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Functional Brain Networks at the Age of 5 Years: Associations with Maternal Perinatal Psychological Distress and Mother-Child Interaction

Anni Copeland

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To my family and friends

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ABSTRACT

The development of the human brain begins at the first trimester of pregnancy and continues with rapid growth, especially during the first years of life. During the period of rapid development, the brain is particularly susceptible to environmental influences, both adverse and protective. Maternal perinatal distress has been linked to detrimental effects on the child's later development and health, whereas positive social interactions may serve as a protective factor that supports healthy development. It has been suggested that these effects are partly mediated through structural and functional brain changes, although the exact mechanisms remain unclear. Understanding the normal variation in functional brain development is crucial to identifying early environmental effects and their potential long-term programming effects on child development. Magnetic resonance imaging provides an excellent tool for studying the brain, although imaging children presents challenges that must be addressed to ensure the acquisition of high-quality imaging data and the achievement of sufficient sample sizes.

The objectives of this dissertation were: 1) to present the methods used for magnetic resonance imaging without anaesthesia in young children; 2) to examine the normative features of intrinsic connectivity networks in 5-year-old children; 3) to investigate the associations between maternal perinatal distress and brain functional connectivity at the age of 5 years; and 4) to investigate the associations between mother–child interaction at 8 and 30 months of age and brain functional connectivity at age 5.

Magnetic resonance imaging of children aged 0–6 years can be achieved without anaesthesia, using age-appropriate methods. The functional networks in 5-year-olds closely resemble those seen in adults. Maternal perinatal depression was associated with local connectivity in the left amygdala, and maternal sensitivity was associated with local connectivity in the prefrontal cortex of 5-year-olds. This dissertation confirms that early exposures influence brain development beyond early childhood, demonstrating that early postnatal maternal distress and early mother–infant interaction are associated with local synchrony of brain regions involved in emotion regulation and executive function.

KEYWORDS: fMRI, functional connectivity, intrinsic connectivity networks, amygdala, prefrontal cortex, maternal perinatal distress, maternal sensitivity

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TIIVISTELMÄ

Ihmisaivojen kehitys alkaa ensimmäisen raskauskolmanneksen aikana ja on nopeaa erityisesti ensimmäisten elinvuosien aikana. Alun nopean kehityksen aikana aivot ovat erityisen alttiit ympäristön haitallisille mutta myös suojaaville vaikutuksille. Äidin perinataalinen psyykkinen stressi on yhdistetty haitallisiin vaikutuksiin lapsen myöhemmässä kehityksessä ja terveydessä, kun taas positiiviset vuorovaikutussuhteet voivat toimia suojaavana tekijänä ja tukea tervettä kehitystä. On arvioitu, että nämä vaikutukset välittyvät osittain aivojen rakenteellisten ja toiminnallisten muutosten kautta, mutta mekanismien yksityiskohdat ovat osittain epäselviä. Kehittyvien aivojen rakenteen normaalivaihtelun ymmärtäminen on oleellista, jotta voidaan tunnistaa varhaisten ympäristövaikutusten aiheuttamia muutoksia sekä niiden mahdollisia pitkäaikaisia ohjelmoivia vaikutuksia. Magneettikuvantaminen mahdollistaa aivojen tutkimisen, mutta lasten kuvantaminen tuo mukanaan haasteita, jotka täytyy tuntea laadukkaan kuvantamisaineiston saavuttamiseksi.

Tämän väitöskirjan tavoitteena oli 1) kartoittaa alle kouluikäisille lapsille ilman anestesiaa toteutettavan magneettikuvantamisen menetelmiä; 2) tarkastella 5-vuotiaiden lasten aivojen toiminnallisia verkostoja; 3) tutkia äidin perinataalisesti esiintyvän psykologisen stressin yhteyksiä lapsen aivojen toiminnallisiin yhteyksiin 5 vuoden iässä; sekä 4) tutkia äidin ja lapsen vuorovaikutuksen (8 ja 30 kuukauden iässä) yhteyksiä lapsen aivojen toiminnallisiin yhteyksiin 5 vuoden iässä.

Alle kouluikäisten lasten laadukas magneettikuvantaminen on toteutettavissa ilman anestesiaa oikeanlaisilla, lapsen ikään sopivilla menetelmillä. 5-vuotiaiden lasten toiminnalliset verkostot olivat osittain aikuisten verkostoja vastaavat. Äidin perinataaliajan masennusoireet olivat yhteydessä mantelitumakkeen paikallisiin toiminnallisiin yhteyksiin ja äidin sensitiivisyys etuotsalohkon toiminnallisiin yhteyksiin 5 vuoden iässä. Tämä väitöskirja vahvistaa, että varhaiset altisteet vaikuttavat aivojen kehitykseen yli varhaislapsuuden. Vaikutukset ovat merkitseviä erityisesti tunnesäätelyn ja toiminnanohjauksen kannalta tärkeillä aivoalueilla.

AVAINSANAT: fMRI, toiminnallinen konnektiivisuus, sisäiset hermoverkkoyhteydet, mantelitumake, etuotsalohko, äidin perinataalinen psykologinen stressi, äidin sensitiivisyys

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Abbreviations

AAL	Anatomical Automatic Labeling
ADHD	Attention deficit hyperactivity disorder
AROMA	Automatic Removal of Motion Artefacts
ART	Artefact Detection Tools
ASD	Autism spectrum disorder
BET	Brain Extraction Tool
BMI	Body mass index
BOLD	Blood oxygen level-dependent
CMT	Composite motion threshold
DMN	Default mode network
DTI	Diffusion tensor imaging
DVARS	Derivative of the root mean square variance
EA	Emotional availability
EAS	Emotional Availability Scales
EPDS	Edinburgh Postnatal Depression Scale
EV	Explanatory variable
FEAT	FMRI Expert Analysis Tool
FLIRT	FMRIB's Linear Image Registration Tool
fMRI	Functional magnetic resonance imaging
FOV	Field of view
FSL	FMRIBs Software Library
FWE	Family-wise error
FWHM	Full width at half maximum
GA	Gestational age
GMV	Grey matter volume
GRAPPA	Generalized Autocalibrating Partially Parallel Acquisition
GW	Gestational week
ICA	Independent Component Analysis
ICN	Intrinsic connectivity network
IV	Independent variable
KCC	Kendall’s coefficient of concordance

MCFLIRT	Motion Correction using FMRIB’s Linear Image Registration Tool
MELODIC	Multivariate Exploratory Linear Decomposition into Independent Components
MNI	Montreal Neurological Institute
mPFC	Medial prefrontal cortex
MPRAGE	Magnetization Prepared Rapid Gradient Echo
MRI	Magnetic resonance imaging
PAT	Parallel acquisition technique
PFC	Prefrontal cortex
PI	Ponderal index
ReHo	Regional homogeneity
ROI	Region of interest
rs-fMRI	Resting-state functional magnetic resonance imaging
RSN	Resting-state network
SCA	Seed-based connectivity analysis
SCL-90	Symptom Checklist-90
SD	Standard deviation
SPSS	Statistical Package for the Social Sciences
T	Tesla
TE	Time of echo
TR	Time of repetition
TSE	Turbo spin echo
WMV	White matter volume

List of Original Publications

This dissertation is based on the following original publications, which are referred to in the text by their Roman numerals:

I Copeland A, Silver E, Korja R, Lehtola SJ, Merisaari H, Saukko E, Sinisalo S, Saunavaara J, Lähdesmäki T, Parkkola R, Nolvi S, Karlsson L, Karlsson H, Tuulari JJ. Infant and Child MRI: A Review of Scanning Procedures. *Frontiers in Neuroscience,* 2021, Volume 15.

II Copeland A, Rajasilta O, Häkkinen S, Kumpulainen V, Silver E, Pulli EP, Saukko E, Jolly A, Saunavaara J, Parkkola R, Lähdesmäki T, Korja R, Karlsson L, Karlsson H, Tuulari JJ. Functional network organization of the 5-year-old brain identified using independent component analysis and evaluation of denoising strategies. (Manuscript)

III Vartiainen E*, Copeland A*, Pulli EP, Kumpulainen V, Silver E, Rajasilta O, Jolly A, Luotonen S, Audah HK, Hashempour N, Bano W, Suuronen I, Saukko E, Häkkinen S, Karlsson H, Karlsson L, Tuulari JJ. Pre- and postnatal maternal depressive symptoms associated with local connectivity of the left amygdala in 5-year-olds. *European Psychiatry*, 2025, Volume 68.

IV Copeland A, Korja R, Nolvi S, Rajasilta O, Pulli EP, Kumpulainen V, Silver E, Saukko E, Hakanen H, Holmberg E, Kataja EL, Häkkinen S, Parkkola R, Lähdesmäki T, Karlsson L, Karlsson H, Tuulari JJ. Maternal sensitivity at the age of 8 months associates with local connectivity of the medial prefrontal cortex in children at 5 years of age. *Frontiers in Neuroscience,* 2022, Volume 16.

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1 Introduction

Magnetic resonance imaging (MRI) is a non-invasive and safe method for studying the human brain across ages. Different MRI techniques, such as structural imaging, diffusion tensor imaging, and functional imaging, have significantly improved our understanding of typical brain development from infancy to adulthood. However, MRI presents challenges, especially when imaging young children, primarily due to excessive movement by the subject during acquisition. MRI is highly sensitive to motion and requires the subject to lie still throughout the scan. Additionally, it generates loud acoustic noise, and the scanning session can last up to an hour. In clinical settings, young children are often scanned under sedation or general anaesthesia, which is usually not an option in research settings when scanning healthy subjects. Various techniques have been developed to conduct imaging without anaesthesia; however, these methods vary, and their effectiveness remains unclear. To obtain high-quality data from this challenging study population, it is crucial to understand the methods used to scan children without anaesthesia.

Throughout early life, the brain undergoes structural changes; white matter volume, grey matter volume, and cortical thickness increase with age (Bethlehem et al., 2022) and likely underlie changes in functional brain development. However, investigating functional brain maturation is challenging, as methodologies used to measure changes in functional connectivity vary, and preprocessing and modelling choices can meaningfully influence the results (Bloom et al., 2022; Botvinik-Nezer et al., 2020). In functional MRI, functional connectivity, that is, the temporal correlation between regional fluctuations of neuronal activity, is measured indirectly from cerebral blood flow using the blood oxygen level-dependent signal. This provides information about connectivity between brain regions that are not necessarily anatomically or structurally connected. It has been suggested that functional brain development undergoes substantial changes during childhood, with connectivity shifting from local to distal, and in network organization from primary sensory regions (e.g., visual, auditory, and sensorimotor) to higher-order networks involved in functions such as attention and executive processing (Sun et al., 2024). This shift from primary to association areas mirrors the development of higher-order cognition during the same period. Despite its importance, functional brain development in early childhood, and especially in children under the age of 7, remains understudied, likely due to the practical challenges associated with MRI in this population.

Early childhood is a critical developmental period with significant development in cognitive functions, behavioural patterns, social competencies, and emotional maturity. These developmental changes are closely linked to structural and functional brain development during this period. Simultaneously, various neurodevelopmental disorders are first identified and diagnosed during childhood, many of which are frequently associated with structural and functional brain changes in preschool-aged children. Therefore, it is important to grasp the mechanisms of structural and functional brain development in normally developing children to better understand the changes related to atypical conditions.

The developing brain is sensitive to environmental influences, such as maternal distress and parenting behaviours. The effects on offspring's later development may be mediated through changes in brain development; however, the exact mechanisms remain unclear. Emerging evidence suggests an association between prenatal maternal distress and alterations in amygdala functional connectivity during infancy (Mandl et al., 2024), while findings from the postnatal period are limited. Additionally, findings are inconsistent, and the effects on childhood functional brain development remain understudied (Manning et al., 2025). Further, there is evidence that infant social interaction, such as the quality of mother–infant interaction, plays a critical role in offspring's brain development (Ilyka et al., 2021). Supportive environments, such as parental sensitivity during early postnatal life, may promote brain development and even mitigate atypical developmental trajectories induced by prenatal stress. Thus, gaining a comprehensive understanding of typical brain maturation during early childhood is crucial for fully understanding brain changes across the human lifespan and the effects of environmental influences on the brain.

Consequently, this thesis aimed to improve methodological practice related to paediatric brain developmental studies by introducing our scanning methods and by reviewing previously used methods. Next, the study aimed to present the organization of the intrinsic connectivity networks in preschool-aged children, and to focus additionally on motion denoising methods, which are crucial when imaging this age group. Finally, the aim was to investigate the effects of maternal perinatal depression and maternal sensitivity on brain functional connectivity in offspring, especially in regions important for emotion regulation and executive functions later in life.

2 Review of the Literature

2.1 Paediatric Magnetic Resonance Imaging

MRI is a non-invasive and safe method for examining the human brain across the entire lifespan (Tocchio et al., 2015). It provides high spatial resolution and excellent soft tissue contrast, which are particularly advantageous for brain imaging. In contrast to computed tomography and X-ray, MRI does not use ionizing radiation, and the image contrast is generated through high magnetic fields and radiofrequency pulses. Thus, it is well-suited also to studies carried out with the paediatric population, including imaging conducted for research purposes. Other non-invasive neuroimaging methods, such as electroencephalography, event-related potentials, and functional near-infrared spectroscopy, are also commonly used in paediatric research; while they do not involve radiation either, they come with their own methodological challenges, such as limited spatial resolution.

MRI is notably sensitive to motion, and therefore the examination requires the subject to lie still during the scan. In clinical contexts, young children below a certain age threshold (typically under 7 years) often require sedation or general anaesthesia. Nevertheless, in research settings involving healthy participants, the use of anaesthetics is discouraged due to ethical considerations and potential complications. Additionally, the acoustic noise of the scanner is high, and the acquisition time typically varies from 15 minutes to over an hour, depending on the type of scan being performed.

Children may experience feelings of fear or anxiety when placed in an unfamiliar and noisy environment. Addressing these challenges requires a child-friendly imaging environment and trained staff experienced in working with children, with the aim of alleviating anxiety and ensuring successful MRI scans. Despite such challenges, MRI plays an important role in paediatric neuroimaging research.

2.1.1 Functional Magnetic Resonance Imaging

Functional MRI (fMRI) serves as a useful tool for investigating brain functional connectivity in all age groups (Grayson & Fair, 2017), both in healthy subjects and patients. It enables the measurement of brain activity by detecting changes in blood flow and oxygenation levels. The underlying principle of fMRI is based on the observation that neuronal activation induces an increased glucose metabolism, which can be measured by an increase in local cerebral blood flow (Gauthier & Fan, 2019). Indirectly, this locally increased blood flow is related to neural activity, which is called the blood oxygen level-dependent (BOLD) signal. Functional MRI can be used, for example, to assess activity in specific brain regions (i.e., how strongly certain brain regions activate), or to assess functional connectivity, or, in other words, the functional coupling between brain regions (i.e., the level of synchronized activity between different brain regions). Functional connectivity between brain regions is considered positive when two brain regions increase and decrease their activity simultaneously, and negative when two brain regions show opposite activity patterns. Additionally, connectivity can increase (i.e., stronger connectivity), indicating that synchronization has strengthened, or decrease (i.e., weaker connectivity), indicating that synchronization has weakened over time or under certain conditions.

Previously, fMRI research has primarily focused on task-related experiments, and fMRI has mainly been used to “map” cognitive functions such as language, memory, and attention to the structural architecture of the brain. Task-based fMRI involves performing cognitive tasks while positioned within the MRI scanner, with subsequent comparison of brain activity patterns across different conditions (task versus control condition). This comparative analysis yields a statistical activation map, which identifies brain regions that are reliably more active in one condition than in another. While this approach can detect and localize minor fluctuations in brain activity, it ultimately ignores a large fraction of the variance arising from task-unrelated, seemingly spontaneous signals. Within paediatric populations, task-based fMRI studies have mostly focused on language organization and lateralization, alongside investigations into neurobehavioural and cognitive disorders.

Over the past decade, there has been a growing interest in examining how brain regions synchronize their activity in the absence of specific tasks, as assessed through resting-state fMRI (rs-fMRI) (Finn, 2021). Rs-fMRI measures spontaneous, high-amplitude, low-frequency BOLD signal fluctuations in subjects at rest. Regions with strongly correlated BOLD activity are thought to represent functional networks, known as “resting state networks” (RSNs) or “intrinsic connectivity networks” (ICNs). The first rs-fMRI study by Biswal et al. (1995) observed spontaneous low-frequency fluctuations in the BOLD signal in the sensorimotor networks, demonstrating that brain regions communicate at rest. When collecting rs-fMRI data in adults, subjects are typically instructed to lie still and keep their eyes open for 6–10 minutes without falling asleep, often with a fixation cross displayed on a screen. Young children are often unable to adequately comply with the demands of resting-state scans. To avoid developmental comparisons that involve sleep, sedation, or cognitive tasks, a common strategy has been to scan young children while they watch movies to investigate functional brain activity (Vanderwal et al., 2019).

2.1.1.1 Naturalistic Paradigms in Paediatric fMRI

Early work by Hasson et al. (2004) demonstrated that individuals watching the same movie exhibit synchronized cortical activity, highlighting the potential of movie-watching as a "naturalistic" stimulus in fMRI research. Subsequently, the use of naturalistic stimuli, such as movies, has become increasingly common across different age groups (Tansey et al., 2024). Compared to traditional resting-state paradigms, movie-watching has been shown to reduce head motion and increase participant engagement and arousal (Vanderwal et al., 2015), while also enhancing the detection of individual differences in behaviourally relevant networks more accurately than traditional resting-state conditions (Finn & Bandettini, 2021). In adults, naturalistic fMRI test-retest reliability is suggested to be good to excellent, with an average 50% increase when compared with resting state conditions (Wang et al., 2017).

The naturalistic movie paradigm typically refers to a dynamic audiovisual stimulus that includes a narrative structure, human interactions, natural soundscapes, and visual scenes that unfold over time. In contrast, *un*-natural characteristics may involve multiple camera angles, zooms, scene cuts, and exaggerated sound effects (Vanderwal et al., 2019). Naturalistic paradigms offer an alternative between highly controlled cognitive paradigms, which often suffer from limited ecological validity, and unconstrained resting-state acquisitions, which are more susceptible to confounding factors and pose challenges in interpretation.

In studies involving preschool-aged children, researchers have employed a variety of age-appropriate naturalistic stimuli to maintain engagement and minimize motion during scanning. These include simple visual displays, such as a lava lamp (Xiao, Friederici et al., 2016) or a video of abstract, screensaver-like animations (Blankenship et al., 2017). While some studies have presented the same age-appropriate movie to all participants (Rohr et al., 2018), others have allowed participants to select their own video (Emerson et al., 2015), which may increase engagement but introduces variability in stimulus exposure. However, cartoons used as a stimulus with children are not as ecologically valid as more naturalistic movies (Vanderwal et al., 2019). Furthermore, to ensure consistent effects across participants and age groups, the stimulus should ideally be standardized to fully understand changes in functional network organization across the lifespan (Sanchez-Alonso et al., 2021).

2.1.2 Challenges in Paediatric MRI

In paediatric MRI, there are numerous challenges. The two main obstacles to overcome are participants' movement and their level of distress or anxiety during the scan. Feelings of distress due to claustrophobia, stress, surprise, or fear can prompt conscious or unconscious urges to move, leading to excessive motion artefacts. However, such distress can be significantly reduced by careful participant preparation, while various strategies exist to minimize motion artefacts (Davis et al., 2022). Within paediatric MRI, both children and their parents commonly experience anxiety or discomfort about the scan, as it represents an extremely unfamiliar situation. Children often sense their parents' emotions, such as nervousness, and this can trigger their own anxiety.

Motion artefacts in MRI can manifest as ghosting, blurring, and signal variations, thus reducing overall image quality (Afacan et al., 2016; Reuter et al., 2015). Even minimal amounts of motion are sufficient to bias results significantly, potentially overshadowing real effects. In fMRI, uncorrected motion effects tend to decrease detected functional coupling across distributed networks, while apparently increasing local functional coupling within these networks (van Dijk et al., 2012).

In paediatric populations, translations in the inferior/superior direction, along with a "nodding" rotational motion, are often evident (Eichhorn et al., 2021; Frew et al., 2022). Such nodding motion can often be attributed to external factors, such as parental presence or the presence of a screen displaying a movie positioned at the end of the scanner bore, and children trying to look outside the bore. Additionally, children have a large head-to-body ratio, are already in a degree of neck flexion when lying supine in the magnet, and the nodding motion may be an effort to regain a neutral neck position. Age emerges as a predictor of head movement, as head motion typically decreases with age (Satterthwaite et al., 2013), at a more rapid rate before approximately 9 years of age (Gao et al., 2023). Furthermore, gender differences are noted, with boys exhibiting greater movement compared with girls (Alexander-Bloch et al., 2016; Frew et al., 2022). Additionally, developmental variables, such as specific temperament characteristics, may predict head movement during scanning (Johnson et al., 2021). The systematic effect of motion presents a notable challenge, as variables of interest, such as sex, age, and cognitive ability, are frequently correlated with the amount of head motion during scanning (Satterthwaite et al., 2019). Creating studies that maximize data retention is a major goal in developmental neuroscience, not only because data loss reduces overall power, but also because excluding data due to motion artefacts may disproportionately affect certain populations (e.g., children with externalizing disorders).

