased correlation with a seed region within a given psychological context (=condition). The variance explained by the interaction term resulting from the PPI represents explained variance above and beyond the variance accounted for by the main effects of task (Self vs Other) and physiological correlation (e.g. regions that are associated anatomically, activated by a third region, etc.). Hence, significant PPI correlations represent the increasing or decreasing connectivity between regions in response to the task.

In order to investigate such fluctuations, we created a multi-subject random-effect GLM of PPI from an ACC seed to our pre-registered ROIs (for the full list of clusters, see Table 2). The resulting map (cluster threshold corrected, Figure 5) indicated that the left insular cortex had increased correlation with ACC in the Self condition compared to the Other condition. This indicates that during the viewing Self stimuli across the individual's attachment history, the transfer of information between ACC and insula is increased.

Finally, we explored the relationship between the magnitude of ACC and insular activations during the Self conditions and the independent coding of maternal and child's social behavior during the interaction. ACC beta values for the Self condition

were positively correlated with child social engagement ($r = 0.375$, $P = 0.007$; Bonferroni corrected, Figure 6), but not with maternal sensitivity ($r = 0.242$, $P = 0.091$). Similarly, insula beta values for the Self condition were moderately correlated with child social engagement ($r = 0.280$, $P = 0.049$; uncorrected) (Figure 6), but not with maternal sensitivity ($r = 0.237$, $P = 0.097$). These findings suggest that the more the child showed initiation of social communications, positive affect, warmth, motivation and involvement during interactions with the mother across development, the greater the ACC and insula activated in response to viewing Self stimuli. Notably, no significant correlations were found between child social engagement and neural response to the Other condition in the ACC ($r = 0.179$, $P = 0.168$) and insula ($r = 0.062$, $P = 0.667$), highlighting the associations between these paralimbic structures and attachment representations.

Discussion

How individuals construct a stable representation of the mother-infant attachment that guides their social and emotional life has been a core issue across multiple theories ranging from attachment theory to psychodynamic 'object relations' models (Winnicott, 1971) and perspectives on socialization and morality (Baumrind, 1967; Hoffman, 1970; Emde, 1992; Maccoby, 1992). Terms such as 'internal working models' (Bowlby, 1969) or 'representations of interactions that have been generalized' (Stern, 1995) were coined to indicate that familiar mother-child behavioral patterns are abstracted to form representations of the relationship that are first sensorimotor-based and then, with development, gain symbolic and representational components (Bretherton and Bates, 1984) and shape other attachments throughout life. Such far-reaching consensus across theories underlines the centrality of the mother-infant attachment and describes how it gains consistency over time and becomes the

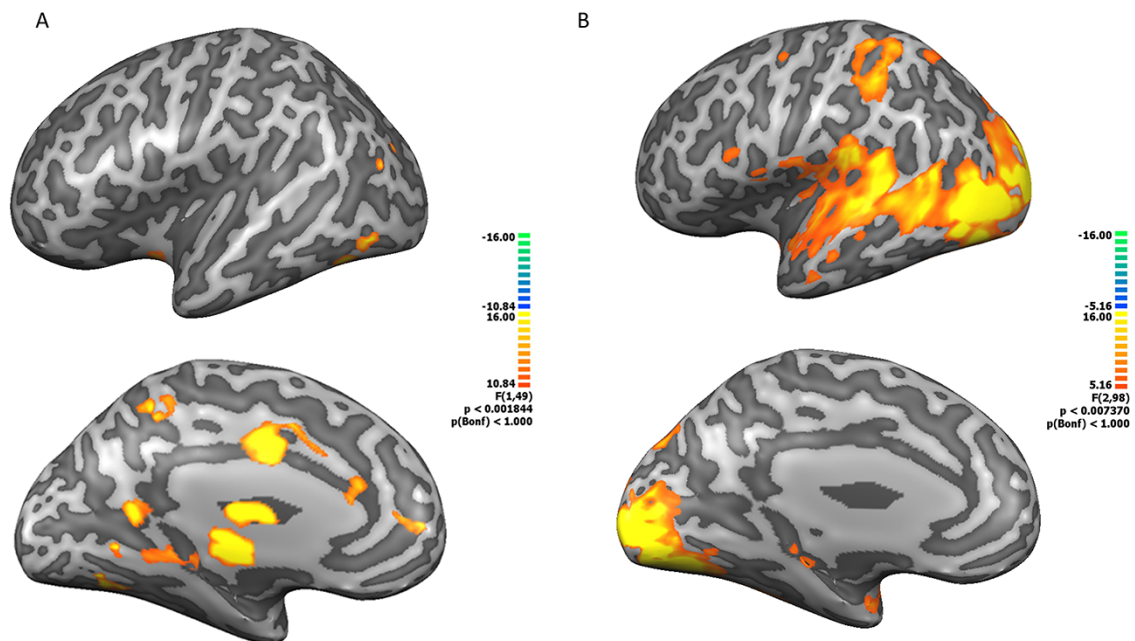


Fig. 3. Whole-brain two factorial repeated measures ANOVA (Attachment (Self/Other) \times Age (Infancy/Childhood/Young Adulthood), analysis dataset ($N = 50$). (A) Main effect for Attachment, clusters in the ACC, thalamus and midbrain. (B) Main effect for time. Clusters in occipital regions, temporal lobe, parietal cortex and limbic regions. There was no Attachment \times Age interaction effect. All maps were FDR corrected ($q(\text{FDR}) < 0.05$) on VMR and projected into an inflated brain for presentation purposes.

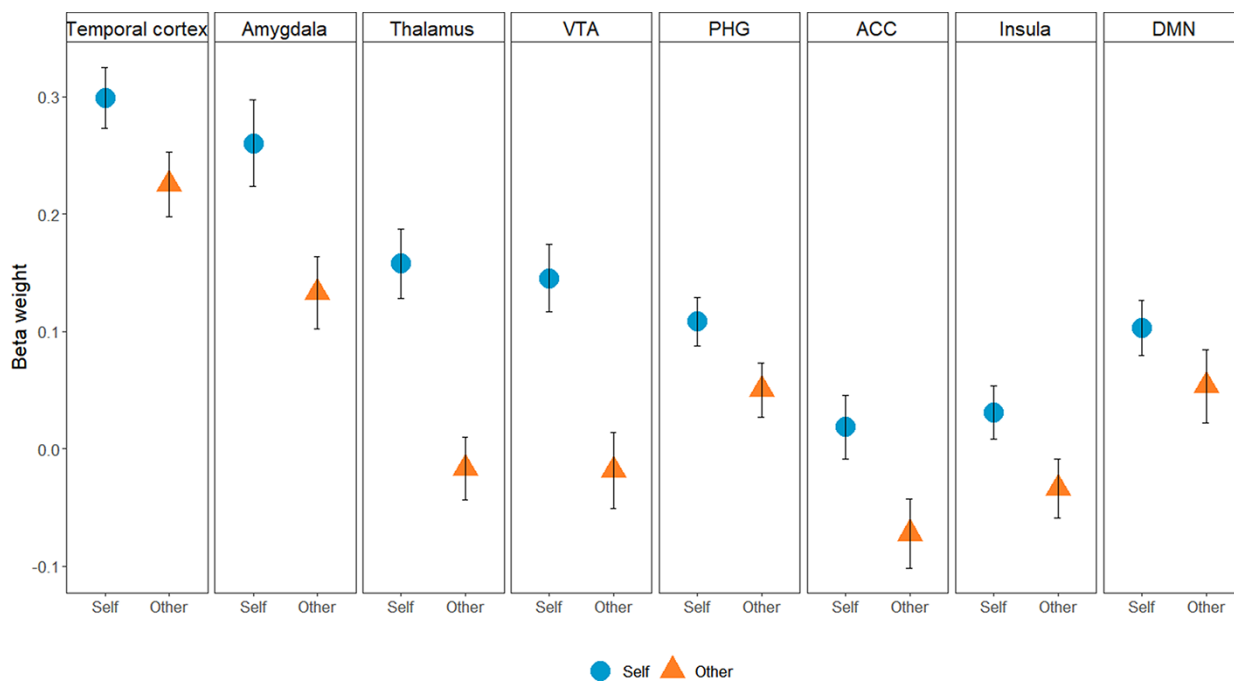


Fig. 4. Attachment main effect in ROIs, analysis dataset, $N = 50$. All ROIs except the DMN showed Attachment main effect, with higher beta values for the self condition. Note the strong effect in the thalamus. Colored shapes mark the average, whiskers mark SE.