The MRI scanning procedure can evoke discomfort due to various factors, such as loud acoustic noise. Rapidly changing currents in the gradient coils, and the presence of a large magnetic field, generate very loud acoustic noise levels, reaching up to 140 dB (peak level) in a 3 Tesla (T) scanner (Moelker & Pattynama, 2003). Furthermore, higher-field scanners, such as a 7 T scanner, can produce even louder noise levels (Akbar et al., 2023). Sounds vary from soft clicks to loud bangs, depending on the acquisition protocol. Although passive protection with earplugs and headphones is used to reduce noise, participants remain exposed to loud acoustic noise. Such intense scanner noise represents a significant source of discomfort and can also cause difficulties in verbal communication during the scan (Moelker et al., 2004).

In this thesis, our primary focus is on the scanning of children aged 0–6 years. However, most of the challenges and procedures described can be also implemented in older age groups. Significantly, children and adolescents with developmental disorders may require extra considerations related to hyperactivity, anxiety, and the ability to perform and maintain attention (Fassbender et al., 2017).

2.1.2.1 Strategies to Minimize Motion in MRI

The strategies used to address motion in paediatric MRI studies vary depending on the age of the child (Barkovich et al., 2019). Infants are often scanned after feeding, while swaddled, and during natural sleep. This technique, referred to as the “feed-and-wrap” or “feed-and-swaddle” method, is inexpensive, easy to implement, and often the first choice in clinical settings (Antonov et al., 2017; Templeton et al., 2020). A successful feed-and-swaddle method requires a well-trained and coordinated team to conduct the procedure (Barkovich et al., 2019). Challenges in data acquisition seem to be less prevalent in infants, as reflected in relatively large sample sizes and the number of studies in this population. A limitation is that this method works best for the age group up to 3 months, although it has also been used with older children (Templeton et al., 2020). Moreover, the sleeping state likely would not affect structural brain examinations, but investigations of functional connectivity may be affected by differing states of consciousness (Lee et al., 2020; Yates et al., 2023).

Imaging young children aged 1–5 years is perhaps the most challenging age group, as these children nap less frequently, are more mobile, and are still often unable to understand verbal instructions. Consequently, considerable variability exists in the methods employed for imaging within this age group (Harrington et al., 2021). Nevertheless, these practical limitations have resulted in a gap in studies in healthy subjects within this age group. In contrast, in older age groups (>5 years) the implementation of behavioural strategies and training before acquisition, such as mock scanner sessions, has consistently been shown to improve success rates and data quality (Cavarocchi et al., 2018; De Bie et al., 2010; Gao et al., 2023; Raschle et al., 2009). Pre-scan procedures may involve providing informative materials to families prior to visits, playing audio recordings of scanner sounds, or presenting videos that explain the scanning procedure. Additionally, websites and smartphone applications offering guidance on the process are available (Runge et al., 2024). More recently, virtual reality preparation has emerged, although its efficacy is unclear (Ashmore et al., 2019; Stunden et al., 2021). At the scanning site, to demonstrate the impact of motion, examples of sharp and blurry pictures can be used, and movement restriction may be illustrated with games, such as the "Freezing-Game" or "Statue-Game" (Raschle et al., 2009). A recent meta-analysis by Suzuki et al. (2023) suggested that participants who underwent a preparation programme were more likely to complete a successful MRI than those who did not undergo a preparation programme (odds ratio 1.98). A limitation is that the meta-analysis included only five studies. Collectively, these preparation methods share the common objective of familiarizing children with the characteristics of an MRI scanner and training them to remain still for extended periods.

Various methods can be used to minimize motion during image acquisition. Restricting head motion can be achieved through the use of foam cushions, inflatable positioning pads, or customised foam head cases. Proper positioning of the head within the base of the head coil is essential. A weighted blanket or small sandbags on the lower legs can be used to improve participants' comfort. During the scan session itself, when scanning older children, playing music or presenting a video during acquisition can improve compliance and reduce motion. Head motion can be significantly reduced by watching a movie, and an additional benefit can be obtained from virtual real-time visual head motion feedback (Greene et al., 2018). Moreover, research findings suggest that movies not only diminish mean head motion but also prevent linear drift in mean head motion over time within a run (Frew et al., 2022). This is particularly crucial, considering the known increase in motion over the duration of the scan, as children tend to lose focus during the scan (Meissner et al., 2020). Previous studies have shown that children as young as 7 tolerate scan sessions of about 45 minutes, with dropout becoming more substantial with increasing time (Achterberg & van der Meulen, 2019; Engelhardt et al., 2017). Verbal communication at regular intervals and the provision of positive feedback regarding performance can also help to maintain motivation (Fassbender et al., 2017). However, it should be noted that visual and auditory distractions may impact the activation of brain regions, potentially confounding resting-state functional connectivity analysis.

2.1.2.2 Strategies to Correct Motion in fMRI

Subject preparation and careful data acquisition should reduce the amount of motion; however, strategies implemented after scanning are also crucial (Zaitsev et al., 2017).

Preprocessing requires striking a delicate balance between conserving signals of interest and removing noise. Preprocessing procedures typically include motion correction, slice-timing correction, spatial smoothing, and high-pass filtering (Zaitsev et al., 2017). Motion correction is the process by which head movements are corrected by realigning volumes across the scan, while slice-timing correction addresses differences in acquisition time between slices within each volume. Spatial smoothing involves applying a filter to remove high-frequency spatial noise, allowing better signal detection. High-pass filtering removes low-frequency signals considered noise of physiological or scanner origin. Importantly, while such routine preprocessing brings all MRI images into alignment and slightly cleans the signal, it does not completely remove the effects of motion, as the image signal is also changed due to movement during the scan. In addition to these standard steps, numerous denoising strategies have been developed to further clean the BOLD signal (Burgess et al., 2016; Caballero-Gaudes & Reynolds, 2017; Satterthwaite et al., 2019). However, no single method offers perfect motion control (Parkes et al., 2018; Zaitsev et al., 2017), and there is currently no preprocessing pipeline regarded as the gold standard. Broadly defined, there are two main approaches to cleaning motion data: 1) removal of motion-affected images (scrubbing, outlier removal) (Power et al., 2012), and 2) signal-preserving, regression-based strategies, such as independent component analysis-based data cleaning (Griffanti et al., 2014). Due to the impact that both head motion and preprocessing choices have on functional connectivity estimates, benchmarking preprocessing steps in high-motion early childhood samples is critical (Graff et al., 2022).

Independent Component Analysis (ICA) automatically decomposes the 4D (space x time) data into maximally independent spatial components (Pruim et al., 2015b). Ideally, in task-free fMRI, these components separate neural signal from noise. Artefact components may then be regressed out, leaving a cleaned signal behind. Typically, over 70% of the components can be classified as noise (Griffanti et al., 2017), highlighting the importance of denoising. Components may be labelled as noise or signal either manually (Griffanti et al., 2017) or automatically, based on spatial and/or temporal features (Salimi-Khorshidi et al., 2014). Manual labelling is time-consuming, subjective, and may be difficult to reproduce (Kelly et al., 2010). Thus, several approaches have been proposed to automate ICA-based denoising. One of these is the Automatic Removal of Motion Artefacts (AROMA), which is an ICA-based method developed to identify and remove motion-related components. This method uses an automatic classifier that categorizes each component as signal or noise based on its high-frequency content, correlation with realignment parameters, and edge and cerebrospinal fluid fractions. It has been shown to effectively remove motion artefacts from rs-fMRI data in adults (Pruim et al., 2015b); however, its performance may decline when applied to data that differs significantly from the datasets for which the method was originally developed.

Finally, a “good” rs-fMRI sequence involves as little displacement of the brain as possible. However, the acceptable amount of motion remains a topic of ongoing debate, and guidelines for determining data usability are expected to differ based on developmental stage and scanning system (Schabdach et al., 2022).

2.2 Early Life Brain Development

The development of the human foetal brain begins during the third week of gestation, undergoing rapid growth throughout the prenatal period, particularly during the third trimester (Clouchoux et al., 2012; Wilson et al., 2021). After birth, the human brain continues to develop and grow in size extremely fast, especially during the first 2 years of life, reaching over 80% of adult brain volume by the age of 2 years (Knickmeyer et al., 2008). A recent study by Bethlehem et al. (2022), combining data from over 100 studies and 120,000 scans, has delineated brain morphometry growth charts (Figure 1). Total grey matter volume (GMV) tends to follow an inverted U-shaped developmental course, showing a strong increase starting from mid-gestation onwards, peaking at approximately 6 years of age, followed by a near-linear decrease. Concurrently, subcortical GMV shows peaks later, in adolescence at 14 years. The developmental trajectory of cortical grey matter follows a regionally specific pattern, as synaptic density peaks first in primary sensory areas, followed by the association areas, and then the prefrontal cortex, cortices that subserve higher cognitive functions (Tau & Peterson, 2010). Finally, total white matter volume (WMV) undergoes rapid growth from mid-gestation to early childhood, reflecting myelination and axonal packing (Reynolds et al., 2019), and reaches its peak at approximately 29 years of age (Bethlehem et al., 2022). The rate of growth (velocity) peaks for both GMV and subcortical GMV in infancy at 5 months, and for WMV during early childhood at 2.4 years. These structural alterations form the basis for the development of the brain’s functional organization and connectivity (Tau & Peterson, 2010).

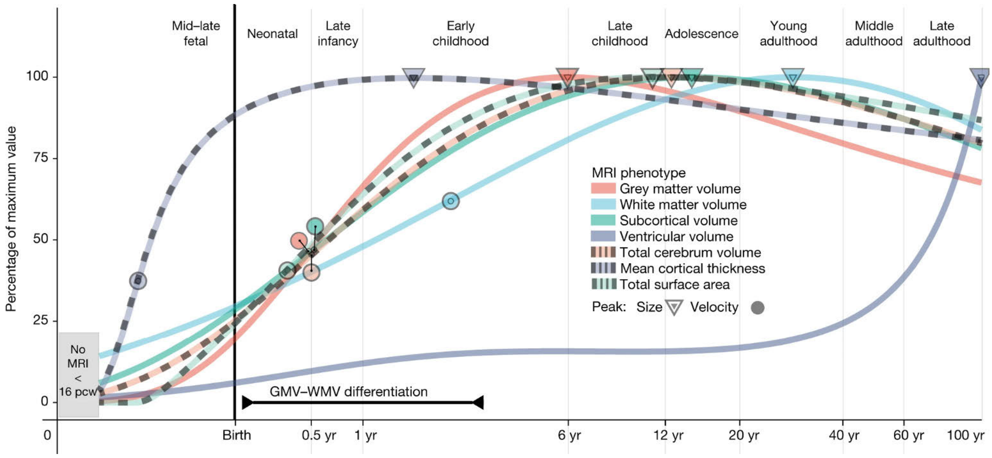

Figure 1. Graphical overview of normative trajectories of brain structural changes, and rates of change, over the lifespan. Modified from an earlier version published in Bethlehem et al. (2022), licensed under a Creative Commons Attribution 4.0 International License (http://creativecommons.org/licenses/by/4.0/).

Functional integration (between-system connectivity) and segregation (within-system connectivity) are two fundamental organizational principles of the human brain functional connectome (Cao et al., 2013). A recent study by Sun et al. (2024) delineated the growth patterns of the functional connectome across multiple scales, spanning ages from 32 postmenstrual weeks to 80 years, based on data from over 33,000 individuals. This study found that the global mean of functional connectivity, which is primarily driven by changes in middle- and long-range connections, does not peak until the late fourth decade of life (38 years), while the global variance of the functional connectome reaches its peak earlier, in the late third decade of life (28 years). These findings suggest that the human brain remains in a state of dynamic adjustment throughout the lifespan.

In utero fMRI has shown that in the human foetal brain, the overall connectivity, short-range connectivity, and interhemispheric connections follow a sigmoid growth pattern, peaking at 26–29 gestational weeks, while long-range connections show a linear increase with no periods of peak development (Jakab et al., 2014). Many forms of cerebral connectivity are present by the third trimester (Thomason et al., 2014) and the key developmental pattern suggests the posterior-to-anterior and proximal-to-distal maturation gradients (Desrosiers et al., 2024). Postnatally, developmental alterations in functional connectivity from infancy to 6 years of age are nonlinear, with more changes occurring during the first postnatal year than the second, followed by the most significant changes from ages 2–4 and 4–6 (Chen et al., 2021b). The progression of brain functional connectivity is characterized by a weakening of short-range, and strengthening of long-range, connections from childhood to adulthood (Supekar et al., 2009), in other words, from a "local to distributed" organization (Fair et al., 2009). This transition from a predominantly local to a more distributed architecture may be attributed to age-dependent systematic pruning of short-range functional connections (Supekar et al., 2009). Weakening of short-range functional connections can serve as a predictor of brain maturity (Dosenbach et al., 2010). Over the course of childhood and adolescence, individuals' overall functional connectivity patterns become more distinct and stabilized, with these changes playing a crucial role in neurocognitive development. Given the heightened plasticity of the developing brain during infancy and early childhood, this period is particularly sensitive to environmental influences, especially in regions crucial for emotion regulation and executive function, such as the amygdala and prefrontal cortex (PFC) (Callaghan & Tottenham, 2016; Ilyka et al., 2021).

2.2.1 Amygdala

The amygdala is a bilateral subcortical grey matter structure located medially within the brain's temporal lobes. It is considered part of the limbic system, connected with a broad range of cortical and subcortical regions (Saygin et al., 2015), and its activation is regulated through these connections. The amygdala has a central role in memory, decision-making, and emotion processing (Sergerie et al., 2008), which mostly develop during childhood. The amygdala appears to play a central role in responses to fear-producing stimuli (Thomas et al., 2001). Dysfunction or dysregulation of the amygdala has been implicated in various psychiatric disorders, including anxiety, depression, and post-traumatic stress disorder (Šimić et al., 2021).

Structurally, the amygdala grows rapidly in volume during the first 2 years of life (Gilmore et al., 2012), and its linear growth continues during the school-age years (Zhou et al., 2021). Structural connections are largely adult-like by early childhood, and by this age, structural connectivity becomes increasingly sparse and localized (Saygin et al., 2015). The amygdala also demonstrates early functionality, maintaining ongoing functional connectivity with subcortical, cortical, and limbic regions during early infancy (Gabard-Durnam et al., 2018; Graham et al., 2016; Rogers et al., 2017). Amygdala functional connectivity growth is nonlinear during the first 2 years of life, featuring dramatic synchronization during the first year, followed by fine-tuning during the second year (Salzwedel et al., 2019). The amygdala does not function independently of other brain regions, but is part of a larger neural circuit, for example, with the medial PFC (mPFC), which regulates the amygdala's reactivity (Tottenham & Gabard-Durnam, 2017). From age 4 to 23 years, the amygdala's functional connectivity with subcortical and limbic regions has been shown to be stable; in contrast, some amygdala-cortical connections (e.g., amygdala-mPFC) suggest age-dependent changes that continue through adulthood (Gabard-

Durnam et al., 2014). These age-related changes in functional connectivity suggest a steady refinement of coupling patterns across childhood and adolescence.

2.2.2 Prefrontal Cortex

The PFC covers the front part of the frontal lobe of the cerebral cortex, and it can be divided into a collection of structurally and functionally different subdomains: the mPFC, lateral PFC, and orbitofrontal cortex (Kolk & Rakic, 2021). When mature, it is connected structurally and functionally with various cortical and subcortical regions. The PFC is critical to many cognitive abilities and forms a large part of the neural system crucial for normal socio-emotional development and executive functioning (Fiske & Holmboe, 2019; Nelson & Guyer, 2011). Most of these characteristics and abilities, as well as the PFC's functionality, continue to develop throughout childhood and adolescence (Casey et al., 2000).

The PFC undergoes one of the longest periods of development of any brain region, taking over two decades to reach full maturity (Diamond, 2009; Gogtay et al., 2004). As the PFC takes so long to fully mature, it also has an extended critical window for environmental exposures. Additionally, the late maturation of the PFC makes it particularly vulnerable to developmental disorders. Studies have described structural and functional changes in the PFC of individuals with autism spectrum disorder (ASD) and attention deficit hyperactivity disorder (ADHD) (Firouzabadi et al., 2022; Li et al., 2024; Lukito et al., 2020). The distinct time courses of the amygdala and PFC may have important implications for the mechanisms of amygdala–PFC connections.

2.2.3 Intrinsic Connectivity Networks

As previously described, functional connectivity of the brain can be delineated into RSNs, comprising brain grey matter regions that exhibit coherent activity in a task-free state. In healthy adults, a distinct set of RSNs has been outlined, including brain regions involved in primary functions, i.e., visual, auditory, and sensorimotor, and higher-order functions encompassing memory, attention, and executive functioning (Damoiseaux et al., 2006; Smith et al., 2009). Various methods have been used to extract these networks, including data-driven methods such as ICA (Beckmann et al., 2005; Damoiseaux et al., 2006), model-driven approaches such as seed-connectivity analysis (SCA) (Biswal et al., 1995), and clustering techniques, which parcellate the cortex into networks of functionally coupled brain regions or whole-brain functional networks (see example in Figure 2) (Yeo et al., 2011). The observed networks and their characteristics depend on the neural processes being evoked, the resting-state or naturalistic context, and analytical choices (Cole et al., 2010), making it difficult to compare study results. Additionally, authors have struggled with the naming of networks, resulting in a lack of a consistent network taxonomy (Uddin et al., 2019). This presents a significant challenge, as it impedes the successful integration of research findings. However, in adults, the most frequently reported networks include the default mode network (DMN), sensory/motor networks, frontoparietal network, central executive network, salience network, visual or occipital networks, ventral attention network, dorsal attention network, auditory network, and limbic network. Previous studies have focused on the changes in connectivity within and between networks, the organization of networks, and changes in organization and connectivity over developmental stages and aging (Betzel et al., 2014).

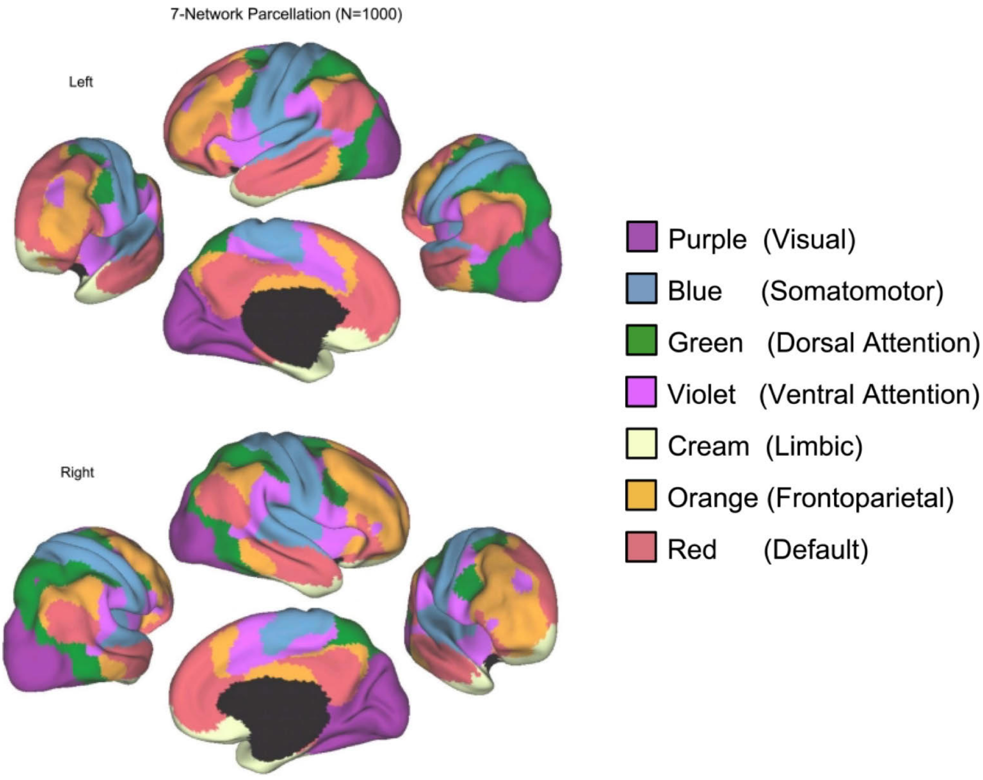

Figure 2. Example of a 7-network cortical parcellation of the human cerebral cortex, and table of colours assigned to networks. Reprinted with permission from the American Physiological Society, combining two originally separate figures side by side from Yeo et al. (2011).

The prenatal and early postnatal periods represent a crucial stage in the establishment of RSNs. *In utero* fMRI has confirmed the presence of primitive forms of functional networks by middle gestation (Turk et al., 2019), indicating that mature functional dynamics originate before birth. The neonatal brain shows early formation of RSNs, with a strong overlap with the mature adult brain (De Asis-Cruz et al., 2015; Rajasilta et al., 2020), especially in primary systems—visual, auditory, and sensorimotor networks—which are functionally synchronized starting from birth (Desrosiers et al., 2024; Gao et al., 2014; Lin et al., 2008; Liu et al., 2008). Visual and sensorimotor networks have been shown to reach adult-like patterns (80% similarity) already in the perinatal period (Sun et al., 2024). The early synchronization of these primary networks can be supported by the adult-like capability for sensory processing and responses to visual (Deen et al., 2017) and auditory stimuli (Wild et al., 2017) during infancy.

In contrast, higher-level networks, which typically include, for example, the central executive network and salience network, are in a premature form at the end of the first postnatal year (Gao et al., 2015) and mature over a more protracted period of time, reaching adult like-patterns (80% similarity) at 4–6 years of age (Sun et al., 2024). This shift from the primary to association areas mirrors the development of higher-order cognition during the same period and environmental stimuli play a crucial role in shaping these connections. Moreover, it has been shown that functional connectivity within RSNs decreases with age, while functional connectivity between RSNs increases with age (Betzel et al., 2014), which is in line with the previously mentioned development from local to distributed. However, these maturation patterns cannot be generalized to all networks, and distinct nonlinear growth patterns are suggested. Sun et al. (2024) found that the distribution scores (defined by the number of spatially discontinuous subregions) of the DMN, frontoparietal, and ventral attention networks developed until early childhood (4–6 years). In contrast, the somatomotor, visual, and dorsal attention networks exhibited a stable pattern of network distribution across the lifespan. Furthermore, the DMN and frontoparietal networks showed the lowest levels of segregation in early development, with segregation increasing rapidly with age and peaking later than other networks, at the end of the third decade. The visual network, however, showed strong segregation across the lifespan, suggesting that it is more functionally specialized and relatively less integrated (Figure 3) (Sun et al., 2024).

Overall, the maturation of RSNs follows a primary-to-higher-order sequence, but different networks demonstrate unique timings and developmental trajectories. Mapping developmental trajectories in typical development lays the groundwork for exploring factors influencing those trajectories, and ultimately for using this knowledge to optimize brain development in healthy and clinical populations.

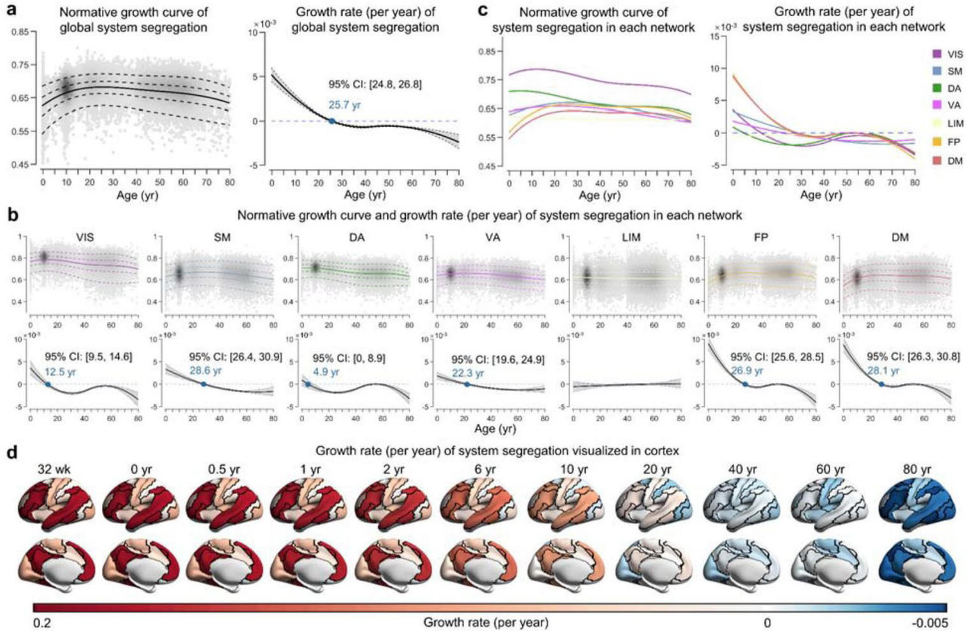

Figure 3. Normative growth rate curves of global system segregation and network segregation. Abbreviations: VIS (visual), SM (somatomotor), DA (dorsal attention), VA (ventral attention), LIM (limbic), FP (frontoparietal), DM (default mode). Network colours as in Figure 2. From Sun et al. (2024), licensed under a CC-BY-NC-ND 4.0 International licence.

2.3 Child Psychological Development

Coinciding with rapid structural and functional brain development during the first years of life, children experience significant increases in motor, social, cognitive, emotional, and language skills during this time, and already before school age. Brain functional maturation is directed by experiences, and, due to brain plasticity especially in early childhood, these early experiences may shape a child's later psychological and cognitive development. Different brain regions are known to have a central role in specific functions, such as the motor cortex, sensory systems' cortical regions, and associative areas. As a child develops, broader functional connections form between different brain regions. This process involves both the organization of distinct neural systems and their integration into more complex functional networks. These neural changes are reflected in the child's development as a noticeable leaps in abilities. Several such developmental shifts typically occur during the early years of life. For example, the emergence of the social smile around 2–3 months of age, and the development of selective attachment between 7 and 9 months, are often reflected in behaviours such as stranger anxiety (Mäntymaa & Tamminen, 1999).

Social and communication skills start to develop early. A newborn is already capable of primitive reciprocal communication, which usually occurs with a caregiver.

Early caregiver–infant communication is based on eye contact, head and body movements, and vocalizations made by both the infant and the caregiver. A typically developing infant begins to produce vocalizations within the first weeks after birth, and these early vocalizations elicit emotional and motivated responses from social partners (Jeong & Ha, 2025). The first words are typically produced around 12 months of age, and most children combine two or a few words at the age of 2 years.

Emotions are an important part of communication from the beginning; emotion regulation skills develop through social interaction, especially in early childhood (Kerr et al., 2019). Self-regulation refers to how a person regulates their thoughts, emotions, and behaviours, achieving a balance between internal experiences and external expectations and demands. These skills are crucial in everyday life, particularly when the state of balance is disturbed by external stress. Infants have limited capabilities for regulating emotions and therefore need caregivers' guidance and support. To manage the intensity of interaction, infants may close their eyes, turn their heads, or avert their gaze, all of which serve as early forms of emotion regulation. Emotion regulation involves not only the reduction of negative feelings, but also the sharing and amplification of positive emotions (Mäntymaa et al., 2003). For the infant, the experience of emotional attunement, especially the transition from a poorly matched emotional state to one of mutual harmony with the caregiver, is deeply rewarding. Over time, the child internalizes and learns regulation skills through experiences with caregivers and others, developing their own emotion regulation abilities. At the brain level, this process involves the formation of new and developing, mostly top-down, regulatory connections, particularly between the PFC, especially the orbitofrontal cortex, and other brain regions such as the ventral striatum, anterior insula, and amygdala (Ahmed et al., 2015; Kerr et al., 2019).

Executive functions are cognitive processes that are essential for goal-directed behaviour. The three core executive functions are inhibitory control, working memory, and cognitive flexibility (Diamond, 2013). Executive function skills are crucial in everyday life, essential for mental and physical health, and develop throughout childhood, while development continues into adolescence and adulthood. There is substantial evidence that the PFC is one of the key brain regions involved in executive functioning (Alvarez & Emory, 2006; Buchsbaum et al., 2005; Nyhus & Barceló, 2009).

Inhibitory control involves being able to control attention, behaviour, thoughts, and emotions, and this term overlaps with self-regulation. During childhood, better inhibitory control skills can, for example, be seen in a child being better at waiting their turn, less easily distracted, and more persistent. These skills are difficult for young children, and inhibitory control continues to mature during adolescence (Luna, 2009). Memory skills start to develop during infancy, as an infant can recognize the mother's voice. The capacity of working memory increases after around 8 months of age, when infants can understand that objects exist even when unseen (Cuevas & Bell, 2010). This is usually examined with the A-not-B task, whereby successful performance also requires inhibition and attention, so these skills also support working memory. This performance is likely determined in part by the development of the PFC, as shown by brain electrical activity measurements (Baird et al., 2002; Bell, 2001). The hippocampus is also known to be a key region involved in memory performance (Liu et al., 2021; Riggins et al., 2016; Warren et al., 2021). Cognitive flexibility builds on inhibitory control and working memory, and emerges later in development (Davidson et al., 2006; Luna et al., 2004). It includes the ability to switch perspectives, whether interpersonally (e.g., understanding someone else's point of view) or spatially (e.g., imagining an object from a different direction). Children as young as 2½ years of age can succeed in a very easy switching task, but more complex and flexible processes develop during school age, while the development of cognitive flexibility continues into adolescence (Diamond, 2013).

Simultaneously with the development of self-regulation and executive functioning skills, other dimensions of cognitive skills, social skills, and motor skills also develop. Before school age, children become proficient in language, begin to think symbolically, develop more sophisticated social communication skills, and show increasing empathy. Gross motor skills develop from crawling to taking first steps, running, and riding a bike. Fine motor skills develop from holding objects to the use of the pincer grasp, then to using a spoon and fork, drawing, and using tweezers. All these skills develop through interplay with the environment and experiences, with repetition reinforcing a child’s skill development. Individual factors, such as temperament and personality, also influence the developmental timeline. Behavioural development and brain development are interactive, bidirectional processes, such that experiences shape the brain, and the brain shapes future changes in behaviour (Geng et al., 2021).

2.4 Factors Affecting Functional Brain Development

Increasing evidence indicates that early-life exposures to both adverse and supportive factors exert significant and enduring impacts on a child’s brain structural and functional development, as well as cognitive and behavioural outcomes. Moreover, adverse early-life experiences represent a prominent risk factor for later mental health issues, problematic alcohol and drug use, as well as self-directed violence (Hughes et al., 2017). Supportive environments, such as social support, cognitive and linguistic stimulation, parental caregiving quality, and socioeconomic status during early postnatal life, may promote brain development and reverse atypical developmental trajectories induced by prenatal stress (see Figure 4) (Nolvi et al., 2023). However, these exposures do not affect all individuals in the same way, as individuals may differ in their receptiveness to environmental experiences, thus there is differential susceptibility to environmental influences. This differential-susceptibility hypothesis suggests that more sensitive individuals may be more susceptible to both conditions ("for better and for worse") (Belsky, 2016).

In previous literature, the term "early-life stress" or "early-life adversity" broadly encompasses various early adverse experiences, such as psychosocial, biological, and environmental stressors, covering a wide range of overlapping adverse exposures (Holz et al., 2023; Lautarescu et al., 2020). Stressors range from maternal depression and anxiety to natural disasters, bereavement, physical abuse, and maternal deprivation or separation during early childhood. As stressors vary, so may the outcomes, which makes it important to define the nature of the stressor. In this thesis, we focus on maternal depression, in some cases combined with anxiety, as an adverse early-life experience, to delineate the scope of the topic. On the other hand, as a supportive early life experience, we focus on normative variations in parenting, especially maternal sensitivity.

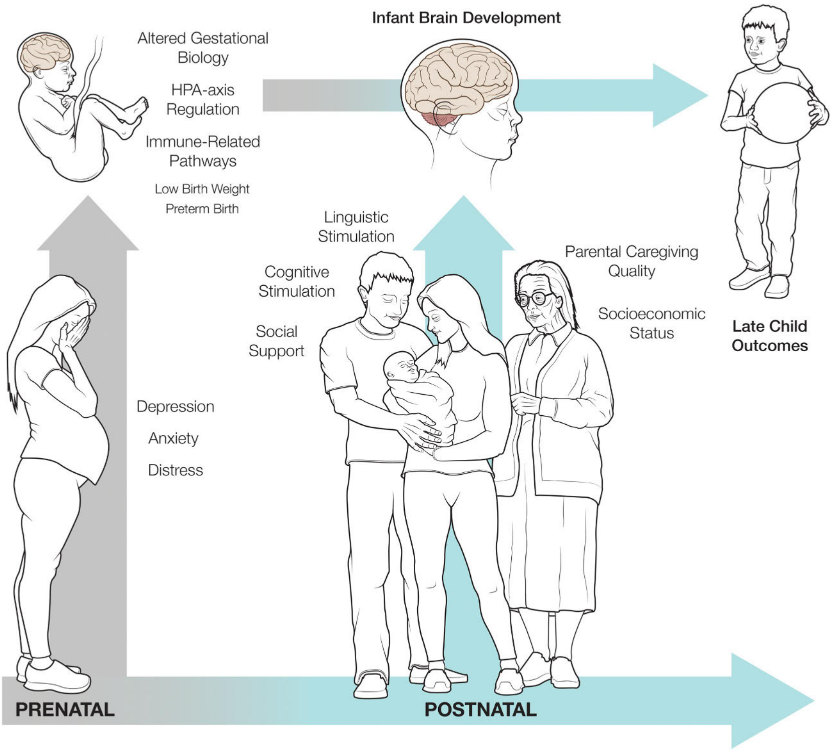

Figure 4. Schematic model of prenatal factors affecting infant brain development and early postnatal factors hypothesized to moderate associations between maternal prenatal stress and infant brain development. Reprinted from Nolvi et al. (2023), licensed under a Creative Commons Attribution 4.0 International Licence (http://creativecommons.org/licenses/by/4.0/).

2.4.1 Maternal Perinatal Depression

Maternal perinatal depression typically refers to a range of depressive episodes, spanning from mild to severe, occurring during pregnancy (prenatal or antenatal depression) or extending up to several months postnatally (postnatal or postpartum depression). A recent meta-analysis by Roddy Mitchell et al. (2023) reported a pooled prevalence rate of perinatal depression of 24.7%, with prevalence rates varying across different income status levels and regions. Maternal perinatal depression constitutes a significant mental health condition, affecting not only the mother herself, but also the developing foetus and the child, thus carrying intergenerational implications.

Maternal perinatal distress is associated with an increased risk of emotional, behavioural, and cognitive problems in the offspring (Korja et al., 2024; Lahtela et al., 2024; Rogers et al., 2020; Stein et al., 2014). Maternal perinatal depressive symptoms have been shown to predict lower social competence in children—an essential aspect of adaptive functioning and socio-emotional development (Korja et al., 2024; Luoma et al., 2001). They are also associated with offspring internalizing and externalizing symptoms (Tung et al., 2023), neurodevelopmental disorders, such as ADHD and ASD (Makris et al., 2023; Tucker & Hobson, 2022), depression (Pearson et al., 2013), and schizophrenia (Guo et al., 2019; Khashan et al., 2008). Increasing evidence also suggests that maternal perinatal distress is a risk factor for somatic conditions, such as allergic and respiratory diseases (Korhonen et al., 2019; Lau et al., 2022; Puosi et al., 2022) and obesity (Li et al., 2010). Furthermore, maternal prenatal distress has been associated with preterm birth, low birth weight, and intrauterine growth restriction, all of these being related to health problems in offspring (Ghimire et al., 2021). The effects of distress may depend on other factors, including the type of stress, timing of stress, foetal sex, and genetic variants (Glover & Hill, 2012). However, not all children exhibit detrimental effects from maternal perinatal distress exposure, and there might be differential susceptibility as mentioned above. Thus, it remains unclear how and when developmental trajectories are influenced by perinatal stress, and which factors may mediate or protect against these effects.

The pathways through which depression may affect child development seem to be different for pre- and postnatal depression. Several mechanisms causing physiological changes that may influence the intrauterine environment have been suggested to underlie adverse developmental trajectories induced by prenatal depression exposure. Depression causes dysregulation of the maternal hypothalamic–pituitary–adrenal axis, resulting in increased maternal cortisol levels (Seth et al., 2016). Elevated maternal cortisol can cross the placenta and affect the developing foetal brain (Buss et al., 2012), potentially altering neuronal growth, migration, and connectivity. Altered maternal hypothalamic–pituitary–adrenal axis functioning can also shape the development of the foetus's own stress-regulation systems, potentially leading to changes in the offspring's stress responses later in life. For example, prenatal stress exposure is suggested to yield an infant who is more stress-reactive (e.g., greater negative affect, difficulty with state regulation, reduced social engagement), which may affect early dyadic interaction. The periods most sensitive to the effects of stress are likely those during which major changes occur in the foetal brain: however, the prolonged duration of exposure, extending across multiple trimesters, might also be significant. Additionally, depression can cause changes in immunological pathways (Lahti-Pulkkinen et al., 2020), as well as placental dysfunction (Blakeley et al., 2013). There is also increasing interest in studies investigating gut–brain interactions (Yeramilli et al., 2023) and epigenetic DNA/histone modifications (Cao-Lei et al., 2020; Malin et al., 2023) following prenatal stress exposure.

Postnatal maternal depressive symptoms are thought to affect child development primarily through their impact on parenting behaviour. Maternal distress may impair mother–child interaction (Binda et al., 2019; Holmberg et al., 2020), which in turn can affect the neurobiological, social, and cognitive development of the child. Maternal depression has been associated with parenting behaviours, including reduced sensitivity, responsiveness, and increased harshness and rigidity (Lovejoy et al., 2000). Depression or other mental health problems may restrain a mother's ability to adjust her behaviour sufficiently to meet the infant's emotional regulation needs (Reck et al., 2004). The interaction difficulties between depressed mothers and their children appear to be universal across different cultures and socioeconomic status groups (Field, 2010). However, findings from a meta-analytic review by Lovejoy et al. (2000) suggest that especially young children, and economically disadvantaged children, appear to be at heightened risk of experiencing the most impaired parenting by depressed mothers. The exact mechanisms underlying the link between parenting behaviour and offspring brain connectivity remain unclear. Although speculative, one possibility is that this occurs through experience-dependent processes that regulate the synaptogenesis and synaptic pruning—key mechanisms driving the maturation of brain networks (Dégeilh et al., 2018).

2.4.1.1 Associations between Maternal Perinatal Depression and Functional Brain Development

Prenatal exposure to psychological distress has been linked to alterations in limbic and frontotemporal networks, as well as the functional and microstructural connections between them (Lautarescu et al., 2020; Scheinost et al., 2016b). The majority of studies have focused on the amygdala and its functional connectivity; however, other critical brain regions, including the PFC, cingulate gyrus, hippocampus, and insula, also play significant roles (Figure 5) (Cattarinussi et al., 2021; Mandl et al., 2024). Scanning infants soon after birth has been a common approach to mitigate potential confounding factors associated with postnatal environmental influences. Nonetheless, findings from fMRI studies have exhibited significant heterogeneity, potentially due to methodological variations, disparate timing of exposure, and variations in the timing of imaging assessments (Cattarinussi et al., 2021; Graham et al., 2015; Holz et al., 2023).

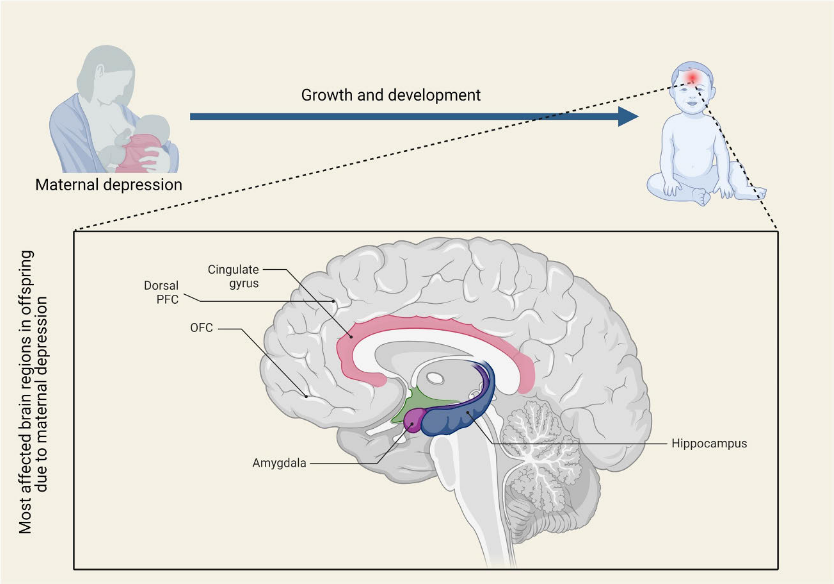

Figure 5. The most commonly affected brain regions in offspring exposed to maternal depression. PFC = prefrontal cortex, OFC = orbitofrontal cortex. Reprinted with permission from Elsevier (Cattarinussi et al., 2021).