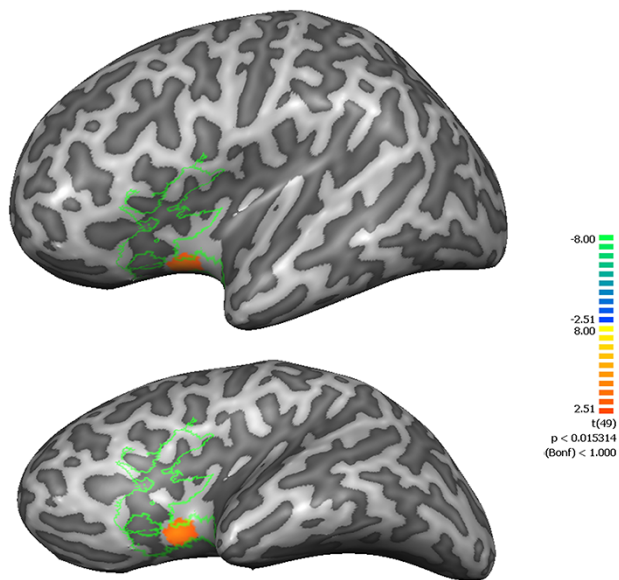


Fig. 5. Psychophysiological interaction analysis, with ACC seed for Self > Other attachment contrast of 50 participants (analysis dataset). Map was corrected using a Monte Carlo cluster-level estimation. A cluster in the left insula, in orange (the insula ROI is outlined in green), shows voxels that increase their interaction with the ACC (seed region) for the self conditions.

most influencing factor in the child's social life, emotional well-being and stable sense of self.

Neuroscientific investigations into the brain basis of attachment were based on the assumption that the centrality of attachment, its key evolutionary role and its far-reaching consequences must have a distinct signature in the brain. Studies uncovered a group of regions in the human brain that were repeatedly shown

to underpin the mother's attachment to her infant and charted its evolutionary origins in mammalian maternal care and comparability across different human attachments (Swain, 2008; Kim et al., 2016; Feldman, 2017, 2020, 2021). Within this framework, our study is the first to address the brain basis of the child-to-parent attachment within a longitudinal design, and our findings lend further support to the consistency hypothesis and tap a new angle in its application. First, we show consistency in the neural underpinnings of the child's attachment to the parent with the network that supports the parent's attachment to the child. Second, we demonstrate consistency in the neural representation of attachment in the adult brain to stimuli depicting his or her attachment relationship from infancy to adulthood, as seen by the findings that most regions of the attachment network exhibited time-invariant activations. Such findings are in line with the aforementioned theories and with research in animal models (Meaney and Champagne, 2001). Our pre-registered ROIs showed greater activations to stimuli representing own mother-child attachment ('Self') as compared to a similar attachment relationship of an unfamiliar mother-child pair ('Other') in the same regions that activate in the parents' brain in response to own parent-child interaction compared to unfamiliar interaction (Ranote et al., 2004; Noriuchi et al., 2008; Musser et al., 2012; Feldman, 2015b; Rigo et al., 2019). These included all regions previously shown to activate when parents or romantic partners observe their attachment targets, including subcortical regions implicated in mammalian caregiving, such as amygdala and hippocampus, as well as cortical areas involved in human affect and reward and nodes of the salience network, including the ACC, insula and temporal regions implicated in simulation and mentalization.

In addition to selective activation to own attachment, we found that neural response to attachment stimuli across the 20-year span were age-invariant. Our Bayesian analysis indicated strong evidence for lack of interaction between the Age and Attachment

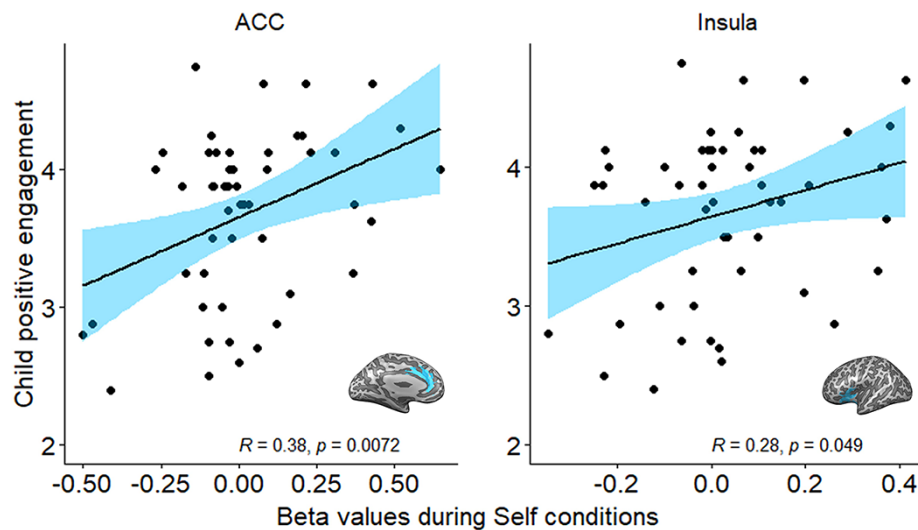


Fig. 6. Child social engagement correlation with activation during Attachment–Self conditions in the ACC and insula, analysis dataset, $N = 50$. Pearson's correlation; ROIs are shown in blue.

Table 2. Clusters of PPI with ACC seed Self > Other map, restricted to pre-registered ROIs

Correlation	Preregistered ROI	BA	Hemisphere	Peak cluster voxel			Cluster size	t	P
				X	Y	Z			
Positive	Insula	13	L	-27	8	-14	550	4.51	0.00004
	Temporal cortex	22	L	-48	-7	-17	110	3.43	0.001252
	PHG		L	-37	-25	-17	81	3.04	0.003801
	Amygdala	53	R	33	-1	-20	42	2.85	0.006412
	VTA		L	-2	-13	-11	28	3.39	0.001379
	Insula	47	R	40	23	-11	17	2.61	0.011836
	VTA		R	3	-13	-10	16	2.76	0.008136
	Insula	13	R	36	14	-8	7	2.68	0.010094
	Insula	47	R	40	20	-14	4	2.55	0.014035
	Insula	47	R	36	26	-8	4	2.63	0.011298
Negative	Temporal cortex	22	R	63	-34	19	179	-3.08	0.003413
	Temporal cortex	21	L	-63	-36	1	53	-3.04	0.00381
	Temporal cortex	39	R	42	-49	25	46	-2.76	0.008204
	DMN	10	R	3	62	10	38	-2.91	0.005434
	ACC	32	R	6	38	16	26	-2.90	0.005549
	DMN	10	R	6	65	22	23	-2.81	0.007161
	ACC	9	R	3	44	19	9	-2.72	0.008941
	Temporal cortex	39	R	39	-57	28	2	-2.52	0.015008
	ACC	9	R	9	38	19	1	-2.51	0.015254