Scheinost et al. (2020) showed that maternal prenatal distress is associated with weaker hippocampal–cingulate cortex and stronger hippocampal–temporal lobe connectivity when scanned in infants shortly after birth. Another study found significant associations between maternal depressive symptoms in the third trimester and their newborns' brain functional connectivity, mainly within the frontal lobe and between the frontal/temporal lobe and the occipital lobe (Na et al., 2023). Posner et al. (2016) found an association between maternal prenatal depression and increased negative functional connectivity between the amygdala and the dorsal PFC in 4–6-week-old infants. This same study found evidence that the connectivity changes were associated with an increase in foetal heart-rate reactivity, resulting from maternal autonomic nervous system stress reactivity. Another infant study found an association between increased prenatal stress and less positive functional connectivity between the amygdala and mPFC, but greater structural connections (Humphreys et al., 2020). In contrast, increasing or peak maternal stress in late pregnancy has been shown to be associated with stronger amygdala functional connectivity to the anterior insula and the ventromedial prefrontal cortex at 1 month of age (Marr et al., 2023). In this same study, the trajectory cluster characterized by increasing stress in late pregnancy was associated with blunted development of infant negative affect over the first 2 years of life. Associations between the amplitude of low-frequency fluctuation (indicative of regional neuronal activity) in newborns' mPFC and maternal prenatal depression and anxiety have been reported (Rajasilta et al., 2023). A recent study found an association between prenatal distress and increased functional connectivity between the amygdala and mPFC during infancy, particularly when reported social support was low (Manning et al., 2022). In this study, social support was a significant predictor of clinically elevated prenatal maternal distress, suggesting that social support in pregnancy may not only support mothers but also mitigate the intergenerational transmission of prenatal stress to their infants. Another study found a positive association between prenatal maternal depression and increased functional connectivity of the amygdala with the left temporal cortex, insula, bilateral anterior cingulate, medial orbitofrontal, and ventromedial prefrontal cortices in 6-month-old children (Qiu et al., 2015). Conversely, a study by Soe et al. (2018) found an association between prenatal depression and weakened functional connectivity of the amygdala to the cortico–striatal circuity, particularly the orbitofrontal cortex, insula, subgenual anterior cingulate, temporal pole, and striatum at the age of 4, in girls but not in boys. In addition, fluctuation of maternal depressive symptoms before and after pregnancy, independent of the severity of depressive symptoms, was associated with lower functional connectivity of the left amygdala with the bilateral subgenual anterior cingulate cortex and left caudate, and with lower functional connectivity of the right amygdala with the left orbitofrontal cortex, insula, and temporal pole, an effect only observed in girls.

Postnatal maternal depressive symptoms have been shown to be associated with the functional connectivity of the mesocortical subnetwork with the mesolimbic and amygdala–hippocampus complex subnetworks in girls, and with the functional connectivity within the mesocortical subnetwork in boys, when scanned at the age of 4 years with rs-fMRI (Wang et al., 2020). Another study in 4-year-old girls showed that postnatal maternal depressive symptoms were positively associated with the medial orbitofrontal cortices' functional connectivity with the visual networks but negatively associated with the cognitive control network (Wang et al., 2019a). Finally, postnatal maternal anxiety and depressive symptoms were negatively associated with amygdala–PFC and frontal pole functional connectivity in 6-year-olds (Uy et al., 2023). This study did not find associations between prenatal distress and amygdala–PFC connectivity.

Taken together, these results suggest that exposure to perinatal maternal depression may influence the development of brain functional connectivity, especially in the amygdala, hippocampus, and frontal cortices. However, comparability between studies is complicated by significant methodological differences related to the timing of the assessments and analysis methods, with some using predefined brain regions and others taking a whole-brain approach. Moreover, many questions remain unanswered, such as the specific timing effects, the role of maternal distress factors in the postnatal period, and long-term influences. Table 1 summarizes previous literature on maternal prenatal and postnatal depression and its associations with alterations in amygdala functional connectivity in offspring.

Table 1. Previous task-free fMRI studies investigating the effects of maternal perinatal stress on functional connectivity in the offspring, with special focus on the amygdala.

Authors	Sample, Cohort	Stress assessment and timing	Age at fMRI	Predefined region of interest	Main findings
(Marr et al., 2023)	N=60 UCI	CES-D, PSS, STAI in early, middle, and late pregnancy and at 1, 3, 6, 9, 12, and 24 months postpartum	1 month	Amygdala – anterior insula / vmPFC	**Prenatal** stress (increasing or peak maternal stress in late pregnancy): • greater FC between the amygdala and the anterior insula and the vmPFC (peak stress in late pregnancy) • greater FC between the amygdala and the vmPFC (increase in stress late in pregnancy)
(Humphreys et al., 2020)	N=32	CRISYS, Life Stressor Checklist 16-32 gw	4-6 weeks	Amygdala-mPFC	**Prenatal** stress ↑: • lower FC between the amygdala and mPFC
(Posner et al., 2016)	N=64	CES-D, PSS, HRS-D gw 34-37	5 weeks	Amygdala functional networks	**Prenatal** depressive symptoms ↑: • greater negative FC between the amygdala and the dorsal PFC bilaterally
(Manning et al., 2022)	N=41 PdP	EPDS, PROMIS, SSEQ gw mean 20.7	3 months	Amygdala-PFC	**Prenatal** distress ↑: • lower FC between the R amygdala and the R superior orbitofrontal cortex and R inferior frontal gyrus • lower amygdala-PFC FC when social support was low, but no association when social support was high
(Qiu et al., 2015)	N=24 GUSTO	EPDS gw 26, 3 months postpartum	6 months	Amygdala functional networks	**Prenatal** depressive symptoms ↑: • grater FC of the L amygdala with the bilateral mPFC, the L superior, middle and temporal cortex, the L entorhinal cortex
(Wang et al., 2020)	N=122 GUSTO	EPDS gw 26, 3 months postpartum BDI-II at 1, 2, 3, and 4.5y postpartum	4,5 years	Reward network including amygdala-hippocampus network	**Postnatal** maternal depressive symptoms ↑: • positive association with the FC of the mesocortical subnetwork and the mesolimbic and amygdala–hippocampus complex subnetworks, in girls • positive association with the FC within the mesocortical reward subnetwork, in boys

(Soe et al., 2018)	N=128 GUSTO	EPDS gw 26, 3 months postpartum BDI-II at 1, 2, 3, and 4.5 years postpartum	4,5 years	Amygdala functional networks	**Prenatal** maternal depressive symptoms ↑: (only in girls) • lower FC of the L amygdala with the right insula, putamen, the bilateral subgenual anterior cingulate cortex, and the caudate • lower FC of the R amygdala with the left orbitofrontal cortex and temporal pole **Greater pre- than postnatal** depressive symptoms: • lower FC of the L amygdala with the bilateral subgenual anterior cingulate cortex and L caudate • lower FC of the R amygdala with the L orbitofrontal cortex, insula, and temporal pole
(Uy et al., 2023)	N = 89 GUSTO	STAI, BDI-II (composite score) gw 26, 3 months, and 1, 2, 3, and 4.5 years postpartum	6 years	Amygdala - PFC	**Postnatal** maternal depressive and anxiety symptoms ↑: • lower FC of the amygdala and PFC and frontal pole

Abbreviations: GUSTO = Growing Up in Singapore Towards healthy Outcomes, Inventory-II; UCI = University of California, Irvine; PdP = Pregnancy during the COVID-19 Pandemic study; EPDS = Edinburgh Postnatal Depression Scale; CES-D = Centre for Epidemiological Studies Depression scale; HRS-D: Hamilton Rating Scale for Depression; CRISYS = Crisis in Family Systems—Revised; PROMIS = Patient-Reported Outcomes Measurement Information System; SSEQ = Social Support Effectiveness Questionnaire; BDI-II = Beck Depression Inventory–II; PSS = Perceived Stress Scale; STAI = State–Trait Anxiety Inventory; SCA = seed-based connectivity analysis; ROI = region of interest; FC = functional connectivity; L = left; R = right; PFC = prefrontal cortex; mPFC = medial PFC, vmPFC = ventromedial PFC

2.4.2 Mother–Child Interaction and Maternal Sensitivity

Maternal attachment, sensitivity, and parenting style are essential for the healthy maturation of an infant's social, cognitive, and behavioural skills. During infancy, children are dependent on caregivers, especially for their emotional and physical regulation, while the infant's own regulation skills are still developing (Eisenberg et al., 1998). An infant relies on parents for the regulation of negative emotions, as well as for the sharing and enhancement of positive emotions. By responding to the infant's physiological, emotional, and social needs in a sensitive and predictable manner during interaction, the parent provides the child with experiences of regulating emotion and behaviour. Parent–child interaction changes when the child develops from infancy to toddlerhood, acquiring cognitive, motor, and language skills and beginning to seek autonomy. These developmental achievements may challenge parents to adjust their responses to the changing developmental levels of their child.

Rocha et al. (2020) reviewed the literature on mother–infant interaction, showing its importance for infant development, especially in language, cognition, and social capabilities. Positive parenting (i.e., sensitive, supportive, structured, warm) has been shown to predict effortful control (Neppl et al., 2020), emotion regulation (Frick et al., 2018), executive function (Gueron-Sela et al., 2018), communicative development (Ollas-Skogster et al., 2025), and social-emotional competence (Lahtela et al., 2024). On the other hand, negative parenting has been shown to predict depression, anxiety, and internalizing outcomes (Yap & Jorm, 2015). Furthermore, positive and negative parenting are not simply opposites of a single continuum, and do not inherently function as direct opposites. For instance, a lack of negative parenting behaviours (e.g., harshness, criticism, and control) does not necessarily indicate a high level of positive parenting. Instead, various degrees of positive and negative parenting can coexist in diverse combinations, potentially exhibiting at least partial independence (Whittle et al., 2014).

Maternal sensitivity is a key element of parenting behaviour. It is considered the cornerstone of secure attachment (Ainsworth et al., 1978; Madigan et al., 2024). Maternal sensitivity refers to the mother's ability to recognize the child's interaction cues, and to respond to them appropriately and in a timely manner from the child's perspective. Even when maternal sensitivity is the focus of evaluation, the interaction is inherently dyadic, with both the mother and the child shaping its quality. Research suggests that at the individual level, maternal sensitivity tends to be relatively stable throughout infancy and toddlerhood (Bigelow et al., 2010; Holmberg et al., 2022). However, it may evolve as children grow and develop, and caregivers adapt their responses to meet the changing needs of their children. One widely used approach to evaluate mother–child interaction, including maternal sensitivity from early infancy onward, is the emotional availability (EA) framework (Biringen et al., 2014).

It evaluates both the parent's and the child's emotional responsiveness and how they emotionally affect each other. In addition to assessing sensitivity, the EA framework offers a multidimensional set of features to assess parent–child interaction, including parent structuring, nonintrusiveness, and nonhostility, and child responsiveness and involvement (Biringen et al., 2014).

2.4.2.1 Associations between Mother–Child Interaction, Maternal Sensitivity, and Functional Brain Development

Parental care plays a vital role in a child's psychosocial development. Previous models suggest that associations between parenting and child psychosocial development may be mediated by the influence of parenting on brain development. However, most research on the relationship between parenting and neurodevelopment has focused on extreme adversities, such as child maltreatment, neglect, and exposure to violence or abuse (Belsky & De Haan, 2011; Bhanot et al., 2021). Less attention has been directed towards normative variations in parenting behaviour that may be less severe but occur more commonly and therefore have the potential to impact a greater proportion of children.

A recent review by Ilyka et al. (2021) examined studies investigating the relationship between adult–infant interactions and measures of child brain structure or function. The review found that most studies have focused on mother–infant interactions rather than father–infant interactions, with maternal behaviours coded from mother–infant interaction, and maternal sensitivity being the most investigated behaviour. Another recent review by Bhanot et al. (2021), which included 82 studies examining associations between parenting and offspring brain structure and function using MRI, found that most studies have focused on subcortical regions, including limbic, striatal, and hippocampal regions, as well as prefrontal cortical areas. Additionally, large-scale functional brain networks, such as the DMN and salience network, have been studied in late childhood and adolescence. However, only a few task-free fMRI studies have examined associations between parenting and functional brain development during early childhood, while most of the studies focused on adolescents (parenting assessment and neuroimaging at >10 years of age). Finally, a review by Farber et al. (2020), focusing on variation within the normative range of parenting and its association with offspring brain structure and function, identified 23 relevant studies, with only four examining brain functional connectivity, and most neuroimaging assessments conducted after childhood. In summary, studies investigating how normative parenting influences brain functional connectivity in offspring during early childhood remain limited.

Maternal sensitivity at 6 months postpartum has been shown to relate to resting-state functional connectivity between the hippocampus and subcortical brain structures during infancy (Rifkin-Graboi et al., 2015) and in preschool-age children (Wang et al., 2019b). Both studies used the hippocampus as a predefined region of interest. As previously discussed, the hippocampus is the crucial brain region for memory skills and also plays an important role in emotion regulation (Lee et al., 2024). Better quality maternal behaviour during infancy, as indexed by higher levels of mind-mindedness (representing a parent's tendency to consider their child as someone who has their own thoughts, feelings, and intentions), and autonomy support, has been linked to the offspring's functional brain development at the age of 10 years (Dégeilh et al., 2018). Specifically, it has been shown to predict stronger negative connectivity between regions of the DMN and the salience network, highlighting the possible long-lasting impact of variation within the normative range of parenting on brain functional connectivity. The authors suggest that this negative relationship in connectivity reflects more mature brain development. The absence of positive parenting is suggested to act functionally differently from the presence of negative parenting (Richmond et al., 2022). Prior research suggests that a lack of positive parenting during childhood may relate to accelerated neurodevelopment (Thijssen et al., 2017). This aligns with the previous stress acceleration hypothesis, which argues that adversity might accelerate the pace of neural development, leading to faster maturation of the emotion circuit in the brain and the behaviours supported by these regions (Callaghan & Tottenham, 2016)—for example, functional connectivity in the amygdala–mPFC circuitry (Gee et al., 2013a).

In conclusion, the role of caregivers, particularly during infancy, seems to be invaluable, given that caregivers' behaviour moderates the relationship between infants' own neural and behavioural measures. Associations between neural patterns of brain structure and function and observed behaviours during mother–infant interactions have been found strikingly early. Furthermore, even the earliest interaction behaviours have been found to carry long-term associations, sometimes months or even years later, in neural (Dégeilh et al., 2018) and behavioural measures (Broomell et al., 2020). However, implicating parenting style in the shaping of neural circuitry has been difficult, in part because of inconsistent research findings, gaps in the literature, and limitations in technology, measurement, and research design. Understanding the influence of parenting on neural systems is crucial because it can inform our knowledge of typical and atypical brain development, and thus lead to neurobiological targets for intervention, including parenting interventions. Table 2 summarizes the relevant literature examining associations between normative-range positive parenting and offspring functional brain development.

Table 2. Previous task-free fMRI studies investigating the effects of normative-range parenting on functional connectivity in offspring.

Authors	**Sample, Cohort**	**Parenting assessment, age at assessment**	**Age at fMRI**	**Predefined region of interest**	**Main findings**
(Rifkin-Graboi et al., 2015)	N = 17 GUSTO	Maternal sensitivity during free play 6 months	6 months	Amygdala and hippocampus functional networks	Maternal sensitivity, positive association with FC between: • R HPC and L/R vmPFC, R dlPFC, L fusiform, and R middle temporal cortex • L HPC and L fusiform, L superior temporal cortex, and L lateral occipital cortex Maternal sensitivity, negative association with FC between: • R HPC and R lingual gyrus, and R posterior cingulate • L HPC and L entorhinal cortex • R amygdala and L inferior temporal cortex • L amygdala L entorhinal cortex and L middle temporal cortex.
(Wang et al., 2019b)	N= 61 N = 76 GUSTO	Maternal sensitivity during free play 6 months	4 years 6 years	Anterior and posterior hippocampus functional networks	Maternal sensitivity • positive association with R aHPC FC with the R precentral gyrus, L postcentral gyrus, R postcentral gyrus at the age of 4 years • negative association with R aHPC FC with the L dorsolateral PFC cortex at the age of 4 years • positive association with R aHPC FC with the L calcarine, R calcarine, R lingual, L cuneus cortex at the age of 6 years

(Thijssen et al., 2017)	N=112 for maternal sensitivity analyses Generation R Study	Maternal and paternal sensitivity during tasks 4 years	6-10 years	Amygdala-mPFC functional connectivity	Combined parental sensitivity x age: • age was related to stronger amygdala–mPFC connectivity in children with a lower combined parental sensitivity score • similar effect for maternal sensitivity Combined parental sensitivity x age x gender: • in daughters from less sensitive parents, amygdala–mPFC connectivity was related to age • in daughters from highly sensitive parents, amygdala–mPFC decreased with age Maternal or paternal sensitivity x age x gender • in daughters of less sensitive mothers or fathers, amygdala-mPFC connectivity was related to age
(Pozzi et al., 2021)	N=95 FACTS	Maternal behaviour during planning Interaction and problem-solving Interaction mean 8.4. years	Wave 1: mean 8.4 years Wave 2: mean 9.9 years	Amygdala functional connectivity Network connectivity and between-network connectivity (DMN, SN, ECN)	Positive parenting: • decreased FC of the superior parietal lobule with ECN at wave 2 compared to wave 1 • no associations in amygdala–whole brain connectivity • no association with RSN connectivity
(Dégeilh et al., 2018)	N= 28	Maternal mind-mindedness during free play (13 months) Autonomy support while doing a puzzle (15 months)	10 years	DMN, SN, CEN	Higher mind-mindedness at 13 months • stronger negative FC between SN and DMN seeds Higher autonomy support at 15 months • stronger negative FC between DMN and SN seeds

Abbreviations: GUSTO = Growing Up in Singapore Towards healthy Outcomes; FACTS = the Families and Childhood Transitions Study; DMN = default mode network; SN = salience network; ECN = executive control network, RSN = resting state networks; HPC = hippocampus; aHPC = anterior hippocampus; pHPC = posterior hippocampus; mPFC = prefrontal cortex; vmPFC = ventromedial prefrontal cortex; dlPFC = dorsolateral prefrontal cortex; FC = functional connectivity; fMRI = functional magnetic resonance imaging; R = right, L = left

3 Aims

In this thesis, we had two main objectives: First, to review and improve practical challenges related to paediatric brain MRI by reviewing recent literature and presenting methods used in the FinnBrain study with newborns and 5-year-olds. Second, this thesis aimed to increase the understanding of normal functional brain development and to bridge that information by investigating the associations between functional connectivity, maternal perinatal psychological well-being, and early mother–child interaction quality.

Specifically, the aims were:

1. To review the methods used for MRI scanning of 0–6-year-old subjects without sedation. Special emphasis was placed on procedures to prepare children for an MRI scan, as well as on the techniques and tools used during the scan to ensure a successful result. The aim was to describe the current knowledge on the topic and assess the quality of reporting of scanning procedures. In addition, we describe the methods used to scan 2–5-week-old infants in the FinnBrain study. (Study I)
2. To describe the protocol for fMRI imaging of 5-year-olds without anaesthesia. The aim was to characterize intrinsic connectivity networks during movie-watching using Independent Component Analysis (ICA). In addition, we aimed to compare how different denoising techniques affect functional brain networks. (Study II)
3. To investigate whether maternal prenatal and postnatal depressive symptoms are associated with local and distal brain functional connectivity at 5 years of age, using regional homogeneity (ReHo) and seed-based connectivity analysis (SCA). Special emphasis was placed on the amygdala's functional connectivity, based on prior literature. (Study III)
4. To investigate how maternal sensitivity at 8 and 30 months is associated with brain functional connectivity at 5 years of age, using ReHo and SCA. (Study IV)

4 Materials and Methods

4.1 Ethical Considerations

All studies were performed in accordance with the Declaration of Helsinki. The neuroimaging measurements for Studies I, II, III, and IV were approved by the Joint Ethics Committee of the University of Turku and the Hospital District of Southwest Finland (ETMK: 31/180/2011). The neuropsychological measurements for Study IV were approved by the same committee (ETMK: 26/1801/2015).

Written informed consent was obtained from parents before the study visit. When scanning 5-year-olds, child assent was confirmed during the recruitment process. All participants were informed about the confidentiality of the study, their voluntary participation, and their right to discontinue the study visit at any time without providing a specific reason.

4.2 Study Design and Participants

The present study sample was drawn from families participating in the FinnBrain Birth Cohort Study (Karlsson et al., 2018). The aim of FinnBrain is to examine the combined influence of environmental and genetic factors on child development and later health outcomes. The initial recruitment took place between December 2011 and April 2015 through personal contact with research nurses stationed at the recruitment sites. The families were recruited during the first-trimester pregnancy ultrasound at 12 gestation weeks (gw) at maternal welfare clinics in Southwest Finland and the Åland Islands. The inclusion criteria for the study were an ultrasound-verified pregnancy and proficiency in Finnish or Swedish (the official languages in Finland). A total of N = 3808 mothers and N = 2623 fathers or other partners of the mother decided to participate. The cohort is representative of the Finnish population, although the prevalence of young, multiparous, and smoking mothers, as well as preterm births, was lower than in the general population (Karlsson et al., 2018).

The study participants in this thesis were drawn from two separate and partly overlapping study populations who attended an MRI scanning visit at two different time points. The first population (Study I) consisted of infants aged 2–5 weeks, and the second population (Studies II–IV) comprised 5-year-old children, with both populations participating in a neuroimaging visit. Participants in Study IV also took part in a mother–child interaction assessment at two different time points (8 months and 30 months), or at least at one of these time points. The main focus of this thesis is on the 5-year-old population, whereas for the infant population we only present the scanning protocol (Study I) and did not use any infant fMRI imaging data for later analyses, as this had already been done in previous publications (Rajasilta et al., 2020, 2023).

Gestational data, including maternal age, gestational weeks at birth, birth weight, and infant biological sex at birth, was retrieved from the Finnish National Birth Register (National Institute for Health and Welfare, www.thl.fi). Other background information, including educational level, monthly income, and parity was collected using questionnaires sent to the entire cohort. Children's weight and height were measured at the 5-year scanning appointment to calculate the relationship between body mass and height using the ponderal index (PI), which was calculated as weight (in kilograms) divided by the cube of height (in metres) (Peterson et al., 2017). Figure 6 presents a schematic timeline of the assessment conducted in Studies II–IV.

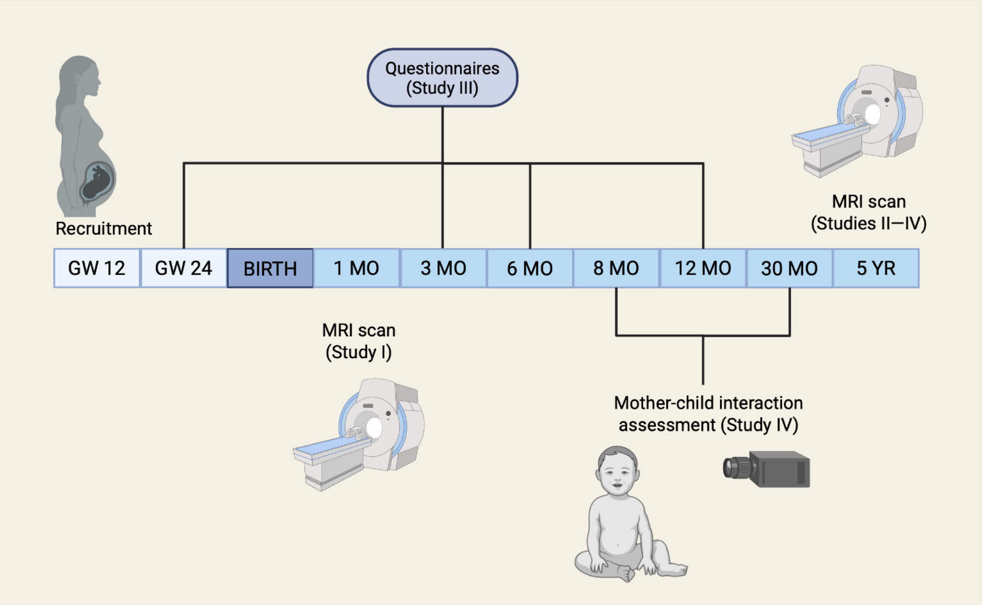

Figure 6. Schematic timeline of the data collection. Abbreviations: GW = gestational week, MO = month, YR = year, MRI = magnetic resonance imaging. Author's illustration. Created with BioRender.com.

4.2.1 Study I

The main focus of Study I was on a literature review of infant and child MRI scanning procedures. Additionally, we presented the infant scanning procedures of the FinnBrain Birth Cohort Study, performed when infants were 2–5 weeks of age. MRI acquisition took place between November 2012 and January 2016 at Turku University Hospital. Recruitment to the study visits was based on a random selection of participants from the FinnBrain Birth Cohort and, depending on willingness and availability, 189 mother–newborn pairs were recruited for an MRI visit. The exclusion criteria for the newborns were as follows: severe perinatal complications with neurological consequences, a previously diagnosed central nervous system anomaly, an abnormal finding on any previous MRI scan, and a birth weight under 1500 grams.

Out of all 189 newborns, 180 (95.2%) sessions were successfully conducted, yielding structural MR images. However, five sessions were excluded due to major motion artefacts, resulting in a total of 175 (92.5%) usable images (94 males and 81 females). Demographic data are presented in a previous publication (Kumpulainen et al., 2020).

4.2.2 Studies II–IV

The participants who attended the neuroimaging visits as part of the 5-year-old data collection were included in Studies II, III, and IV. The MRI data collection took place between October 2017 and March 2021 at Turku University Hospital. However, due to the COVID-19 pandemic, imaging sessions were temporarily paused between March 2020 and May 2020. For the 5-year-old neuroimaging visits, we primarily recruited participants who had previously attended the 5-year neuropsychological visits (these data were not used in this thesis). Participants for the 5-year-old neuropsychological visits (and later neuroimaging visits) were drawn from the Focus Cohort families (i.e., those with maternal prenatal distress scores in the highest or lowest quartile; see Karlsson et al. (2018) for details) and from families who had actively participated in earlier FinnBrain study visits. In total, 203 children attended the neuroimaging visits at the age of 5 years.

The exclusion criteria for the 5-year-old neuroimaging visits were the following:

1. Born before gw 35 (gw 32 for those with exposure to maternal prenatal synthetic glucocorticoid treatment),
2. Developmental or major organ abnormalities in sensation or communication (e.g., blindness, deafness, congenital heart disease),
3. Known long-term medical diagnosis (e.g., epilepsy, autism),

4. Ongoing medical examinations or clinical follow-up in a hospital,
5. Continuous daily medication (desmopressin was allowed),
6. History of head trauma (defined as concussion necessitating clinical follow-up in a health care setting),
7. Metallic ear tubes,
8. Routine MRI contraindications.

In total, 11 children did not start the MRI scanning, typically due to anxiety or discomfort related to the scanning procedure, resulting in 192 out of 203 participants (94.6%) starting the acquisition. Of those, 118 out of 192 (61.5%) started the fMRI sequence, which was the final sequence in our protocol. In total, 96 participants completed the 7-minute fMRI sequence with all 170 volumes. Other reasons for exclusion were excess motion during fMRI (N=9) and technical problems during acquisition (N=10). Thereafter, 77 participants had high-quality fMRI data and were included in later analyses.

For Study II, all participants (N=77) with full (170 volumes) fMRI data were included. For Study III, all participants with full fMRI data and EPDS questionnaires collected at least at the 3-month postpartum time point (N=68) were included. For Study IV, all participants with full fMRI data and mother–child interaction data from at least one age point (8 months or 30 months) were included, defining a final cohort of 17 mother–child dyads with mother–infant interaction data at the age of 8 months and 39 mother–child dyads at the age of 30 months. There was only a partial overlap between the mother–child interaction sample and the 5-year-old neuroimaging sample, which led to a reduced sample size in Study IV. The selection of the subjects is described in Figure 7. The demographics of the subjects in Studies II–IV are presented in Table 3.

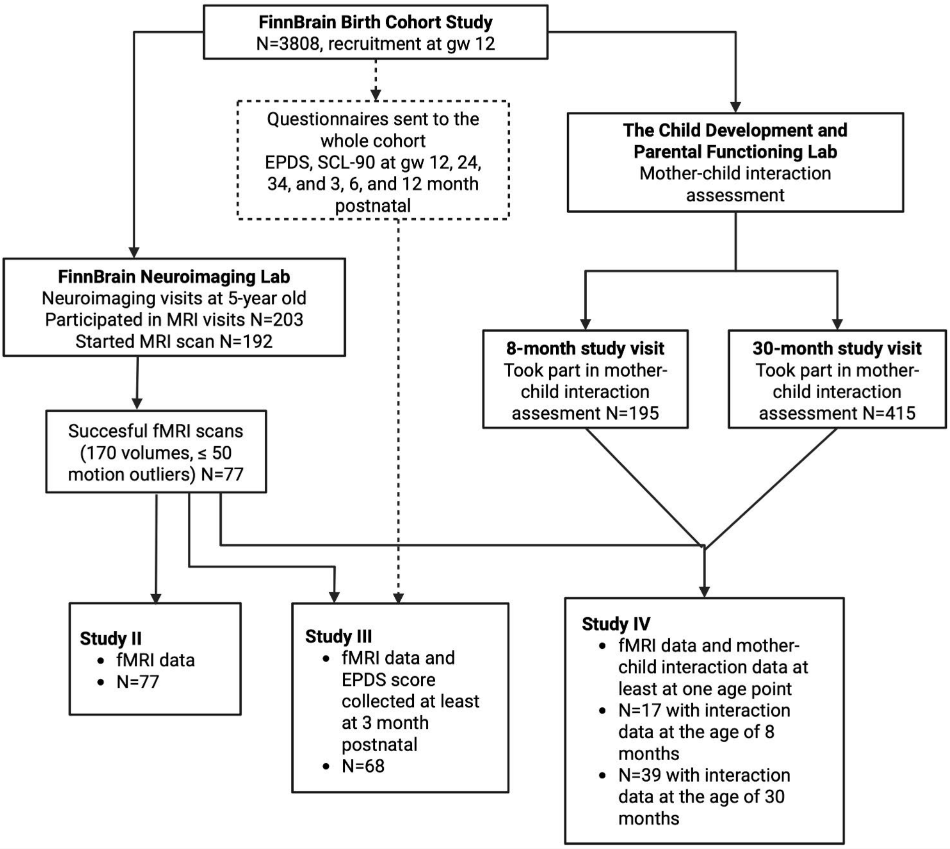

Figure 7. Flow chart of the FinnBrain data collection points from which data were included in the present thesis (Studies II-IV). Abbreviations: gw = gestational week, MRI = magnetic resonance imaging, fMRI = functional MRI, EPDS = Edinburgh Postnatal Depression Scale, SCL-90 = Symptom Checklist-90. Author's illustration. Created with BioRender.com.

Table 3. Summary of the descriptive characteristics of the subjects in Studies II–IV. Study IV included 17 mother–infant dyads (interaction assessment at 8 months) and 39 mother–toddler dyads (interaction assessment at 30 months). The demographics of the two groups are presented separately.

	STUDY II N=77	**STUDY III** N=68	**STUDY IV** N=17 / N=39
Continuous variables, mean (SD)			
GA at birth (weeks)	39.81 (1.51)	39.83 (1.34)	39.75 (1.59) / 39.88 (1.32)
Birth weight (grams)	3544.13 (442.07)	3551.07 (429.50)	3552.06 (526.51) / 3547.00 (488.44)
Age at scan (years)	5.40 (0.13)	5.39 (0.12)	5.43 (0.15) / 5.38 (0.11)
Maternal age at childbirth (years)	30.26 (4.77)	30.40 (4.63)	31.12 (4.68) / 30.92 (4.61)
Maternal BMI before pregnancy (kg/m^2)	23.66 (4.18) *	23.52 (3.99)	24.16 (4.66) / 23.60 (4.31)
Categorical variables, number (%)			
Sex			
Male	33 (42.9)	28 (41.2)	6 (35.3) / 13 (33.3)
Female	44 (57.1)	40 (58.8)	11 (64.7) / 26 (66.7)
Maternal background			
Finnish	75 (97.4)	66 (97.1)	17 (100) / 39 (100)
Other	1 (1.3)	1 (1.5)	0 / 0
Missing	1 (1.3)	1 (1.5)	0 / 0
Maternal smoking during pregnancy			
No smoking	73 (94.8)	64 (94.1)	16 (94.1) / 39 (100)
During 1st trimester	2 (2.6)	2 (2.9)	1 (5.9) / 0
During 3rd trimester	2 (2.6)	2 (2.9)	0 / 0
Missing	0	0	0 / 0
Maternal education level			
Low	17 (22.1)	14 (20.6)	5 (29.4) / 9 (23.1)
Middle	18 (23.4)	17 (25.0)	3 (17.6) / 9 (23.1)
High	41 (53.2)	36 (52.9)	9 (52.9) / 21 (53.8)
Missing	1 (1.3)	1 (1.5)	0 / 0
Maternal monthly income (euros)			
≤1500	23 (29.9)	20 (29.4)	4 (23.5) / 9 (23.1)
1501–2500	42 (54.5)	37 (54.4)	12 (70.6) / 23 (59.0)
2501–3500	9 (11.7)	8 (11.8)	0 (0) / 6 (15.4)
≥3501	1 (1.3)	1 (1.5)	1 (5.9) / 0 (0)
Missing	2 (2.6)	2 (2.9)	0 (0) / 1 (2.6)

Abbreviations: SD = standard deviation, GA = gestational age, BMI = body mass index, * =1 missing. The maternal background data, maternal education data, and maternal monthly income estimate data were collected via questionnaires at 14 weeks of gestation.

4.3 Methods

4.3.1 Literature Search (Study I)

In Study I, which included a literature review, we focused on reviewing the methods used to prepare a child for an MRI scan, but also on the techniques and tools used during scanning to enable a successful scan. Additionally, we evaluated how studies reported the scanning procedures, success rates, and reasons for data loss.

A literature search was conducted using the PubMed database. To identify relevant articles, we used the following search terms: (‘Magnetic Resonance Imaging’[Mesh] OR ‘MR imaging∗’ OR ‘MRI’ OR ‘NMRI’ OR ‘fMRI’ OR ‘DTI’ OR ‘diffusion tensor imaging’) AND (‘Brain/growth and development’[Mesh] OR ‘brain growth*’ OR ‘brain develop*’) AND (‘Infant’[Mesh] OR ‘infant*’ OR ‘toddler*’). No languages were excluded at this point. To capture the most recent and relevant work in the field, a starting date limit was enforced to include only papers published after 1 January 2012. The final search included literature published between 1 January 2012 and 1 January 2021. After duplicates were removed, the search resulted in 1098 publications.

Titles and abstracts were used to screen articles in the first phase. During this screening, our primary goal was to exclude studies outside the age range and/or studies with participants showing potential “abnormal” development, including those born prematurely or with low birth weight. In addition, we aimed to exclude studies focusing on disease or treatment. The exclusion criteria in the first phase were as follows, in descending order of priority:

1. Publications written in a language other than English.
2. Studies not conducted on humans.
3. Studies including subjects born prematurely or with low birth weight.
4. Studies focusing on disease or treatment.
5. Studies in which living 0–2-year-old subjects were not MR imaged.

If a publication met multiple exclusion criteria, only the highest was considered as the reason for exclusion. If the exclusion criterion was identified in the title, the abstract was not used to determine a higher-priority exclusion criterion. A total of 721 articles were screened out, while 377 publications were deemed potentially relevant.

During the second phase, the 377 publications were reviewed based on their abstracts, full texts, and supplementary data when applicable. Initially, all review articles were excluded. Secondly, the exclusion criteria (1–5) from the first phase were applied. Subsequently, articles that met the following criteria were included in the final study:

1. All subjects were scanned between 0 and 6 years of age.
2. All scans were performed without sedation, and MRI was not clinically indicated. To make sure no sedatives were used, the study had to state it, or mention that scans were made during *natural* sleep or awake. If this was not mentioned, the publication was excluded due to insufficient information about the scanning procedure.
3. All subjects were born at a gestational age (GA) of 35 weeks or later. If a study set a lower limit than 35 weeks for GA, it was excluded regardless of the subjects' GA. If a study did not set a limit for GA and the range was not reported, the mean GA was ≥37 weeks with a standard deviation ≤2 weeks (and mean GA minus SD was ≥35 weeks). Finally, regarding studies with no mention of GA, only longitudinal studies were included.

Because we were also interested in how studies report their procedures, we did not exclude articles that used the same data. Thus, the reviewed studies may contain overlapping participant populations. During the second phase, 291 publications did not meet the criteria and were excluded. Finally, a total of 86 articles were included in the review. The flowchart of study selection is presented in Figure 8.

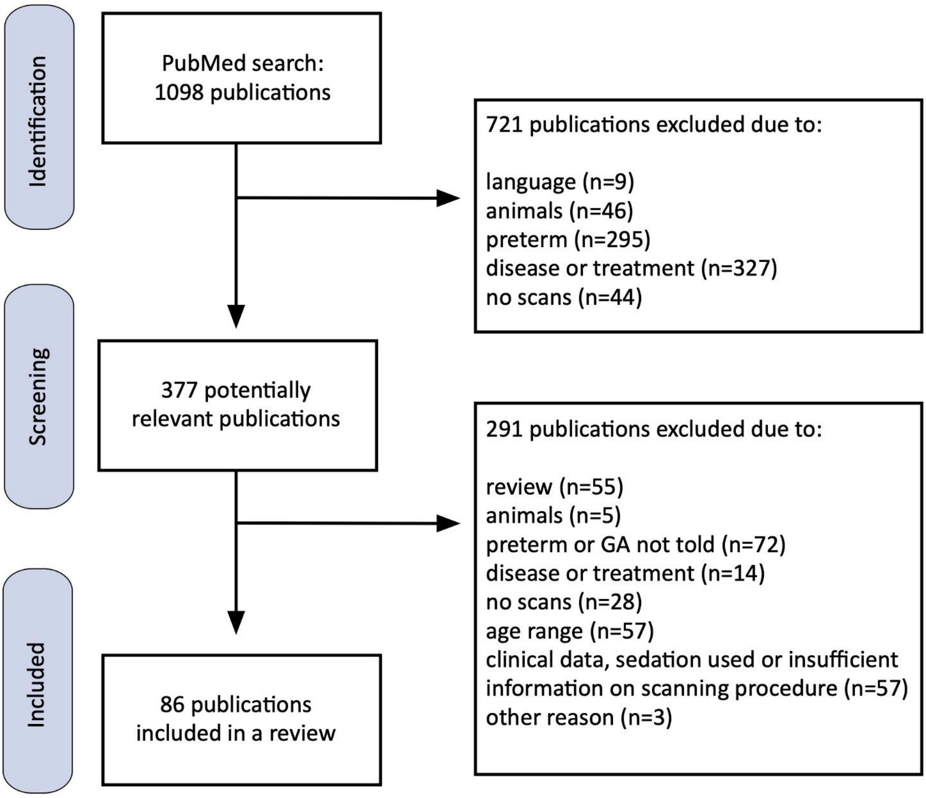

Figure 8. Flow diagram explaining the study selection protocol in the literature review (Study I). Author's illustration. Modified from Study I.

4.3.2 MRI Scanning Visits

All MRI scans were performed for research purposes, and participants were scanned without sedation. All brain images (T1 and/or T2) were reviewed by a paediatric neuroradiologist for possible incidental findings. Within the sample of 175 infants, 13 (7.4%) had an incidental finding, and within the sample of 192 5-year-olds, 13 (6.8%) had an incidental finding. When incidental findings were detected, a paediatric neurologist informed the families about them so that any immediate questions or concerns of the parents were appropriately assessed (Kumpulainen et al., 2020).

4.3.2.1 Preparation and MRI Imaging Visits of Infants (Study I)

Scanning was executed at the Department of Radiology, Turku University Hospital, Finland. The scanning usually occurred during a weekday afternoon or evening (16:30–20:00), although some scans were performed during the day on weekends as well. The enrolment to the neuroimaging sub-study happened via a telephone call to the family. The purpose and protocol of the study were explained to the parent(s), after which they signed a written informed consent, also on behalf of their newborn.