L=left; R=right.

factors in the ROIs, indicating that the greater activation to the 'Self' stimuli observed within an attachment context did not differ as a function of age. This is particularly striking as stimuli differed substantially across ages. While the interaction of a 3-month-old infant and that of a 20-year-old adult with the mother differ on any possible sensory and mental attachment-related parameter—looks (body, face), verbal content, temporal distance, self-similarity, affective expression or mentalization—it appears that the identification of the stimuli with one's own self interacting with the attachment figure trumps these differences, and activations in the attachment nodes were mainly consistent from infancy to adulthood. These findings are the first to show that representation of the primary attachment by adults is consistent across their entire relational history, lending some support to theoretical models postulating that the consistency of attachment

is a possible mechanism that underpins the pervasive impact of early attachment on human adults (Dykas and Cassidy, 2011; Keller, 2016). However, a caveat that must be remembered is that our study showed consistency in young adult's response to stimuli representing different epochs of their attachment history. A full demonstration of continuity across ages would necessitate repeated neural measurements, which are beyond the scope of the current data. Our study highlights the need to include a longitudinal perspective and multiple brain-imaging sessions in social neuroscience studies, a practice that is rarely presented in the literature. Another important argument is that this consistency may relate to domain-general circuits of affect, motivation or salience that participate in the processing of such stimuli; however, the consistently higher activations to own attachment reminders as compared to similar stimuli of unfamiliar pair

suggest that greater resources are allocated to attachment representations, possibly as they attract more attention and trigger greater affect and reward.

One possible explanation for the time-invariant representation of attachment across a 20-year span can be drawn from perspectives on the 'self' and its neural underpinnings, as our paradigm presented participants with stimuli of the 'self-within-attachment relationships' where the attachment context is inseparable from observing the self, a practice consistent with research on the parent-to-child attachment. Studies on the neural representation of the 'self' indicate that it combines the bodily (Blanke, 2012; Salomon, 2017), social (Decety and Sommerville, 2003; Yeshurun et al., 2021) and narrative (Christoff et al., 2011; Peer et al., 2015) aspects of the 'self' into an integrated whole (Northoff et al., 2006) that, similar to attachment, is considered a stable organizational construct across time and place (Allen and Tsakiris, 2018; Rubianes et al., 2020). It has been repeatedly suggested that the sense of self and its neural foundations develop within the attachment context (Rochat, 2003; Ciaunica and Crucianelli, 2019; Montirosso and McGlone, 2020) which integrates its bodily, social and salience-attributing features (Allen and Tsakiris, 2018; Ciaunica and Crucianelli, 2019; Montirosso and McGlone, 2020). Our paradigm, included several key aspects previously addressed in neuroscientific studies on the self (Northoff et al., 2006; Peer et al., 2015), including visual and auditory self-recognition (Uddin et al., 2005; Qin and Northoff, 2011; Salomon et al., 2012, 2020), autobiographical memory, affective self-relevance (Kelley et al., 2002; Schäfer et al., 2020) and 'self-relatedness' factors (mother's face, mother's voice, my home). These were encoded within the 'narrative self', the 'story' the individual builds of his or her personal development, attachment relationships and childrearing environment (Gergen and Gergen, 1988; Miller et al., 1990). Our findings accord with perspectives suggesting that the development of the self and its bodily functions are embedded within the mother-infant bond (as initially suggested Freud, 1923 in his article "The ego and the id (1923)") and, over time, gain consistency of representation through ongoing transactions between the consolidation of the self and internal models of attachment (Fonagy et al., 2007; Feldman, 2015a). However, since we did not compare stimuli of the mother-child attachment with those of the self alone from the three age groups, these points are presented as suggestions and should be treated with caution. Much further research is needed to examine the ongoing relationship between the neural underpinnings of the self and those of attachment relationships.

Stimuli of one's own attachment elicited not only greater activations but also increased inter-region coherence. The PPI analysis indicated that our seed region in the ventral ACC showed increased connectivity with the insula during the observation of own attachment stimuli. The ACC is a key hub that receives exteroceptive inputs from all primary sensory and associative cortices, which are integrated into a higher-order percept (Beckmann et al., 2009). The ACC contains projections to the amygdala, striatum, and VTA and these connections mark stimuli with salience and reward value (Fujiwara et al., 2009). The ACC also links with the hippocampus to create higher-order representations of memorized events (Rolls, 2019). Finally, upstream projections of the ACC to the OFC enable the processing of reward value and the prioritizing of action on the basis of such valuation (Burgos-Robles et al., 2019).

It has long been known (Papez, 1937) that the ACC plays a key role in affective processing, which underpins the formation of attachment bonds. The ACC is implicated in evaluative

emotional processing (Esslen et al., 2004), assessment of the motivational value of stimuli (Fujiwara et al., 2009), generation of behavioral emotional response (Etkin et al., 2011) and top-down monitoring of affective information (Carter et al., 2001). The ACC integrates social functions relevant for the formation of human attachments. It contains neurons that respond specifically to cues related to 'self' vs 'nonself' (Sturm et al., 2013) and integrates sensory, cognitive and affective information into a coherent percept that prioritizes motivation (Porter et al., 2019; Lee and Reeve, 2020), forms predictions, regulates affect (Ochsner et al., 2009), consolidates memories (Restivo et al., 2009; Vetere et al., 2011) and shapes the individual's mode of operation in social contexts (Krill and Platek, 2009; Vassena et al., 2017). Such integration of functions related to self, affect and social processing renders the ACC as a key region for the representations of attachment and their consistency over time.

Extensive reciprocal projections connect the ACC with the insula, which monitors interoceptive signals from the body. These projections connect insula-monitored interoceptive signals with ACC-controlled exteroceptive cues into an integrative interface that enables embodiment, emotional mirroring, and higher-order representation (Craig, 2009; Seth, 2013; Park et al., 2018). Both the ACC and insula contain layer V Von Economo neurons that afford rapid communication among the two regions as well as with other upstream or downstream targets (Allman et al., 2011) and both contain areas of overlap between self and others' pain (Corradi-Dell'Acqua et al., 2016; Smith et al., 2021), which mark them as regions for the interplay of connection and separation between self and partner that define the basis of attachment bonds throughout life. Our results on the increased connectivity between the ACC and insula during the processing of self-within-attachment stimuli suggest that this interface becomes more functionally coupled in response to attachment reminders in order to provide the neural underpinnings for the consistent representation of attachment relationships.

Interestingly, our seed region in the ACC was also found to play an important role in representation of the self. Several meta-analyses (Northoff et al., 2006; Qin et al., 2020) indicated that midline cortical structures, including our seed region, are integrated across the ventral and dorsal midline to sustain the multiple dimensions of the self, including proto-self, self-'qualia', bodily self, facial self-recognition and mental self (Northoff and Bermpohl, 2004; Uddin et al., 2007; Northoff and Panksepp, 2008; Moran et al., 2009). The ventral part of the midline cortical structures includes an area of overlap among the post-genual ACC, our seed region, the ventro-medial prefrontal cortex (vmPFC) and the medial orbitofrontal cortex (mOFC), and is particularly linked with the narrative self, which matures in the context of the mother-infant attachment (Northoff et al., 2006; Araujo et al., 2013; Salomon et al., 2014). Notably, a recent meta-analysis (Qin et al., 2020) differentiated on the basis of all available neural studies of the self between three levels: the bodily—the interoceptive monitoring of one's body, the environmental—the self-relevant exteroceptive signals and the mental—the representational dimension of the self. While the insula is represented at all three levels of the self, the ventral ACC is implicated only in the mental level. This level expands the representations of the self beyond the bodily or immediate sensory into autobiographical memory, personal perspective and self-reference. This autobiographical 'narrative' self assembles from the affective components of early attachments and integrates into a stable concept. Again, the parallels and reciprocal relationships between the neural underpinnings of self and the brain basis of attachment

require much further research, and we present these thoughts only as directions for future research, as our study did not separate the neural response to the self from the neural response to attachment reminders and the associations between self and attachment could not be empirically tested.