At the start of the visit, the families were received by a trained and experienced radiographer and the researchers. The scanning protocol was reviewed with the parents and the absence of safety risks (inner ear implants, pacemakers, or other metal devices) was confirmed by the personnel. Before entering the scanner, the newborns were fed with either breastmilk or formula, and then swaddled into a vacuum mattress to limit movements. Deformable wax earplugs and custom-sized earmuffs were used for hearing protection. If willing, the parents were present in the scanning room throughout the scan and could stop the study at any point during the visit. Parents were provided with standard earplugs and earmuffs if they stayed in the scanning room during the scanning session. The personnel observed the scanning from the control room through a window with a microphone contact to the parent. A loudspeaker transmitted the sounds from the scanning room to the control room, allowing the staff to hear if the infant woke up. If this occurred, the parent or personnel tried to calm the infant back to sleep if possible. Calming could be done by gently reaching for the infant even within the scanner bore with relatively simple measures that rely on infant reflexes and/or calming touch. The ongoing sequence continued during soothing, as abrupt changes in the surrounding noises risked waking up the infant. After soothing, the sequences were reacquired, i.e., sequences obtained during soothing were considered invalid and therefore excluded from the analyses. The session was terminated if the infant did not fall asleep before scanning or failed to resume sleep during the scan. The total duration of the visit was less than 2 hours.

4.3.2.2 Preparation and MRI Imaging Visits of 5-Year-Olds (Studies II–IV)

Imaging was performed at the Department of Radiology, Turku University Hospital, on Sundays from the morning to early evening hours (9:00–20:00). During recruitment, each family was personally contacted via telephone. If the parents were interested in participating, they were advised to explain the process to their child and confirm the child’s assent before deciding on their willingness to participate.

Getting ready for the scanning visit started with preparations at home. Various familiarization techniques were recommended to parents, including reading stories, watching videos, describing the visit, playing scanner sounds, encouraging the child to practise lying still "like a statue", and using a homemade mock scanner to help them acclimate to the enclosed space inside the MRI head coil. Additionally, a link to an *Inscapes* movie was provided for further familiarization. Several weeks before the scheduled scanning day, a member of the research team, often the research nurse, made a home visit to deliver earplugs (Mack's® Soft Moldable Silicone Putty Earplugs) and headphones (3M™ Peltor™ Kid Earmuff) for practice. Detailed information about the scanning visit was provided, and the research staff member was available to address any remaining questions or concerns.

On the scanning day, at the start of the visit, the families were welcomed by trained research staff, including the same research nurse who made the home visit, a PhD student, and a radiographer. Preparations were conducted in a separate room with kitchen and toilet facilities and free space for playing. The main goal was to reduce anxiety and distress and create a comfortable and child-friendly environment. The preparations were tailored according to the child's needs. The imaging situation was simulated with the aid of a self-made wooden mock scanner head coil. Imaging was trained by "imaging" the child's own toy. The effects of motion were illustrated by taking sharp and blurry pictures using a mobile phone camera. To facilitate communication during scanning, children were trained to use a soft silicone ball and a gentle leg-press system. Throwing the ball indicated a desire to speak or stop the scan, whereas a gentle press on the child's legs signalled that they were moving too much. These communication methods were practised in advance. Participants were able to watch the *Inscapes* movie beforehand, and it was displayed on a tablet screen. At the end of the preparation, a light meal was served. The preparation phase lasted 1–2 hours.

After preparations, the participant and research staff were moved to the scanning suite located in the same building. Participants were able to wear their own clothing (if MRI compatible) during acquisition. A comfort item (e.g., a stuffed animal) could be taken into the scanning room. To increase comfort and minimize head motion, foam padding was positioned around the child's head inside the head coil. A leg cushion placed under the knees and weighted blankets (50 cm x 50 cm; 2 kg and 150 cm x 130 cm; 3.8 kg; tikkitakki.fi) were provided if desired. As the MRI room can be cold, a blanket was also provided if needed. For noise attenuation, earplugs (Mack's® Soft Moldable Silicone Putty Earplugs) and MRI-compatible headphones (Siemens Medical Solutions) were provided. Through the headphones, participants were able to listen to a movie or TV show and communicate with the control room.

4.3.3 Image Acquisition

4.3.3.1 MRI Acquisition in Infants (Study I)

All scans were obtained using a Siemens Magnetom Skyra fit 3T scanner (Siemens Medical Solutions, Erlangen, Germany). A 12-element Head Matrix coil allowed the use of generalized autocalibrating partially parallel acquisition (GRAPPA) to accelerate acquisitions (a parallel acquisition technique [PAT] factor of 2 was used). The sequences comprised an axial T2 Dual Echo TSE (Turbo Spin Echo), a sagittal T1-weighted 3D MPRAGE (magnetization-prepared rapid gradient echo), and three diffusion tensor imaging (DTI) sequences. The acquisition times for sequences were 6 min 50 s (T2 Dual Echo TSE), 4 min 3 s (3D-T1), 5 min 3 s (DTI 1), 5 min 33 s (DTI 2), and 5 min 42 s (DTI 3). Sequence parameters were optimized so that "whisper" gradient mode could be used in PD-T2-TSE and 3D-T1 sequences to reduce acoustic noise during the scan. A 6-minute functional MRI sequences were added to the protocol starting in June 2015 and continued until the end of the study. We acquired task fMRI measurements investigating touch responses and a resting-state fMRI scan. Functional MRI sequence consisted of 120 volumes, with a voxel size of 3 × 3 × 3 mm, a repetition time (TR) of 2500 ms, an echo time (TE) of 30 ms, a flip-angle of 80 degrees, and 42 slices without gaps. Sixty minutes was the maximum duration of the complete scanning protocol.

4.3.3.2 MRI Acquisition in 5-Year-Olds (Studies II–IV)

All scans were obtained using a Siemens Magnetom Skyra fit 3T scanner (Siemens Medical Solutions, Erlangen, Germany). A 20-element head/neck matrix coil allowed the use of the GRAPPA technique to accelerate acquisitions, with a PAT factor of 2. The scans included a high-resolution T1-weighted MPRAGE, a T2 TSE, DTI, and a 7-minute fMRI, respectively. Functional MRI consisted of 170 volumes with a voxel size of 3.0 x 3.0 x 3.0 mm, TR 2500 ms, TE 30.0 ms, a flip angle of 80°, and 42 axial slices without gaps. During 30–45 min of structural scanning, children were able to watch a movie or TV show of their choice. If the child had fallen asleep during structural scanning, they were gently awakened before the fMRI sequence. During fMRI scanning, children were instructed to watch the *Inscapes* movie, a paradigm featuring abstract shapes without a narrative or scene cuts (Figure 9). The movie was designed to provide enough stimulation to improve compliance related to motion and wakefulness while minimizing cognitive load during functional imaging data collection (Vanderwal et al., 2015). Parents were asked not to touch or make eye contact with the child during functional imaging. The total scanning time was limited to 1 hour.

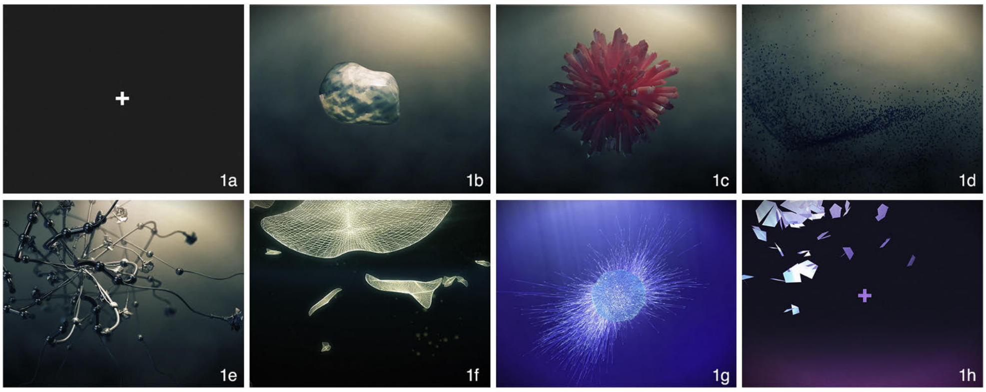

Figure 9. Images captured from the *Inscapes* movie. It features a series of technological-looking, abstract shapes. The movie is nonverbal, avoids explicit social references, has no direct story or narrative, and does not use scene cuts. Reprinted with permission from Elsevier (Vanderwal et al., 2015).

4.3.4 Measures of Maternal Perinatal Distress (Study III)

In Study III, maternal depressive symptoms were used as the main variable of interest, and maternal anxiety scores as covariates. In addition, maternal depressive symptoms were used as covariates in Study IV. In FinnBrain, maternal depressive symptoms were assessed during pregnancy (at gw 14, 24, and 34) and in the postnatal period (3, 6, and 12 months postpartum) with the EPDS (Cox et al., 1987). Maternal anxiety symptoms were assessed with the anxiety subscale of the Symptom Checklist 90 (SCL-90) questionnaire (Derogatis et al., 1973) at the same time points as the EPDS, except at 12 months postpartum, when it was not used.

The EPDS is a widely used self-report screening tool designed to detect symptoms of postnatal depression (Cox et al., 1987), later validated for use during pregnancy (Bergink et al., 2011). The scale consists of 10 short statements, with depression symptoms rated according to how they have been experienced during the past 7 days. It is scored on a 4-point Likert scale from 0 to 3, and the total score ranges between 0 and 30. A higher score reflects greater levels of depressive symptoms. In this thesis, the total sum score was used as a continuous variable, and no cut-off points were used.

The SCL-90 anxiety subscale is a reliable measure of anxiety symptoms that is widely used in clinical and research settings (Derogatis et al., 1973). This self-report questionnaire consists of 10 items and assesses anxiety symptoms experienced during the past 7 days. Items are scored on a 5-point Likert scale from 0 to 4. The total score ranges from 0 to 40, and a higher score reflects a greater level of anxiety symptoms. In this thesis, the total sum score was used as a continuous variable.

4.3.5 Measures of Mother–Child Interaction and Maternal Sensitivity (Study IV)

Maternal sensitivity was used as the main variable of interest in Study IV. Mother–child interaction assessments were conducted as part of the Child Development and Parental Functioning Lab study visits when children were aged 8 months and 30 months. Recruitment to the study visits for mothers and children was primarily based on the Focus Cohort (Karlsson et al., 2018), and there were no exclusion criteria for the mother–child interaction assessment besides the original recruitment criteria for the FinnBrain Birth Cohort. A total of 195 mother–infant dyads took part in the interaction assessment at the age of 8 months, and 415 mother–toddler dyads at the age of 30 months. The collection of mother–infant interaction data was added to the 8-month study visit protocol later, at which point approximately half of the neuropsychological assessments had already been conducted. This led to a smaller subsample at this time point. Study visits were conducted by graduate students and supervised by psychologists. The mothers were instructed to play with their children in a similar manner to that which they were used to, either with or without toys. The 20-min (8 months) and 15-min (30 months) play sessions were videotaped and later coded. Mother–child interaction sessions are presented in Figure 10.

Figure 10. Mother–child interaction assessments at 8 months of age (left side) and 30 months of age (right side). The photos are from the FinnBrain Birth Cohort's archives, and written consent was obtained from the participants for their use.

Maternal sensitivity was assessed using the Emotional Availability Scales (EAS) 4th Edition (Biringen et al., 2008). The EAS is characterized by a dyadic perspective rather than a unidirectional reaction of the caregiver to the child's signals, meaning that both caregiver and child contribute to the overall quality of the interaction. It consists of four dimensions regarding parental behaviour: sensitivity, structuring, non-intrusiveness, and non-hostility, and two regarding the child: child responsiveness and child involvement. All dimensions are scored using either a 3- or 7-point scale, with subscale scores yielding a total score from 7 to 29. The dimensions were also scored on a Likert-type scale to yield a direct score of 1–7, reflecting the evaluator's overall view of emotional availability, where higher scores indicate warm and healthy emotional availability and lower scores indicate reasons for concern regarding the relationship (Saunders et al., 2015). In the present study (Study IV), the direct score of maternal sensitivity (with measurements at 8 and 30 months) was used as a continuous variable. Higher scores refer to higher maternal sensitivity. Maternal sensitivity was chosen because it is a key aspect of mother–child interaction and crucial for child development. Maternal sensitivity refers to a mother's behaviours and emotions that create and maintain a healthy and positive connection with her child. It also includes how well the mother responds to the child's physical and emotional needs in a timely and suitable manner. Although the mother is the rated target, EAS conceptualizes sensitivity as inherently dyadic: scores are interpreted relative to the child's cues and availability. The coding was performed by two (at 8 months) and three (at 30 months) blinded, trained, and reliable coders. Interrater reliability was assessed for 10% of the videotapes. The intraclass correlation coefficient was 0.80 for sensitivity at 8 months and ranged from 0.83 to 0.91 at 30 months.

4.3.6 Image Preprocessing and Analysis

4.3.6.1 Image Preprocessing (Studies II–IV)

As the first step, functional images were visually inspected for whole-brain FOV coverage, signal blurring, or artefacts. We ascertained the length of the time-series manually and included only subjects with a total number of 170 volumes. T1-weighted structural images were quality controlled and collected as reference images for all subjects.

Data quality assessment included motion outlier detection. Motion outliers were estimated using artefact detection tools (ART) (http://www.nitrc.org/projects/artifact_detect). We tagged the images as outliers if they had a composite motion threshold (CMT) >2 mm or a derivative of the root mean square variance (DVARS) >9, which are the default parameters in the ART toolbox. CMT combines the movement parameters from the six realignment parameters (translation and rotation in the X, Y, and Z directions) to calculate an overall motion estimate for each volume. DVARS calculates the temporal derivative of the root mean square of the fMRI signal across all voxels in the brain, and a high value indicates a large change in the signal between volumes. At this point, we excluded subjects with more than 50 volumes tagged as outliers. Finally, all children included in the final sample had a full fMRI sequence of 170 volumes, and a maximum of 50 volumes (50/170 = 30%) were tagged as outliers by ART. Figure 11 presents an example of motion-corrupted data from a randomly selected excluded subject.

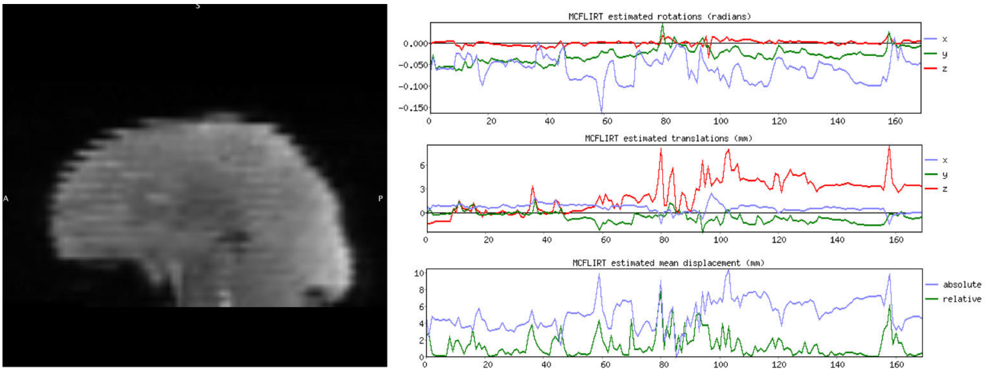

Figure 11. Representative example of high-motion data from a 5-year-old subject in our dataset who was excluded from the final sample due to excessive motion. The left side shows an fMRI image with typical “striping” motion artefacts, and the cerebellum is partially out of the field of view. The right side displays motion estimated from MCFLIRT: the first graph represents estimated rotations (radians), the second represents estimated translations (millimetres), and the third represents estimated mean displacement (millimetres). The mean absolute displacement was 5.2 mm and the mean relative displacement 1.35 mm.

In Study II, fMRI data preprocessing was carried out using FEAT (FMRI Expert Analysis Tool) Version 6.00, part of FSL (FMRIBs Software Library, www.fmbrib.ox.ac.uk/fsl). The following pre-statistics processing steps were applied: motion correction using MCFLIRT (Motion Correction using FMRIB’s Linear Image Registration Tool) (Jenkinson et al., 2002); slice-timing correction using Fourier-space time-series phase-shifting; non-brain removal using BET (Brain Extraction Tool) (Smith, 2002); spatial smoothing using s Gaussian kernel of FWHM (Full Width at Half Maximum) of 5 mm; grand-mean intensity normalization of the entire 4D dataset by a single multiplicative factor; and high-pass temporal filtering (Gaussian-weighted least-squares straight-line fitting, with sigma = 50.0 s). Registration to the Montreal Neurological Institute (MNI) template space was performed via high-resolution structural T1-weighted images using FLIRT (FMRIB's Linear Image Registration Tool) (Jenkinson et al., 2002; Jenkinson & Smith, 2001).

In Studies III and IV, functional MRI data were slice-timing corrected, and motion corrected using FSL version 6.00 (Jenkinson et al., 2012) relative to a manually chosen reference volume, free of major artefacts. Anatomical masks for white matter and cerebrospinal fluid were defined in the MNI standard space and registered to functional data with an affine transformation. Average signal in white matter and cerebrospinal fluid, as well as 24 motion covariates (the six realignment parameters and their temporal derivatives and quadratic terms) were included as nuisance covariates. Taken together, denoising consisted of outlier rejection, nuisance regression, detrending, and high-pass filtering (0.008 Hz).

4.3.6.2 Independent Component Analysis (Study II)

In Study II, ICA was used to capture intrinsic functional networks. ICA is a model-free, data-driven approach, ideal for exploratory analysis and in cases where no suitable hypothesis is available. ICA decomposes functional data into several independent components, in the form of spatial maps, which are temporally correlated (Beckmann et al., 2005). However, the underlying cause of the perceived synchrony within the components may be non-neural in origin (such as breathing or pulsation). Further, ICA can also be employed as part of preprocessing to isolate noise components.

In our study, ICA was carried out using Probabilistic ICA (Beckmann & Smith, 2004; Hyvärinen, 1999) as implemented in MELODIC (Multivariate Exploratory Linear Decomposition into Independent Components) Version 3.15, part of FSL. Subject-level ICA was utilized for optimization and quality control of the preprocessing step for group-level ICA, as well as separating noise and signal components for manual denoising. For noise removal, the spatial distribution, time course, and power spectrum of components in each participant were visually inspected, and components were identified as signal or noise following previously published criteria (Griffanti et al., 2017). Components identified as noise during manual labelling were removed using the “fsl_regfilt”, part of FSL. We ran the AROMA pipeline as described by Pruim et al. (2015b).

We then ran three versions of the group-ICA with different cleaning approaches: 1) manual denoising (M), 2) non-aggressive AROMA (AN), and 3) aggressive AROMA (AA). All versions were run using a limited dimensionality of 40. We thus ran the group-ICA from the command line using FSL’s “melodic” and “dual_regression” to obtain component time courses from the preprocessed data, and used FSLnets to assess the component power spectra (https://fsl.fmrib.ox.ac.uk/fsl/fslwiki/FSLNets).

4.3.6.3 Regional Homogeneity (Studies III and IV)

In Studies III and IV, the main derived brain metric was regional homogeneity (ReHo). It is a voxel-based measure of brain activity, which evaluates the similarity or synchronization between the time series of a given voxel and its nearest neighbours across the whole brain (Zang et al., 2004). It is based on calculating Kendall's coefficient of concordance (KCC) over a target voxel and neighbouring voxels. It assumes that a given voxel is temporally similar to its neighbours, and that intrinsic brain activity is manifested by clusters of voxels rather than single voxels. Depending on whether neighbouring voxels are taken to include those on the side, edge, or corner of a given voxel, cluster size can be 7, 19, or 27 voxels, respectively. Values of KCC range from 0 to 1, with higher values indicating greater similarity. Voxel-based maps are then generated based on KCC values and standardized using Z-scores to perform group analysis.

In Studies III and IV, ReHo was computed as implemented in DPABI (http://rfmri.org/DPABI), with the number of KCC cluster size set at 27 voxels. Motion outliers (outlier detection described above) were removed from the data before estimating the ReHo maps. For group analysis, ReHo maps were normalized non-linearly using FSL FNIRT to $1.0 \times 1.0 \times 1.0\ \mathrm{mm}^3$ MNI space. Finally, the data were smoothed with a Gaussian filter of 6 mm FWHM.

4.3.6.4 Seed-Based Connectivity Analysis (Studies III and IV)

In Studies III and IV, SCA was employed to assess the BOLD response within an anatomically defined seed region of interest (ROI). SCA is a model-based, hypothesis-driven approach, usually used for testing specific connectivity hypotheses, as it requires a priori determination of the seed. It calculates connectivity by correlating the time series of a seed voxel (or ROI) with the time series of all other voxels in the brain. The result of SCA is a connectivity map showing Z-scores for each voxel, reflecting the strength of its correlation with the seed region's time series.