Connectivity between the ACC and AI, which subserves key functions such as interoception and affective processing (Craig, 2009; Seth, 2013), appears to play an important role in the parent-to-child attachment. Connectivity of the ACC and AI in the parental brain has been associated with parent–infant synchrony in infancy and predicted the child’s emotion regulation and cortisol reactivity in preschool and lower behavior problems at 7 years (Abraham et al., 2016b; Abraham and Feldman, 2018). The coupling between the ACC and insula in response to attachment stimuli shown in our study anchors the representation of the mother–child attachment in the bodily and non-verbal sensory, as seen by the insular involvement, yet integrates this interoceptive level into adult representation, as seen by our seed region in the ACC (Morita et al., 2014). Insular activations in the maternal brain are thought to provide external-regulatory function for the infant’s emerging ability to recognize his/her own bodily signals and, over time, develop interoceptive representations (Atzil et al., 2018). Furthermore, as part of the sociotemporal brain (Schirmer et al., 2016), the insula monitors the duration and patterns of social events, including the early patterns of mother–infant non-verbal synchronous interactions that later expand into symbolic and verbal exchanges that are individually stable and provide the background for consistent attachment relationships from infancy to adulthood (Ulmer Yaniv et al., 2021).

It is interesting to note that the same brain regions sustaining human attachment overlap with the so-called ‘interoceptive network’, particularly, as recent models on interoception suggest that viewing the self often triggers activation in this ‘interoceptive network’ (Chen et al., 2021). For adults, viewing the self while interacting with the mother as an infant may be an especially strong reminder of caregiving and bodily contact. It has been suggested (Chen et al., 2021) that interoceptive information is first processed in the brainstem nucleus of the solitary tract and then projects to the thalamus, from where it is relayed to higher targets: the amygdala, insula and ACC. As seen in our data (Figure 2), the same nodes of the interoceptive network were found here to differentiate Self from Other’s attachment: thalamus-to-brainstem, amygdala, hippocampus, insula and ACC. This suggests some overlap between the attachment network and the interoception network and raises the possibility that the primary attachment and the experience of caregiving provide the earliest context for the infant’s capacity to first sense, then identify and finally form representations of signals from the body. Further study on the overlap in the brain basis of interoception and attachment may be a fruitful avenue of research and may shed further light on this important topic.

Finally, the magnitude of ACC and insular activations correlated with the degree of child social engagement, which defines the degree of positive involvement, motivation for social connection and initiation of social communication the child exhibits during interactions with the mother across the 20-year span. Child social engagement is an important feature of the mother–child interaction that has received significantly less research as compared with maternal sensitivity, albeit its role in shaping social-emotional competencies and the social brain appears to be just as critical. Child social engagement is an individually stable disposition that develops on the basis of both maternal

sensitivity and the child’s temperamental sociality (Feldman et al., 2010; Feldman, 2021). No study, to our knowledge, tracked the expression of children’s social engagement during interaction with the mother across two decades, and thus, our findings that show stability in this orientation from infancy to adulthood are novel and important and likely represent the longest timespan for which such stability in children’s behavioral social orientation is reported. This suggests that features of the infant’s behavior within the first social relationship may persist throughout life, and thus, high-risk conditions associated with dampened child social engagement, such as maternal postpartum depression or high contextual risk, should receive intervention that help mothers increase infant social engagement already in early infancy. Notably, activation of the ACC and insula was not significantly related to maternal sensitivity, the key variable in attachment research that often views attachment from the mother’s perspective (van Ijzendoorn et al., 1995), but with the child’s own behavior as an infant, child and adult. Interestingly, while maternal sensitivity has been repeatedly shown to serve as a buffer against harsh rearing conditions, beginning in late childhood the child’s social engagement charts a unique pathway to resilience, independent of the maternal path (Halevi et al., 2017), suggesting that children’s own social behavior becomes more important beginning in late childhood. Our findings indicate that in adulthood, the neural representation of the mother–child attachment, particularly the paralimbic interface that becomes functionally coupled in response to attachment cues, shows closer associations with markers of the ‘self’ and its contribution to the relationship, including the degree of engagement, valuation and motivation for the interaction, than with the mother’s behavior. These results highlight, again, the ongoing relationship between representations of the ‘self’ and internalization of the primary attachment as they mutually evolve across development and cohere into a time-invariant representation.

Several study limitations should be considered. First, we did not measure mothers’ neural response to the same stimuli, and our ROIs were based on prior research with mothers using the same naturalistic paradigm. Only a design that includes both mother and child can definitively demonstrate that own attachment stimuli trigger similar activations in both mother and child. Second, similar to all neural studies of the self, it is possible that self-related stimuli are allotted more attentional resources than non-self-relevant stimuli. However, this attentional account would also suggest that the novel attachment stimuli from the earlier ages would probably elicit greater attention; still our data show no difference between ages, suggesting that these findings do not stem from differential attentional engagement. Third, stimuli presentation order was counterbalanced for ‘attachment’ (Self vs Other), but not for ‘Age’ presentation order. This stemmed from our desire to present a coherent narrative account of the mother–child relationship from infancy to adulthood and describe the unfolding of the attachment relationship across the individual’s developmental history. Still, the lack of counterbalance in age is a study limitation and should be taken into account when interpreting the Age effect. Additionally, as in all ecological studies, our stimuli varied on numerous visual and auditory properties. Despite these limitations, we found consistent activation across our pre-registered ROI, which speak to the robustness of the effect above and beyond the specific stimuli. Much further research is needed to characterize the development of the neural basis of attachment across ages and relationships, understand its impact on the consolidation of the self and representation of

the bodily milieu, and tease apart the impact of culture, context, habit and risk conditions on the maturation of the neural representation of attachment bonds throughout life.

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Conflict of interest

The authors declare no competing financial interests.

Supplementary data

Supplementary data is available at SCAN online.

References

- Abraham, E., Hendler, T., Shapira-Lichter, I., et al. (2014). Father's brain is sensitive to childcare experiences. *Proceedings of the National Academy of Sciences*, **111**, 9792–7.
- Abraham, E., Hendler, T., Zagoory-Sharon, O., et al. (2016a). Network integrity of the parental brain in infancy supports the development of children's social competencies. *Social Cognitive and Affective Neuroscience*, **11**, 1707–18.
- Abraham, E., Hendler, T., Zagoory-Sharon, O., et al. (2016b). Network integrity of the parental brain in infancy supports the development of children's social competencies. *Social Cognitive and Affective Neuroscience*, **11**, 1707–18.
- Abraham, E., Gilam, G., Kanat-Maymon, Y., et al. (2017). The human coparental bond implicates distinct corticostriatal pathways: longitudinal impact on family formation and child well-being. *Neuropsychopharmacology*, **42**, 2301–13.
- Abraham, E., Feldman, R. (2018). The neurobiology of human allo-maternal care; implications for fathering, coparenting, and children's social development. *Physiology and Behavior*, **193**, 25–34.
- Acevedo, B.P., Aron, A., Fisher, H.E., et al. (2012). Neural correlates of long-term intense romantic love. *Social Cognitive and Affective Neuroscience*, **7**, 145–59.
- Ainsworth, M.D., Blehar, M.C., Waters, E., Wall, S. (1978). *Patterns of Attachment: A Psychological Study of the Strange Situation*. Hillsdale, NJ: Erlbaum.
- Allen, M., Tsakiris, M. (2018). The body as first prior: interoceptive predictive processing and the primacy of self-models.
- Allman, J.M., Tetreault, N.A., Hakeem, A.Y., et al. (2011). The von Economo neurons in the fronto-insular and anterior cingulate cortex. *Annals of the New York Academy of Sciences*, **1225**, 59–71.
- Araujo, H.F., Kaplan, J., Damasio, A. (2013). Cortical midline structures and autobiographical-self processes: an activation-likelihood estimation meta-analysis. *Frontiers in Human Neuroscience*, **7**, 548.
- Atzil, S., Hendler, T., Feldman, R. (2011). Specifying the neurobiological basis of human attachment: brain, hormones, and behavior in synchronous and intrusive mothers. *Neuropsychopharmacology: Official Publication of the American College of Neuropsychopharmacology*, **36**, 2603–15.
- Atzil, S., Hendler, T., Feldman, R. (2014). The brain basis of social synchrony. *Social Cognitive and Affective Neuroscience*, **9**, 1193–202.
- Atzil, S., Gao, W., Fradkin, I., et al. (2018). Growing a social brain. *Nature Human Behaviour*, **2**, 624–36.
- Bartels, A., Zeki, S. (2004). The neural correlates of maternal and romantic love. *NeuroImage*, **21**, 1155–66.
- Baumrind, D. (1967). Child care practices anteceding three patterns of preschool behavior. *Genetic Psychology Monographs*, **75**, 43–88.
- Beauregard, M., Lévesque, J., Bourgouin, P. (2001). Neural correlates of conscious self-regulation of emotion. *Journal of Neuroscience*, **21**(18), RC165.
- Beckmann, M., Johansen-Berg, H., Rushworth, M.F.S. (2009). Connectivity-based parcellation of human cingulate cortex and its relation to functional specialization. *Journal of Neuroscience*, **29**, 1175–90.
- Belsky, J., Fearon, P. (2002). Early attachment security, subsequent maternal sensitivity, and later child development: does continuity in development depend upon continuity of caregiving? *Attachment and Human Development*, **4**, 361–87.
- Benjamini, Y., Hochberg, Y. (1995). Controlling the false discovery rate: a practical and powerful approach to multiple testing. *Journal of the Royal Statistical Society. Series B (Methodological)*, **57**, 289–300.
- Blanke, O. (2012). Multisensory brain mechanisms of bodily self-consciousness. *Nature Reviews Neuroscience*, **13**, 556–71.
- Boccia, M.L., Petrusz, P., Suzuki, K., et al. (2013). Immunohistochemical localization of oxytocin receptors in human brain. *Neuroscience*, **253**, 155–64.
- Bowlby, J. (1969). *Attachment and loss*, Volume 1: Attachment.
- Bretherton, I. (2010). Fathers in attachment theory and research: a review. *Early Child Development and Care*, **180**, 9–23.
- Bretherton, I., Bates, E. (1984). The development of representation from 10 to 28 months. In: *Continuities and Discontinuities in Development*, Boston, MA: Springer. pp. 229–61.
- Buchheim, A., Erk, S., George, C., et al. (2006). Measuring attachment representation in an fMRI environment: a pilot study. *Psychopathology*, **39**, 144–52.
- Burgos-Robles, A., Gothard, K.M., Monfils, M.H., et al. (2019). Conserved features of anterior cingulate networks support observational learning across species. *Neuroscience and Biobehavioral Reviews*, **107**, 215–28.
- Bush, G., Luu, P., Posner, M.I. (2000). Cognitive and emotional influences in anterior cingulate cortex. *Trends in Cognitive Sciences*, **4**, 215–22.
- Carter, C.S., MacDonald, A.W., Ross, L.L., et al. (2001). Anterior cingulate cortex activity and impaired self-monitoring of performance in patients with schizophrenia: an event-related fMRI study. *American Journal of Psychiatry*, **158**, 1423–8.
- Chae, Y., Goodman, M., Goodman, G.S., et al. (2018). How children remember the strange situation: the role of attachment. *Journal of Experimental Child Psychology*, **166**, 360–79.
- Chen, W.G., Schloesser, D., Arensdorf, A.M., et al. (2021). The emerging science of interoception: sensing, integrating, interpreting, and regulating signals within the self. *Trends in Neurosciences*, **44**, 3–16.
- Christoff, K., Cosmelli, D., Legrand, D., et al. (2011). Specifying the self for cognitive neuroscience. *Trends in Cognitive Sciences*, **15**, 104–12.
- Ciaunica, A., Crucianelli, L. (2019). Minimal self-awareness from within: a developmental perspective. *Journal of Consciousness Studies*, **26**, 207–26.
- Corradi-Dell'Acqua, C., Tusche, A., Vuilleumier, P., et al. (2016). Cross-modal representations of first-hand and vicarious pain, disgust and fairness in insular and cingulate cortex. *Nature Communications*, **7**, 1–12.