In Studies III and IV, the SCA was performed with FSL tools using the same preprocessing and nuisance regression as for the ReHo analyses, except that in Study III the interquartile range (obtained via *fsl_motion_outliers*) of DVARS was used for removal of motion-corrupted volumes after confirming that it matched the ReHo pipeline. In Study III, the bilateral amygdala were set as the ROIs, and the average time series of the seed ROIs were extracted from normalized data using the "fslmeants" command after creating a binary amygdala mask for the left and right sides from the Anatomical Automatic Labeling (AAL) template (Tzourio-Mazoyer et al., 2002). In Study IV, the seed ROI was defined by a 3-mm-radius sphere generated in FSL's FSLeyes and corresponding to the location of the ReHo result, the mPFC, at the cluster peak MNI coordinate (-6, 44, 28). The average time series of the seed ROI was extracted from normalized data using the "fslmeants" command. Subject-level seed-based connectivity maps were generated using the FSL v6.00 fMRI Expert Analysis Tool (Woolrich et al., 2001). The resulting Z-score maps for each participant were then normalized to MNI space, and statistical tests were conducted with FSL FEAT higher-level analysis.

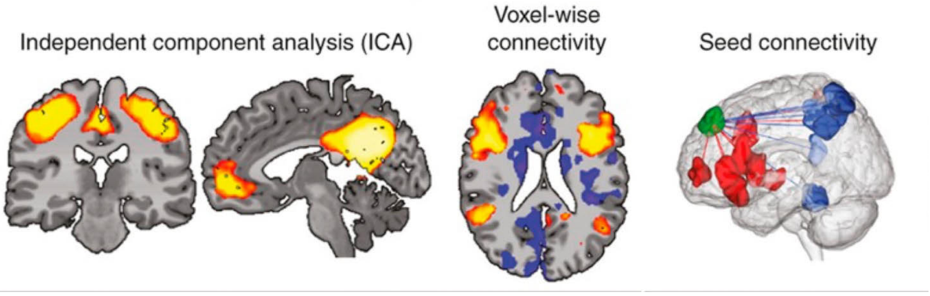

Figure 12. Representative examples of measures used to study functional connectivity in this thesis. From left to right: Independent Component Analysis (Study II), voxel-wise connectivity representing regional homogeneity (Study III ja IV), and seed-based connectivity analysis, where the example seed is shown in green (Study III and IV). The figure is a modified version from an article by Scheinost et al. (2016b), which is licensed under a Creative Commons Attribution-NonCommercial-ShareAlike 4.0 International Licence.

4.3.7 Statistical methods

4.3.7.1 Study II

Demographic data were analysed with IBM SPSS Statistics (version 29). Differences between groups in continuous variables were compared using the independent-samples t-test. Differences in categorical variables between two groups were compared using the chi-square test.

4.3.7.2 Study III

ReHo analyses were conducted with the general linear model using the "multiple regression" option of SPM12 (https://www.fil.ion.ucl.ac.uk/spm/software/spm12/). First, the EPDS score (performed separately for each time point: gw 24, 3 months, 6 months, and 12 months postpartum) was set as the main explanatory variable (EV) and child age at scan and sex were set as the independent variables (IVs) of no interest. Second, IVs of no interest, including maternal socioeconomic status (SES) measured by maternal education level, maternal pre-pregnancy body mass index (BMI, kg/m^2), and child's PI, as well as maternal anxiety symptom score (SCL-90 score), were added to the model. Additionally, in analyses using postnatal EPDS scores, EPDS at gw 24 was added as an IV of no interest to account for the possible continuum of depressive symptom levels from prenatal to the postnatal period. The a priori threshold for voxel-level statistical significance was set to $p < 0.005$, and a family-wise error (FWE) correction at the cluster level was set to $p < 0.0125$ (taking into account four separate statistical models for the EPDS time points).

Linear regression models were conducted in RStudio (https://www.R-project.org/) to examine associations between bilateral amygdala ReHo values and IVs in line with SPM models. The ReHo values were extracted using binary masks from the AAL atlas and estimated with FSLmaths. Separate models were run for the left and right amygdala. The first model included EPDS scores (gw 24 and 3, 6, and 12 months postpartum), child sex, and child age at scan. The second model added maternal SES, pre-pregnancy BMI, and child's PI. A final model incorporated maternal anxiety symptoms (SCL-90 scores) to assess the specificity of associations with depressive symptoms. Regression assumptions were verified, with variance inflation factors <2.3 and normally distributed residuals through visual inspection of Q-Q plots and histograms of the residuals. Uncorrected p-values were reported, but given eight tests (2 amygdala regions, 4 EPDS time points), the Bonferroni corrected threshold was $p < 0.00625$.

4.3.7.3 Study IV

ReHo analyses were conducted as in Study III, using maternal sensitivity as the main EV and child age at scan and sex as the IVs of no interest. The a priori threshold for voxel-level statistical significance was set to $p < 0.005$, and an FWE correction at the cluster level to $p < 0.05$. We also systematically tested whether the results survived a more stringent threshold at $p < 0.001$.

For visualization, we plotted the association between the mean ReHo values of the previously identified cluster of ReHo analysis and maternal sensitivity scores in IMB SPSS Statistics (version 27). To assess the robustness of this association against potential confounders, we calculated a partial correlation analysis following the SPM model, while additionally controlling for maternal age at childbirth, maternal pre-pregnancy BMI, smoking during pregnancy, education level, perinatal depressive symptoms, and child gestational age. There were a few (1–2) missing EPDS scores depending on the time point used, and they were handled as missing data, that is, no imputation was performed.

FSL GLM one-sample t-tests were used to determine mean seed-based connectivity from subject-level SCA maps. Additionally, an FSL GLM regression model examined associations between subject-level SCA maps and maternal sensitivity, with child sex and age as covariates. Analyses were limited to grey matter using an inclusive grey-matter mask covering cortical and subcortical regions.

5 Results

5.1 Infant and Child MRI Scanning

5.1.1 Findings from the Literature Review (Study I)

The review included 86 articles using brain MRI in healthy subjects aged 0–6 years. Included studies are listed in Supplementary Table 1 of the original publication (Study I). The number of participants ranged from nine to 288. Fifty-two studies were cross-sectional, with one scan per subject, and 34 were longitudinal with serial scans.

All subjects underwent MRI scanning without sedation, as sedation or anaesthesia was an exclusion criterion in our literature search. Infants and children under the age of 4 years slept during acquisition in most studies. Fifteen studies included children aged 4–6 years; in most, scanning was performed while the child was awake, e.g., watching a movie or a TV show, if tolerated.

Only a few studies reported the timing of the visits. When reported, MRI sessions were scheduled according to the participant's usual sleeping/diurnal rhythm. Naptime imaging was typically used for the youngest participants, whereas evening and nighttime scans were commonly used with older participants.

Few studies reported home preparations, including habituating infants to scanner noise, earplugs, and swaddling. Additionally, sleep deprivation was used by asking parents to wake the child earlier, skip a nap, or keep the child busy throughout the day. Preparations at MRI facilities included feeding the infant before scanning and then swaddling in sheets to promote sleep. Replicating typical bedtime or naptime routines was also reported.

Motion prevention was conducted with specific vacuum immobilization mats, bags, or pillows to stabilize the child and reduce natural movement from breathing. Some studies reported that subjects' heads were separately secured in a vacuum fixation device. Additionally, foam cushions, foam pads, and viscoelastic mattresses were used to keep the head in place and fill the space between the subject and the head coil.

A major part of the studies reported the use of noise attenuation during acquisition. The most reported passive measure was ear protection, including

MiniMuffs, earplugs, headphones, sound-attenuating ear protectors, electrodynamic headphones, or a custom-made acoustic hood used as single, double or triple protection. In addition, noise levels were reduced by a noise-insulating bore liner or foam insert fitted inside the scanner bore. Furthermore, some studies reported reducing scanner noise actively by selecting specific imaging parameters, slowing the gradient switching rate, and reducing the maximum gradient amplitudes.

Numerous studies mentioned monitoring subjects throughout the scan. To confirm that the child remained asleep, a physician, nurse, research assistant, or a member of the research team was present and visually monitored the subject. A few studies reported using an MRI-compatible camera or infrared camera to monitor subjects during the scan. In addition to visual monitoring, a pulse oximeter, pulse oximetry socks, and electrocardiography were used to monitor heart rate and oxygen saturation.

The majority of studies did not directly report the total duration of the imaging protocol. The acquisition time could often be calculated using the provided sequences, which, however, does not reveal the total/maximum time in the scanner. Only one study reported the total visit duration.

Reporting of success rates and data losses varied considerably between studies, and about half reported either the number of excluded scans or the success rate for included data. The most common reason for data loss was movement during the scan, which caused motion artefacts. Additional scanning-related factors included the subject failing to fall asleep before scanning, waking up during transition to the scanning bed, or awakening during MRI acquisition. Exclusions were also made due to demographic factors, analytical issues, ages falling outside the study-specific range, missing measurements in other parts of the study, and the presence of a brain anatomical anomaly. Thus, not all exclusion criteria were directly related to imaging failure.

5.1.2 MRI Scanning of 2–5-week-old Infants in FinnBrain

In Study I, we outlined the protocol used in scanning 2–5-week-old infants in the FinnBrain Birth Cohort Study (see Methods 4.3.2.1). In total, 189 families participated in MRI sessions, and 180 infants were scanned. Five subjects were excluded due to major artefacts, reducing the total number of images to 175 (94 males, 81 females). Later, after image quality control, success rates were 69% (n=125/180) for structural scans (Acosta et al., 2020), 96% (n=172/180) for at least 20 good-quality diffusion-weighted images out of the acquired 96 images (N = 157 for 30 directions, N = 142 for 40 directions, and N = 121 for 60 directions) (Merisaari et al., 2019), 69% (n=18/26) for task fMRI (Mariani Wigley et al., 2023) and 75% (n = 21/28) for resting-state fMRI (Rajasilta et al., 2020).

To provide practical advice, we also reported the procedures used to calm infants who woke up during scanning. These relatively simple measures, which relied on infant reflexes and/or calming touch, included gently reaching for the infant within the scanner bore, moving a pacifier side-to-side or up-and-down, brushing the cheek, tapping the thigh, moving the legs side-to-side, rubbing the tummy or sides, or covering the infant's vision with a sheet placed over the scanner coil. Such methods were typically applied when the infant was sleeping restlessly at the start of the session or began moving during acquisition. The ongoing sequence was maintained to avoid abrupt changes in surrounding noise, but the sequence was later repeated to acquire clear images. We did not record the total number of infants who woke up, were successfully calmed, or the duration required to calm them.

5.1.3 Functional MRI Scanning of 5-year-old Children in FinnBrain

In Study II, we outlined the protocol for scanning 5-year-old children in the FinnBrain Birth Cohort Study (see Methods 4.3.2.2), focused on success rates of functional imaging. In total, 203 participants attended neuroimaging visits, of whom 192 (94.6%) began the acquisition and 118 (61.5%) commenced the fMRI acquisition. In total, 96 participants completed the 7-min fMRI acquisition; nine were excluded due to motion, and 10 due to technical problems.

The final sample included 77 children (mean age = 5.40 years; range 5.25–5.76 years; 44 girls). When comparing included (n = 77) and excluded (n = 126) participants, the included sample had more girls (44 [57.1%] vs 46 [36.5%]; $\chi2(1) = 8.25$, $p = 0.004$ and their mothers had lower pre-pregnancy BMI (mean = 23.66, SD = 4.19; vs mean = 25.01, SD = 4.54; $p = 0.037$).

5.2 Intrinsic Connectivity Networks During Movie-Watching (Study II)

In Study II, after three different denoising techniques, group-ICA with a dimensionality of 40 yielded 19 components with manual denoising, 21 components with non-aggressive AROMA, and 20 components with aggressive AROMA that were identified as potential ICNs. Components were numbered from 1 to 40 for each denoising strategy independently and were labelled with the following abbreviations: M for manual denoising, AN for non-aggressive AROMA, and AA for aggressive AROMA. We named the networks based on anatomical location, noting that there is variability in how components are named in previous literature (Uddin et al., 2019). Figure 13 presents three examples of spatial maps of spatially well-matching components across the different denoising techniques. All signal spatial maps are presented in the Appendix.

Occipital components were captured in three main regions: medial, lateral, and the occipital pole, across all denoising techniques. These networks closely matched previously known visual networks (Chen et al., 2021a; Muetzel et al., 2016). Components M_C1, AN_C14, and AA_C23 correspond to the primary visual network in the occipital pole. M_C2, AN_C7, and AA_C1 show bilateral activation in the striate and parts of the peristriate cortex, previously named the anterior or medial visual network. M_C3 represents the lateral visual or secondary visual network. Aggressive AROMA showed the lateral visual network separately as the left (AA_C9) and right (AA_C14), while non-aggressive AROMA showed only the left (AN_C5).

Cingulate components were identified in two main parts: the posterior cingulate cortex/precuneus, including the angular gyrus (M_C5), and the anterior cingulate cortex (M_C29). M_C5 aligns with the posterior DMN and was also captured using both AROMA-based approaches (AN_C12, AA_C4). M_C29 represents the anterior cingulate cortex as a local cluster, resembling patterns of the salience network (Uddin et al., 2019). A corresponding component was found with aggressive AROMA (AA_C27), but not with non-aggressive AROMA.

Prefrontal components varied between denoising techniques. Manual denoising identified four bilateral components: the medial (M_C6), dorsolateral (M_C15), orbitofrontal (M_C16), and ventrolateral (M_C21) prefrontal cortex, all appearing as local clusters without widespread connectivity. Aggressive AROMA showed a left lateral prefrontal component (AA_C26), and non-aggressive AROMA showed two right lateral components (AN_C17, AN_C26) and one left lateral (AN_C29) prefrontal component.

Parietal components included the bilateral superior parietal cortex (M_C8, AN_C15, AA_C12), bilateral angular gyrus (M_C11), and left lateralized intraparietal sulcus (M_C19). M_C8 covered the intraparietal sulcus and showed slight distal spatial distribution with a few voxel-signal clusters in the frontal eye field, resembling the dorsal attention or dorsal frontoparietal networks (Yeo et al., 2011). M_C11 represents the bilateral posterior part of the DMN, while non-aggressive AROMA showed a similar DMN component left lateralized (AN_C25) and aggressive AROMA left (AA_C22) and right (AA_C33) lateralized.

Sensorimotor components corresponded to previously reported RSNs, including lateral (M_C22) and medial (AN_C11, AA_C13) somatosensory networks, as well as primary motor networks (M_C26, AN_C36, AA_C35) (Chen et al., 2021a). Lateralized somatosensory components were identified in the left hemisphere across all denoising methods (M_C27, AN_C10, AA_C20) and right lateralized with both AROMA-based approaches (AN_C28, AA_C28).

Temporal components varied between denoising techniques. The bilateral insular network (M_C25), also known as the auditory network, showed a more pronounced middle temporal configuration in both AROMA-based approaches (AN_C32, AN_C33, AA_C31, AA_C36) and a more superior localization with manual denoising.

The thalamic network was detected only with non-aggressive AROMA (AN_C31). No cerebellar networks were identified, likely due to a limited FOV excluding the parts of the cerebellum in some participants.

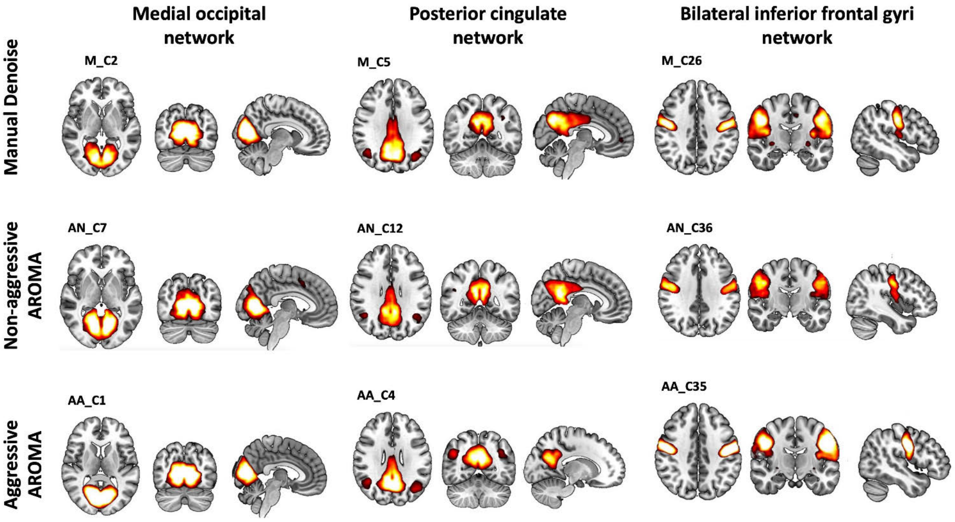

Figure 13. Examples of occipital, cingulate, and sensorimotor networks showing high spatial correspondence across denoising techniques. Images are shown in the radiological convention. Modified from Study III.

5.2.1 Summary of the Findings (Study II)

Altogether, the results suggest that most intrinsic connectivity networks commonly reported in previous studies with children and adults were also present in our sample of 5-year-olds during movie-watching. Consistent with prior research, networks supporting basic motor and sensory processing showed robust functional organization, closely resembling adult patterns. In contrast, networks associated with higher-order functions appeared more immature or fragmented. These potentially immature higher-order functional networks may reflect cognitive skills that are still developing at the age of 5. However, functional connectivity varies between scanning conditions (e.g., rest vs. movie stimuli), which may limit cross-study comparability. Finally, our results indicate that manual denoising, as well as both non-aggressive and aggressive AROMA, yielded largely similar components, with minor differences in 5-year-old children.

5.3 Maternal Perinatal Depressive Symptoms and Association with Amygdala Connectivity (Study III)

In Study III, we examined associations between maternal depressive symptoms during the pre- and postnatal phases and amygdala connectivity at age 5 (N = 68; mean age 5.39 years; 28 boys). Mean EPDS sum scores across measurement points were 5.12 (SD = 4.23; range 0–21) at gw 24, 3.97 (SD = 3.52; range 0–12) at 3 months postnatally, 5.19 (SD = 4.63; range 0–19) at 6 months postnatally, and 4.39 (SD = 4.32; range 0–21) at 12 months postnatally. The corresponding SCL-90 scores were 3.41 (SD = 3.55; range 0–14) at gw 24, 2.00 (SD = 3.11; range 0–15) at 3 months postnatally, and 3.21 (SD = 4.75; range 0–24) at 6 months postnatally.

5.3.1 Whole-Brain Voxel-Wise Associations

There was a positive association between mothers' EPDS scores at 3 months postnatally and the child's brain ReHo map in the left amygdala region when controlling for child's sex and age at scan [$p < 0.005$, $p = 0.002$ FWE corrected, cluster size (kE) 1522]. The association remained significant when maternal pre-pregnancy BMI, maternal SES, and child PI were included as covariates [$p < 0.005$, $p = 0.007$ FWE corrected, cluster size (kE) 1281], and when EPDS scores at gw 24 were controlled as well [$p < 0.005$, $p = 0.008$ FWE corrected, cluster size (kE) 1213] (Figure 14). However, the association did not remain significant when the SCL-90 score was included as a covariate.

Additionally, mothers' EPDS scores at 12 months postnatally were positively associated with the ReHo map in the left amygdala region when child sex and age at scan were included as covariates [$p < 0.005$, $p = 0.005$ FWE corrected, cluster size (kE) 1325], but not with any other covariates.

There were no associations between maternal EPDS scores and ReHo values in the left amygdala at gw 24 or 6 months postnatally. No negative associations were observed between amygdala ReHo values and maternal EPDS scores at any time point.

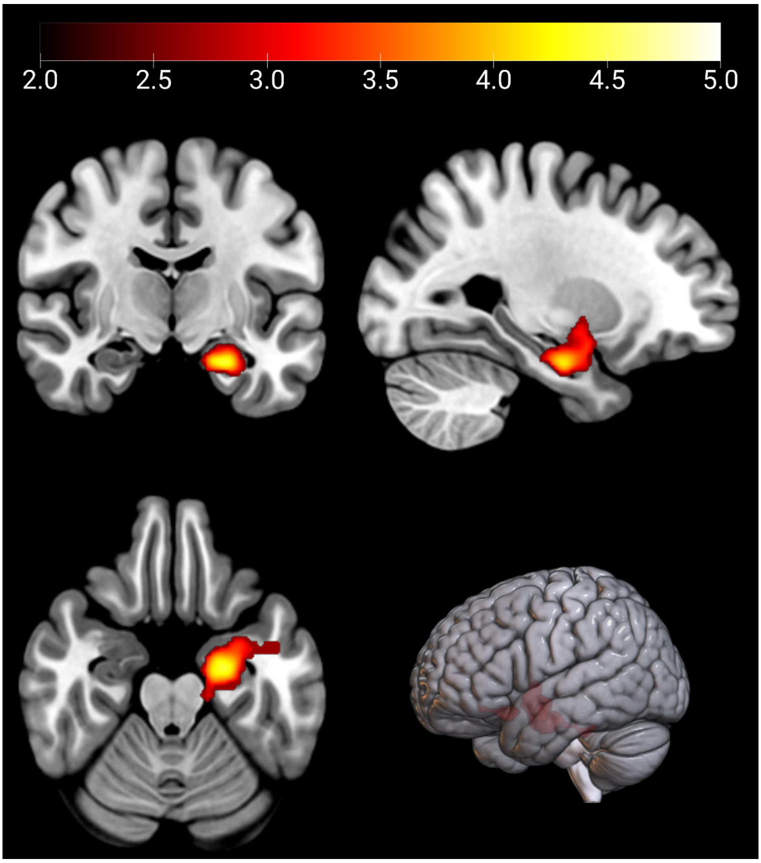

Figure 14. ReHo values of the left amygdala are positively associated with maternal EPDS scores at 3 months postnatally, controlling for child sex, age at scan, maternal pre-pregnancy BMI, maternal socioeconomic status, child's ponderal index, and EPDS score at gw 24. The cluster also extends to the surrounding cortex, anterior hippocampus, cerebellum, and globus pallidus (all in the left hemisphere). The colour bars depict t-values. Images are shown in the radiological convention. Modified from Study III.