- Craig, A.D. (2003). Interoception: the sense of the physiological condition of the body. *Current Opinion in Neurobiology*, **13**, 500–5.
- Craig, A.D. (2009). How do you feel - now? The anterior insula and human awareness. *Nature Reviews Neuroscience*, **10**, 59–70.
- Decety, J., Sommerville, J.A. (2003). Shared representations between self and other: a social cognitive neuroscience view. *Trends in Cognitive Sciences*, **7**, 527–33.
- Dykas, M.J., Cassidy, J. (2011). Attachment and the processing of social information across the life span: theory and evidence. *Psychological Bulletin*, **137**, 19–46.
- Elmadih, A., Wan, M.W., Downey, D., et al. (2016). Natural variation in maternal sensitivity is reflected in maternal brain responses to infant stimuli. *Behavioral Neuroscience*, **130**, 500–10.
- Emde, R.N. (1992). Social referencing research. In: *Social Referencing and the Social Construction of Reality in Infancy*. US: Springer, 79–94.
- Eslinger, P.J., Anders, S., Ballarini, T., et al. (2021). The neuroscience of social feelings: mechanisms of adaptive social functioning. *Neuroscience and Biobehavioral Reviews*, **128**, 592–620.
- Esslen, M., Pascual-Marqui, R.D., Hell, D., et al. (2004). Brain areas and time course of emotional processing. *NeuroImage*, **21**, 1189–203.
- Etkin, A., Egner, T., Kalisch, R. (2011). Emotional processing in anterior cingulate and medial prefrontal cortex. *Trends in Cognitive Sciences*, **15**, 85–93.
- Fan, Y., Duncan, N.W., de Greck, M., et al. (2011). Is there a core neural network in empathy? An fMRI based quantitative meta-analysis. *Neuroscience and Biobehavioral Reviews*, **35**, 903–11.
- Feldman, R. (1998). Coding Interactive Behavior. *Ramat Gan Bar Ilan University Israel*, 1–54.
- Feldman, R. (2010). The relational basis of adolescent adjustment: trajectories of mother-child interactive behaviors from infancy to adolescence shape adolescents' adaptation. *Attachment and Human Development*, **12**, 173–92.
- Feldman, R., Gordon, I., Zagoory-Sharon, O. (2010). The cross-generation transmission of oxytocin in humans. *Hormones and Behavior*, **58**, 669–76.
- Feldman, R. (2012). Parent-infant synchrony: a biobehavioral model of mutual influences in the formation of affiliative bonds. *Monographs of the Society for Research in Child Development*, **77**, 42–51.
- Feldman, R., Bamberger, E., Kanat-Maymon, Y. (2013). Parent-specific reciprocity from infancy to adolescence shapes children's social competence and dialogical skills. *Attachment and Human Development*, **15**, 407–23.
- Feldman, R., Golan, O., Hirschler-Guttenberg, Y., et al. (2014). Parent-child interaction and oxytocin production in pre-schoolers with autism spectrum disorder. *British Journal of Psychiatry*, **205**, 107–12.
- Feldman, R. (2015a). Mutual influences between child emotion regulation and parent-child reciprocity support development across the first 10 years of life: implications for developmental psychopathology. *Development and Psychopathology*, **27**, 1007–23.
- Feldman, R. (2015b). Sensitive periods in human social development: new insights from research on oxytocin, synchrony, and high-risk parenting. *Development and Psychopathology*, **27**, 369–95.
- Feldman, R. (2016). The neurobiology of mammalian parenting and the biosocial context of human caregiving. *Hormones and Behavior*, **77**, 3–17.
- Feldman, R. (2017). The neurobiology of human attachments. *Trends in Cognitive Sciences*, **21**, 80–99.
- Feldman, R. (2020). What is resilience: an affiliative neuroscience approach. *World Psychiatry*, **19**, 132–50.
- Feldman, R. (2021). Social behavior as a transdiagnostic marker of resilience. *Annual Review of Clinical Psychology*, **17**, 153–80.
- Fonagy, P., Steele, H., Steele, M. (1991). Maternal representations of attachment during pregnancy predict the organization of infant-mother attachment at one year of age. *Child Development*, **62**, 891–905.
- Fonagy, P., Gergely, G., Target, M. (2007). The parent-infant dyad and the construction of the subjective self. *Journal of Child Psychology and Psychiatry and Allied Disciplines*, **48**, 288–328.
- Forman, S.D., Cohen, J.D., Fitzgerald, M., et al. (1995). Improved assessment of significant activation in functional magnetic resonance imaging (fMRI): use of a cluster-size threshold. *Magnetic Resonance in Medicine*, **33**, 636–47.
- Fraley, R.C. (2002). Attachment stability from infancy to adulthood: meta-analysis and dynamic modeling of developmental mechanisms. *Personality and Social Psychology Review*, **6**, 123–51.
- Freeman, H., Brown, B.B. (2001). Primary attachment to parents and peers during adolescence: differences by attachment style. *Journal of Youth and Adolescence*, **30**, 653–74.
- Freud, S. (1923). The ego and the id (J. Strachey, Trans.). *The Standard Edition of the Complete Psychological Works of Sigmund Freud*, **19**, 12–66.
- Friston, K.J., Buechel, C., Fink, G.R., et al. (1997). Psychophysiological and modulatory interactions in neuroimaging. *NeuroImage*, **6**, 218–29.
- Frith, U., Frith, C.D., Frith, C.D., Wolpert, D.M. (2003). Development and neurophysiology of mentalizing. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **358**, 459–73.
- Fujiwara, J., Tobler, P.N., Taira, M., et al. (2009). Segregated and integrated coding of reward and punishment in the cingulate cortex. *Journal of Neurophysiology*, **101**, 3284–93.
- Gergen, K.J., Gergen, M.M. (1988). Narrative and the self as relationship. *Advances in Experimental Social Psychology*, **21**, 17–56.
- Glasser, M.F., Coalson, T.S., Robinson, E.C., et al. (2016). A multimodal parcellation of human cerebral cortex. *Nature*, **536**, 171–8.
- Göbel, A., Barkmann, C., Arck, P., et al. (2019). Couples' prenatal bonding to the fetus and the association with one's own and partner's emotional well-being and adult romantic attachment style. *Midwifery*, **79**, 102549.
- Goossens, F.A., Van Ijzendoorn, M.H., Tavecchio, L.W.C., et al. (1986). Stability of attachment across time and context in a dutch sample. *Psychological Reports*, **58**, 23–32.
- Halevi, G., Djalovski, A., Kanat-Maymon, Y., et al. (2017). The social transmission of risk: maternal stress physiology, synchronous parenting, and well-being mediate the effects of war exposure on child psychopathology. *Journal of Abnormal Psychology*, **126**, 1087–103.
- Hamilton, C.E. (2000). Continuity and discontinuity of attachment from infancy through adolescence. *Child Development*, **71**, 690–4.
- Hoffman, M.L. (1970). Conscience, personality, and socialization techniques. *Human Development*, **13**, 90–126.
- Insel, T.R., Harbaugh, C.R. (1989). Lesions of the hypothalamic paraventricular nucleus disrupt the initiation of maternal behavior. *Physiology and Behavior*, **45**, 1033–41.
- JASP Team (2020). JASP (Version 0.12) [Computer software].
- Keller, H. (2016). Attachment. A pancultural need but a cultural construct. *Current Opinion in Psychology*, **8**, 59–63.
- Kelley, A.W.M., Macrae, C.N., Wyland, C.L., et al. (2002). Finding the self? An event-related fMRI study. *Journal of Cognitive Neuroscience*, **14**, 785–94.
- Kelter, R. (2020). Bayesian alternatives to null hypothesis significance testing in biomedical research: a non-technical introduction to Bayesian inference with JASP. *BMC Medical Research Methodology*, **20**, 1–13.

- Keysers, C., Gazzola, V., Wagenmakers, E.J. (2020). Using Bayes factor hypothesis testing in neuroscience to establish evidence of absence. *Nature Neuroscience*, **23**, 788–99.
- Kim, P., Feldman, R., Mayes, L.C., et al. (2011). Breastfeeding, brain activation to own infant cry, and maternal sensitivity. *Journal of Child Psychology and Psychiatry and Allied Disciplines*, **52**, 907–15.
- Kim, P., Strathearn, L., Swain, J.E. (2016). The maternal brain and its plasticity in humans. *Hormones and Behavior*, **77**, 113–23.
- Krill, A., Platak, S.M. (2009). In-group and out-group membership mediates anterior cingulate activation to social exclusion. *Frontiers in Evolutionary Neuroscience*, **1**, 1.
- Lamm, C., Rütgen, M., Wagner, I.C. (2019). Imaging empathy and prosocial emotions. *Neuroscience Letters*, **693**, 49–53.
- Laurita, A.C., Hazan, C., Spreng, R.N. (2017). Dissociable patterns of brain activity for mentalizing about known others: a role for attachment. *Social Cognitive and Affective Neuroscience*, **12**, 1072–82.
- Lee, W., Reeve, J. (2020). Remembering pleasure and personal meaning from episodes of intrinsic motivation: an fMRI study. *Motivation and Emotion*, **44**, 810–8.
- Leibenluft, E., Gobbi, M.I., Harrison, T., et al. (2004). Mothers' neural activation in response to pictures of their children and other children. *Biological Psychiatry*, **56**, 225–32.
- Lewis, M., Feiring, C., Rosenthal, S. (2000). Attachment over time. *Child Development*, **71**, 707–20.
- Lorenz, K. (1935). Der Kumpan in der Umwelt des Vogels. *Journal für Ornithologie*, **83**, 289–413.
- Maccoby, E.E. (1992). The role of parents in the socialization of children: an historical overview. *Developmental Psychology*, **28**(6), 1006.
- Mar, R.A. (2011). The neural bases of social cognition and story comprehension. *Annual Review of Psychology*, **62**, 103–34.
- Margulies, D.S., Kelly, A.M.C., Uddin, L.Q., et al. (2007). Mapping the functional connectivity of anterior cingulate cortex. *NeuroImage*, **37**, 579–88.
- Meaney, M.J., Champagne, F.A. (2001). Like mother, like daughter: evidence for non-genomic transmission of parental behavior and stress responsivity. *Progress in Brain Research*, **133**, 287–302.
- Meins, E., Fernyhough, C., Fradley, E., et al. (2001). Rethinking maternal sensitivity: mothers' comments on infants' mental processes predict security of attachment at 12 months. *Journal of Child Psychology and Psychiatry*, **42**, 637–48.
- Mikulincer, M., Shaver, P.R. (2005). Attachment theory and emotions in close relationships: exploring the attachment-related dynamics of emotional reactions to relational events. *Personal Relationships*, **12**, 149–68.
- Mikulincer, M., Shaver, P.R. (2012). An attachment perspective on psychopathology. *World Psychiatry*, **11**, 11–5.
- Miller, P.J., Potts, R., Fung, H., et al. (1990). Narrative practices and the social construction of self in childhood. *American Ethnologist*, **17**, 292–311.
- Montiroso, R., McGlone, F. (2020). The body comes first. Embodied reparation and the co-creation of infant bodily-self. *Neuroscience and Biobehavioral Reviews*, **113**, 77–87.
- Moran, J.M., Heatherton, T.F., Kelley, W.M. (2009). Modulation of cortical midline structures by implicit and explicit self-relevance evaluation. *Social Neuroscience*, **4**, 197–211.
- Morita, T., Tanabe, H.C., Sasaki, A.T., et al. (2014). The anterior insular and anterior cingulate cortices in emotional processing for self-face recognition. *Social Cognitive and Affective Neuroscience*, **9**, 570–9.
- Murty, V.P., Shermohammed, M., Smith, D.V., et al. (2014). Resting state networks distinguish human ventral tegmental area from substantia nigra. *NeuroImage*, **100**, 580–9.
- Musser, E.D., Kaiser-Laurent, H., Ablow, J.C. (2012). The neural correlates of maternal sensitivity: an fMRI study. *Developmental Cognitive Neuroscience*, **2**, 428–36.
- Noriuchi, M., Kikuchi, Y., Senoo, A. (2008). The functional neuroanatomy of maternal love: mother's response to infant's attachment behaviors. *Biological Psychiatry*, **63**, 415–23.
- Northoff, G., Heinzel, A., de Greck, M., et al. (2006). Self-referential processing in our brain: a meta-analysis of imaging studies on the self. *NeuroImage*, **31**, 440–57.
- Northoff, G., Bermpohl, F. (2004). Cortical midline structures and the self. *Trends in Cognitive Sciences*, **8**, 102–7.
- Northoff, G., Panksepp, J. (2008). The trans-species concept of self and the subcortical-cortical midline system. *Trends in Cognitive Sciences*, **12**, 259–64.
- Numan, M. (2020). *The Parental Brain: Mechanisms, Development, and Evolution*. Oxford University Press.
- Ochsner, K.N., Hughes, B., Robertson, E.R., et al. (2009). Neural systems supporting the control of affective and cognitive conflicts. *Journal of Cognitive Neuroscience*, **21**, 1842–55.
- Oxley, G., Fleming, A.S. (2000). The effects of medial preoptic area and amygdala lesions on maternal behavior in the juvenile rat. *Developmental Psychobiology*, **37**, 253–65.
- Papez, J.W. (1937). A proposed mechanism of emotion. *Archives of Neurology and Psychiatry*, **38**, 725–43.
- Park, H.D., Bernasconi, F., Salomon, R., et al. (2018). Neural sources and underlying mechanisms of neural responses to heartbeats, and their role in bodily self-consciousness: an intracranial EEG study. *Cerebral Cortex (New York, N.Y.)*, **28**, 2351–64.
- Pascuzzo, K., Cyr, C., Moss, E. (2013). Longitudinal association between adolescent attachment, adult romantic attachment, and emotion regulation strategies. *Attachment and Human Development*, **15**, 83–103.
- Pavlovlić, D.M., Pavlovlić, A.M., Lačković, M. (2009). The anterior cingulate cortex. *Archives of Biological Sciences*, **61**, 659–73.
- Peer, M., Salomon, R., Goldberg, I., et al. (2015). Brain system for mental orientation in space, time, and person. *Proceedings of the National Academy of Sciences of the United States of America*, **112**, 11072–7.
- Peterson, B.S., Skudlarski, P., Gatenby, J.C., et al. (1999). An fMRI study of stroop word-color interference: evidence for cingulate subregions subserving multiple distributed attentional systems. *Biological Psychiatry*, **45**, 1237–58.
- Porter, B.S., Hillman, K.L., Bilkey, D.K. (2019). Anterior cingulate cortex encoding of effortful behavior. *Journal of Neurophysiology*, **121**, 701–14.
- Pratt, M., Goldstein, A., Feldman, R. (2018). Child brain exhibits a multi-rhythmic response to attachment cues. *Social Cognitive and Affective Neuroscience*, **13**, 957–66.
- Pratt, M., Zeev-Wolf, M., Goldstein, A., et al. (2019). Exposure to early and persistent maternal depression impairs the neural basis of attachment in preadolescence. *Progress in Neuro-Psychopharmacology and Biological Psychiatry*, **93**, 21–30.
- Qin, P., Wang, M., Northoff, G. (2020). Linking bodily, environmental and mental states in the self—a three-level model based on a meta-analysis. *Neuroscience and Biobehavioral Reviews*, **115**, 77–95.
- Qin, P., Northoff, G. (2011). How is our self related to midline regions and the default-mode network? *NeuroImage*, **57**, 1221–33.
- R Core Team. (2020). R: a language and environment for statistical computing.

- Raam, T., McAvoy, K.M., Besnard, A., et al. (2017). Hippocampal oxytocin receptors are necessary for discrimination of social stimuli. *Nature Communications*, **8**, 1–14.
- Ranote, S., Elliott, R., Abel, K.M., et al. (2004). The neural basis of maternal responsiveness to infants: an fMRI study. *NeuroReport*, **15**, 1825–9.
- Restivo, L., Vetere, G., Bontempi, B., et al. (2009). The formation of recent and remote memory is associated with time-dependent formation of dendritic spines in the hippocampus and anterior cingulate cortex. *Journal of Neuroscience*, **29**, 8206–14.
- Rigo, P., Kim, P., Esposito, G., et al. (2019). Specific maternal brain responses to their own child's face: an fMRI meta-analysis. *Developmental Review*, **51**, 58–69.
- Rochat, P. (2003). Five levels of self-awareness as they unfold early in life. *Consciousness and Cognition*, **12**(4), 717–31.
- Rolls, E.T. (2019). The cingulate cortex and limbic systems for emotion, action, and memory. *Brain Structure and Function*, **224**, 3001–18.
- Rubianes, M., Muñoz, F., Casado, P., et al. (2020). Am I the same person across my life span? An event-related brain potentials study of the temporal perspective in self-identity. *Psychophysiology*, **58**(1), e13692.
- Rushworth, M.F., Buckley, M.J., Behrens, T.E., et al. (2007). Functional organization of the medial frontal cortex. *Current Opinion in Neurobiology*, **17**, 220–7.
- Salomon, R., van Elk, M., Aspell, J.E., et al. (2012). I feel who I see: visual body identity affects visual-tactile integration in peripersonal space. *Consciousness and Cognition*, **21**, 1355–64.
- Salomon, R., Levy, D.R., Malach, R. (2014). Deconstructing the default: cortical subdivision of the default mode/intrinsic system during self-related processing. *Human Brain Mapping*, **35**, 1491–502.
- Salomon, R., Ronchi, R., Dönz, J., et al. (2016). The insula mediates access to awareness of visual stimuli presented synchronously to the heartbeat. *Journal of Neuroscience*, **36**, 5115–27.
- Salomon, R. (2017). The assembly of the self from sensory and motor foundations. *Social Cognition*, **35**, 87–106.
- Salomon, R., Progin, P., Griffo, A., et al. (2020). Sensorimotor induction of auditory misattribution in early psychosis. *Schizophrenia Bulletin*, **46**, 947–54.
- Scatliffe, N., Casavant, S., Vittner, D., et al. (2019). Oxytocin and early parent-infant interactions: a systematic review. *International Journal of Nursing Sciences*, **6**, 445–53.
- Schäfer, S., Wentura, D., Frings, C. (2020). Creating a network of importance: the particular effects of self-relevance on stimulus processing. *Attention, Perception, and Psychophysics*, **82**, 3750–66.
- Schirmer, A., Meck, W.H., Penney, T.B. (2016). The socio-temporal brain: connecting people in time. *Trends in Cognitive Sciences*, **20**, 760–72.
- Selcuk, E., Günaydin, G., Sumer, N., et al. (2010). Self-reported romantic attachment style predicts everyday maternal caregiving behavior at home. *Journal of Research in Personality*, **44**, 544–9.
- Seth, A.K. (2013). Interoceptive inference, emotion, and the embodied self. *Trends in Cognitive Sciences*, **17**, 565–73.
- Shimon-Raz, O., Salomon, R., Bloch, M., et al. (2021). Mother brain is wired for social moments. *eLife*, **10**, 1–32.
- Singer, T., Critchley, H.D., Preusschoff, K. (2009). A common role of insula in feelings, empathy and uncertainty. *Trends in Cognitive Sciences*, **13**, 334–40.
- Smith, M.L., Asada, N., Malenka, R.C. (2021). Anterior cingulate inputs to nucleus accumbens control the social transfer of pain and analgesia. *Science*, **371**, 153–9.
- Sroufe, L.A., Carlson, E.A., Levy, A.K., et al. (1999). Implications of attachment theory for developmental psychopathology. *Development and Psychopathology*, **11**, 1–13.
- Sroufe, L.A. (2005). Attachment and development: a prospective, longitudinal study from birth to adulthood. *Attachment and Human Development*, **7**, 349–67.
- Stern, D.N. (1995). The Motherhood Constellation. In: *A Unified View of Parent-Infant Psychotherapy*, New York (Basic Books) 1995.
- Strathearn, L., Fonagy, P., Amico, J., et al. (2009). Adult attachment predicts maternal brain and oxytocin response to infant cues. *Neuropsychopharmacology: Official Publication of the American College of Neuropsychopharmacology*, **34**, 2655–66.
- Sturm, V.E., Sollberger, M., Seeley, W.W., et al. (2013). Role of right pregenual anterior cingulate cortex in self-conscious emotional reactivity. *Social Cognitive and Affective Neuroscience*, **8**, 468–74.
- Swain, J., Leckman, J., Mayes, L., et al. (2004). Neural substrates of human parent-infant attachment in the postpartum.
- Swain, J.E., Lorberbaum, J.P., Kose, S., et al. (2007). Brain basis of early parent? Infant interactions: psychology, physiology, and in vivo functional neuroimaging studies. *Journal of Child Psychology and Psychiatry*, **48**, 262–87.
- Swain, J.E. (2008). Baby stimuli and the parent brain: functional neuroimaging of the neural substrates of parent-infant attachment. *Psychiatry (Edgmont (PA.: Township))*, **5**, 28–36.
- Swain, J.E., Kim, P., Spicer, J., et al. (2014). Approaching the biology of human parental attachment: brain imaging, oxytocin and coordinated assessments of mothers and fathers. *Brain Research*, **1580**, 78–101.
- Tinbergen, N. (1963). On aims and methods of ethology. *Zeitschrift für Tierpsychologie*, **20**, 410–33.
- Uddin, L.Q., Kaplan, J.T., Molnar-Szakacs, I., et al. (2005). Self-face recognition activates a frontoparietal 'mirror' network in the right hemisphere: an event-related fMRI study. *NeuroImage*, **25**, 926–35.
- Uddin, L.Q., Iacoboni, M., Lange, C., et al. (2007). The self and social cognition: the role of cortical midline structures and mirror neurons. *Trends in Cognitive Sciences*, **11**, 153–7.
- Ulmer Yaniv, A., Salomon, R., Waidergoren, S., et al. (2021). Synchronous caregiving from birth to adulthood tunes humans' social brain. *Proceedings of the National Academy of Sciences*, **118**, e2012900118.
- Ulmer-Yaniv, A., Djalovski, A., Yirmiya, K., et al. (2017). Maternal immune and affiliative biomarkers and sensitive parenting mediate the effects of chronic early trauma on child anxiety. *Psychological Medicine*, **48**, 1020–33.
- Ulmer-Yaniv, A., Djalovski, A., Priel, A., et al. (2018). Maternal depression alters stress and immune biomarkers in mother and child. *Depression and Anxiety*, **35**, 1145–57.
- Valadez, E.A., Tottenham, N., Tabachnick, A.R., et al. (2020). Early parenting intervention effects on brain responses to maternal cues among high-risk children. *American Journal of Psychiatry*, **177**, 818–26.
- van Ijzendoorn, M.H., Juffer, F., Duyvesteyn, M.G.C. (1995). Breaking the intergenerational cycle of insecure attachment: a review of the effects of attachment-based interventions on maternal sensitivity and infant security. *Journal of Child Psychology and Psychiatry*, **36**, 225–48.
- Vassena, E., Holroyd, C.B., Alexander, W.H. (2017). Computational models of anterior cingulate cortex: at the crossroads between prediction and effort. *Frontiers in Neuroscience*, **11**, 316.

- Vassena, E., Deraeve, J., Alexander, W.H. (2020). Surprise, value and control in anterior cingulate cortex during speeded decision-making. *Nature Human Behaviour*, **4**, 412–22.
- Verhage, M.L., Schuengel, C., Madigan, S., et al. (2016). Narrowing the transmission gap: a synthesis of three decades of research on intergenerational transmission of attachment. *Psychological Bulletin*, **142**, 337–66.
- Vetere, G., Restivo, L., Cole, C.J., et al. (2011). Spine growth in the anterior cingulate cortex is necessary for the consolidation of contextual fear memory. *Proceedings of the National Academy of Sciences of the United States of America*, **108**, 8456–60.
- Waters, E., Hamilton, C.E., Weinfield, N.S. (2000). The stability of attachment security from infancy to adolescence and early adulthood: general introduction. *Child Development*, **71**, 678–83.
- Weinfield, N.S., Whaley, G.J., Egeland, B. (2004). Continuity, discontinuity, and coherence in attachment from infancy to late adolescence: sequelae of organization and disorganization. *Attachment and Human Development*, **6**, 73–97.
- Weisz, E., Zaki, J. (2018). Motivated empathy: a social neuroscience perspective. *Current Opinion in Psychology*, **24**, 67–71.
- Winnicott, D.W. (1971). *Playing and reality*. London: Tavistock Publications. pp. 1–156.
- Wickham, H., Averick, M., Bryan, J., et al. (2019). Welcome to the tidyverse. *Journal of Open Source Software*, **4**, 1686.
- Yeshurun, Y., Nguyen, M., Hasson, U. (2021). The default mode network: where the idiosyncratic self meets the shared social world. *Nature Reviews Neuroscience*, **22**, 181–92.
- Zaki, J., Davis, J.I., Ochsner, K.N. (2012). Overlapping activity in anterior insula during interoception and emotional experience. *NeuroImage*, **62**, 493–9.
- Zimmermann, P., Iwanski, A. (2015). Attachment in middle childhood: associations with information processing. *New Directions for Child and Adolescent Development*, **2015**, 47–61.