5.3.2 Region-of-Interest Analyses of ReHo in the Bilateral Amygdala

There was a positive association between left amygdala mean ReHo values and EPDS scores at gw 24 when controlling for child sex and age at scan ($p < 0.05$, $\beta = 0.25$). This association did not persist when maternal SES, maternal pre-pregnancy BMI, and child's PI, or when SCL-90 score at gw 24 were controlled for. No associations were found between right amygdala mean ReHo values and EPDS scores at gw 24.

There was a positive association between left amygdala mean ReHo values and EPDS scores at 3 months postnatally when child sex and age at scan were included as covariates ($p < 0.001$, $\beta = 0.48$), and when maternal SES, maternal pre-pregnancy

BMI, and child's PI were added as covariates ($p < 0.001$, $\beta = 0.47$). When SCL-90 score at 3 months postpartum was additionally included, the association remained significant, but attenuated ($p < 0.05$, $\beta = 0.34$). Further, right amygdala mean ReHo values and EPDS scores at 3 months postnatally were statistically significantly associated when child sex and age at scan were controlled for ($p < 0.05$, $\beta = 0.28$), and the association remained significant when further controlling for maternal SES, maternal pre-pregnancy BMI, and child's PI ($p < 0.05$, $\beta = 0.29$), but did not remain significant when the SCL-90 score at 3 months postnatally was also included.

Left amygdala mean ReHo values and EPDS scores at 6 months postpartum were positively associated when controlling for sex and age ($p < 0.01$, $\beta = 0.38$), and when further controlling for maternal SES, maternal pre-pregnancy BMI, and child's PI ($p < 0.01$, $\beta = 0.37$). The association did not remain significant when the SCL-90 score at 6 months postnatally was additionally controlled for. There were no associations between right amygdala mean ReHo values and EPDS scores at 6 months postpartum.

There was a positive association between left amygdala mean ReHo values and EPDS scores at 12 months postnatally when child sex and age at scan were controlled for ($p < 0.001$, $\beta = 0.42$), and it remained significant when further controlling for maternal SES, maternal pre-pregnancy BMI, and child's PI ($p < 0.01$, $\beta = 0.39$). No associations were found between right amygdala mean ReHo values and EPDS scores at 12 months postnatally. A summary of the statistically significant results of the regression analyses is represented in Table 4.

Table 4. Summary of statistically significant results of regression analyses for bilateral amygdala mean ReHo and maternal perinatal EPDS sum scores. Modified from Study III.

RELATION	CONTROLLED COVARIATES	β	*P*
L Amygdala ReHo and EPDS at gw 24	Child sex, and age at scan	0.25	< 0.05
L Amygdala ReHo and EPDS at 3 mo	Child sex, and age at scan	0.48	< 0.001
L Amygdala ReHo and EPDS at 3 mo	Child sex, age at scan, maternal SES, maternal pre-pregnancy BMI, and child's PI	0.47	< 0.001
L Amygdala ReHo and EPDS at 3 mo	Child sex, age at scan, maternal SES, maternal pre-pregnancy BMI, child's PI, and SCL-90 sum score at 3 months	0.34	< 0.05
R Amygdala ReHo and EPDS at 3 mo	Child sex, and age at scan	0.28	< 0.05
R Amygdala ReHo and EPDS at 3 mo	Child sex, age at scan, maternal SES, maternal pre-pregnancy BMI, and child's PI	0.29	< 0.05
L Amygdala ReHo and EPDS at 6 mo	Child sex, and age at scan	0.38	< 0.01
L Amygdala ReHo and EPDS at 6 mo	Child sex, age at scan, maternal SES, maternal pre-pregnancy BMI, and child's PI	0.37	< 0.01
L Amygdala ReHo and EPDS at 12 mo	Child sex, and age at scan	0.42	< 0.001
L Amygdala ReHo and EPDS at 12 mo	Child sex, age at scan, maternal SES, maternal pre-pregnancy BMI, and child's PI	0.39	< 0.01

Abbreviations: L= left, R = right, ReHo = regional homogeneity; EPDS = Edinburgh Postnatal Depression Scale; SES = socioeconomic status; BMI = body mass index; SCL-90 = Symptom Checklist.

5.3.3 Seed Connectivity Analysis of the Bilateral Amygdala

There were no significant associations in the seed connectivity of our region of interest (bilateral amygdala) with the rest of the brain and maternal EPDS scores.

5.3.4 Summary of the Findings (Study III)

In whole-brain analyses, higher maternal depressive symptoms at 3 and 12 months postnatally were associated with higher ReHo in the offspring's left amygdala at age 5 years. A higher ReHo reflects greater local signal similarity, which may indicate more intense local connectivity or abnormal hyperconnectivity. While an increase in amygdala ReHo suggests heightened local synchronization, its functional meaning remains unclear. The amygdala is commonly associated with processing emotions, particularly fear and threat, as well as influencing memory and decision-making. The observed associations may relate to these functions either at the time of measurement or at other time points in development, but further research is needed to clarify these links.

Region-of-interest analyses of bilateral amygdala revealed positive associations between maternal depressive symptoms at gw 24 and at 3, 6, and 12 months postnatally, and the offspring's left amygdala mean ReHo at age 5 years, with the largest effect size observed for symptoms at 3 months postnatally. At this time point, maternal depressive symptoms were also positively associated with offspring right amygdala mean ReHo. These findings support the notion that the timing of maternal depressive symptoms may play an important role when examining the effects on offspring brain development.

5.4 Maternal Sensitivity and Its Association with Medial Prefrontal Cortex Connectivity (Study IV)

In Study IV, we examined how maternal sensitivity at 8 and 30 months of age is associated with brain functional connectivity at 5 years of age. The final sample included 17 mother–child dyads with interaction data at 8 months (mean 8.0 months) and 39 mother–child dyads with interaction data at 30 months (mean 30.1 months). Of the included dyads, 13 participated in interaction assessments at both time points. Maternal sensitivity scores were 5.2 (SD = 1.4, range 2–7) at 8 months and 5.2 (SD = 1.1, range 3–7) at 30 months.

5.4.1 Whole-Brain Voxel-Wise Associations

There was a positive association between maternal sensitivity at 8 months and the child's brain ReHo map of the mPFC when controlling for child sex and age at scan [$p < 0.005$, $p = 0.027$ FWE-corrected, cluster size (kE) 704] (Figure 15A). Based on the Automatic Anatomic Labeling Atlas (AAL), the peak cluster (-6, 44, 28) was located in the left medial superior frontal gyrus, with extensions to the right medial superior frontal gyrus and the right anterior cingulate and paracingulate. There were no negative associations between maternal sensitivity and ReHo maps.

We estimated a mean ReHo value from the peak cluster across 704 voxels for sensitivity analyses. There was a statistically significant positive partial correlation ($r = 0.80$, $p < 0.001$) between mean ReHo values (mean = 1.29, SD = 0.28) and maternal sensitivity scores (mean = 5.18, SD = 1.42), corrected for child sex and age at scan (Figure 15B). The effects on the correlation map between ReHo and maternal sensitivity remained statistically significant with additional covariates: child gestational age, maternal age at childbirth, maternal pre-pregnancy BMI, maternal smoking during pregnancy, maternal education level, and perinatal maternal depressive symptoms.

We also ran sensitivity analyses in SPM by adding each of the variables used in the partial correlation models individually as an additional covariate of no interest (one variable at a time). These analyses revealed that our main finding (frontal cluster) was consistently identified, but most of the models did not survive as statistically significant, which was likely due to the small sample size.

No associations were found between maternal sensitivity at 30 months and ReHo at 5 years.

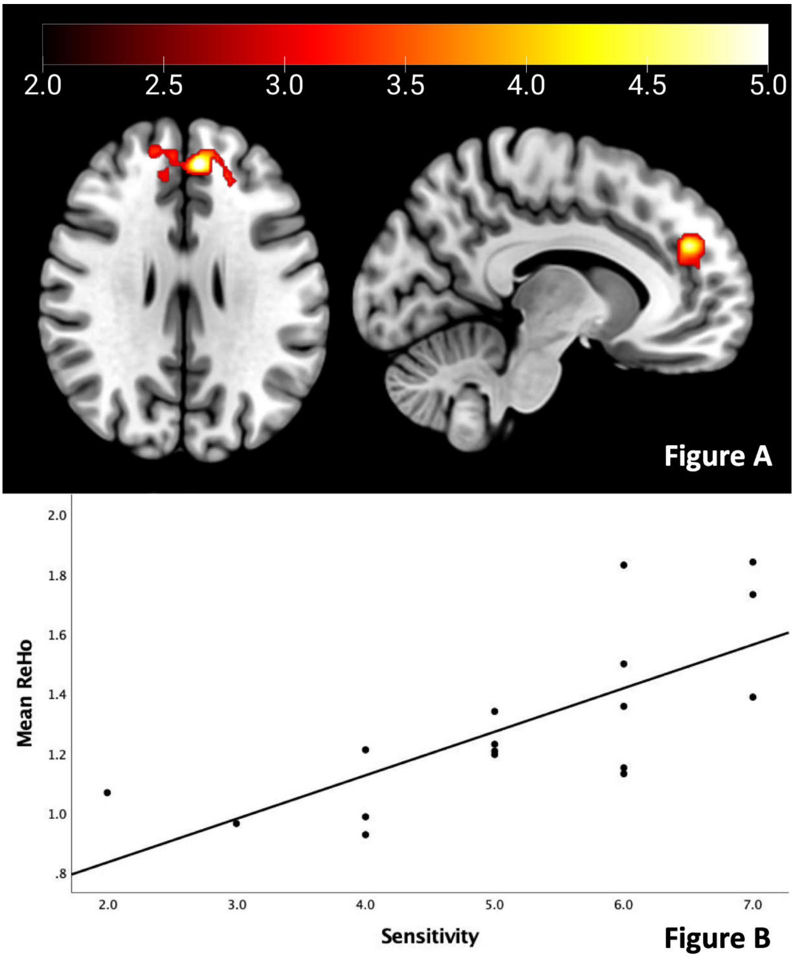

Figure 15. Figure A: ReHo values of the mPFC are positively associated with maternal sensitivity scores at 8 months, controlling for child sex and age at scan. The colour bar depicts t-values. Images are shown in the radiological convention. Figure B: Scatterplot (for display purposes only) showing the relation between maternal sensitivity and mean ReHo in the mPFC. Modified from Study IV.

5.4.2 Seed Connectivity Analysis of mPFC

There were no associations in the seed connectivity analysis of our seed region of interest (location of our ReHo result) with the rest of the brain and maternal sensitivity at 8 months. However, the group mean SCA with the ReHo-based seed showed positive correlations across widespread brain regions.

5.4.3 Summary of the Findings (Study IV)

Higher maternal sensitivity at 8 months was associated with increased ReHo in the offspring's mPFC at age 5 years, whereas no such association was found at 30 months. The functional significance of elevated ReHo in the PFC remains unclear and warrants further investigation. Nonetheless, given the mPFC's central role in emotional regulation and executive functions, and its susceptibility to early environmental influences, these findings suggest that maternal sensitivity in infancy may contribute to prefrontal cortex development. In addition, the findings suggest that variation within the normative range of parenting is still relevant for functional brain development. Caution is warranted in interpreting these results due to the limited sample size.

6 Discussion

In this thesis, we demonstrated that infant and child MRI can be conducted with age-appropriate methods without the need for anaesthesia. We also highlighted the importance of sufficient reporting of the methods used, to enable future studies to make informed choices based on their efficacy, strengths, and possible limitations. Second, we identified intrinsic connectivity networks in 5-year-old children during movie-watching. While most networks showed adult-like spatial organization, those related to higher-order cognitive functions exhibited more immature patterns. Third, maternal perinatal depressive symptoms were found to be associated with local functional connectivity in the left amygdala. The strongest association was found when maternal depressive symptoms were measured at 3 months postnatally. Finally, maternal sensitivity during mother–infant interaction at 8 months was associated with PFC local functional connectivity at the age of 5 years. These findings indicate that early exposures may inflict long-term effects on functional brain development, especially in areas critical for self-regulation and executive functions.

6.1 Infant and Child MRI

The first aim of this thesis was to review and present methods for scanning children under the age of 6 years without anaesthesia. In our literature review, we found that the feed-and-wrap (or feed-and-swaddle) method is the most frequently used, particularly in infant samples. In general, swaddled infants arouse less and sleep longer (Van Sleuwen et al., 2007), which is beneficial for MRI imaging. Infants younger than 3 months appear easiest to scan (Hendrix & Thomason, 2022), although previous studies report successful use of this method up to 6 months (Templeton et al., 2020; van der Veen et al., 2025). The feed-and-swaddle method is also applied in clinical neuroimaging, where most infant brain MRI scans can be conducted without anaesthesia and with high success rates (Greer et al., 2024). This method worked well also in our sample of 2–5-week-old infants.

From 1 to 3 years (Hendrix & Thomason, 2022), or even up to 5 years of age, (Barkovich et al., 2018) appears to be the most challenging period for scanning without sedation. Based on the reviewed studies, scanning while the child is awake is most commonly initiated at around 4 years of age. However, some studies have conducted scans during natural sleep at this age, while others have successfully scanned even younger children while awake (Thieba et al., 2018; Vannest et al., 2014). There is no clear evidence indicating the optimal age to begin awake scanning, and it is likely that individual child characteristics, such as temperament (Johnson et al., 2021) and cognitive ability (Thieba et al., 2018), play a role.

From a developmental perspective, 4-year-olds begin to show the ability to follow verbal instructions, and their attention and self-regulation skills are emerging, which may facilitate awake scanning. Due to the exclusion and inclusion criteria of our original literature search, we were not able to broadly review methods for scanning children awake (see limitations). However, previous studies with preschool- and school-aged children emphasize strategies to minimize anxiety and create a child-friendly, age-appropriate environment to enhance cooperation. These strategies include mock-scanner training, virtual-reality stimulation, videos, stories, mobile apps, and other behavioural methods (Carter et al., 2010; Staab et al., 2024; Stunden et al., 2021). One randomized control trial found no differences between home-based preparation materials, training with a child life specialist, or mock scanner training with a child life specialist in children aged 3–7 years (Fletcher et al., 2023). Earphones for music and goggles for viewing movies are widely used strategies. Having a parent present in the scanner room can also help reduce anxiety. In our sample of 5-year-olds, home preparation, mock-scanner training, and video viewing during acquisition worked well. However, our success rate for functional MRI was relatively low, likely due to the long duration of scanning before the fMRI sequence, and because the child's own movie was stopped and replaced with the *Inscapes* movie.

Other important aspects to consider are motion restriction and sound attenuation during scanning. Based on our review, swaddling was the most common technique for restricting motion in infants. Additionally, vacuum immobilizer mats, cushions, and foam pads were used to stabilize body and head position. Appropriate sound attenuation is crucial for both safety and comfort. Our review suggests that the most common approaches were ear protection using earplugs (silicone, foam, or wax), soft-shell earmuffs (Minimuffs), or regular ear protectors, usually in combination. Well-fitted earplugs or earmuffs typically provide noise attenuation of around 10–30 dB, which generally brings noise exposure within acceptable limits (McJury, 2022). However, such passive noise control methods have certain limitations, including discomfort, fitting issues, and, most importantly, insufficient noise reduction in some cases. Therefore, active methods, like quiet sequences, have been developed. These approaches, however, may lead to longer scanning times and reduced data quality (McJury, 2022; McJury & Shellock, 2000). Combining noise attenuation methods is particularly important when using high-field MRI scanners

(7 T), which produce greater acoustic noise due to higher field strength and faster gradient switching (Akbar et al., 2023b).

Successful scanning is dependent upon the participant's ability to remain still during acquisition, and our review found that motion is the most common cause of data loss. Scanning time is a crucial factor, as children are often unable to remain still for extended periods. While our study could not provide detailed information on scanning times, a previous survey study of infant and toddler neuroimaging protocols reported durations ranging from 10 to 80 minutes (Hendrix & Thomason, 2022). Shorter scanning times would probably improve success rates, and several techniques have been developed to accelerate MRI acquisition and shorten scanning times (Gallo-Bernal et al., 2023).

Success rates for infant scans are usually reported to be high (80–95%) (Dean et al., 2018; Lugo-Candelas et al., 2018; Qiu et al., 2013). In contrast, success rates for toddlers and preschool-aged children show considerable variability both within and between studies. For example, one study reported 54–71% success in 4-year-olds (De Bie et al., 2010), another found 48% success for all sequences and 72% for some high-quality data in 2–5-year-olds (Thieba et al., 2018), and yet another reported a 95% success rate in 4–6-year-olds (Runge et al., 2018). Even when data are successfully acquired, up to 51% may be rejected during analyses due to excessive motion (Hendrix & Thomason, 2022). These findings underscore the importance of optimizing methods used during the scanning process.

Considering the findings in our review, we recommend comprehensive reporting of the procedures used when scanning infant and child samples, particularly with respect to potential effects of scanning conditions on results in functional imaging. Identifying the most effective strategies for different age groups may later improve data quality and facilitate larger sample sizes across all ages.

6.2 Intrinsic Connectivity Networks

The second aim of this thesis was to investigate intrinsic connectivity networks in typically developing 5-year-olds during movie-watching. To our knowledge, our study (Study II) is the first to present ICNs during a movie-watching paradigm in this narrow age range. Our main finding was that most adult-like networks are already present at the age of 5 years, while some, especially those known to support higher-order functions, appear more fragmented and possibly immature. Furthermore, we found that ICA-based manual denoising and AROMA (both non-aggressive and aggressive) yielded broadly similar spatial organizations of the networks in our data. The primary visual, sensorimotor, and auditory networks were largely consistent across denoising techniques and showed high spatial correspondence with previously reported networks (Damoiseaux et al., 2006;

Muetzel et al., 2016). This aligns with previous findings that these networks display an adult-like topography already in infancy and undergo only minimal topological changes during the first year of life (Gao et al., 2015).

A major difference compared to adult studies was the decomposition of the DMN into several components. In adults, the DMN generally appears as a single network including the mPFC, inferior parietal lobule, and posterior cingulate cortex. The DMN is typically most active during rest and internally focused cognitive processes (such as mind-wandering) and becomes less active when attention is directed toward tasks requiring cognitive effort (Fernandino & Binder, 2024; Sambuco, 2024). For this reason, it is often classified as a "task-negative" network. It supports a variety of higher-level functions, such as self-referential processing, social cognition, and inhibitory control (Menon, 2023; Rebello et al., 2018), which are still developing at the age of 5 years. In our data, we identified a posterior cingulate cortex component extending to the inferior parietal lobule bilaterally, along with a separate parietal component. Additionally, a distinct prefrontal component was identified. Evidence from seed-based rs-fMRI studies suggests that the basic architecture of the DMN is already present in a basic form in infancy, as indicated by the coactivation of the posterior cingulate cortex, bilateral inferior parietal lobule, and mPFC (Gao et al., 2015). However, ICA-based studies in infants suggest that the DMN is decomposed into multiple components (Rajasilta et al., 2020). Furthermore, ICA-based studies in children have generally reported the DMN as divided into multiple subcomponents, typically into separate anterior and posterior components (Chen et al., 2021a; de Bie et al., 2012; Muetzel et al., 2016; Thornburgh et al., 2017). Increasing ICA dimensionality may lead to the splitting of components into sub-networks (Smith et al., 2009). However, previous studies have mostly identified the DMN as separate components in children even when applying lower dimensionalities (20–30) than those used in our study (Chen et al., 2021a; de Bie et al., 2012; Muetzel et al., 2016; Thornburgh et al., 2017). In a previous naturalistic viewing study, children aged 4–6 years showed more variable patterns of activation compared to adults, particularly within regions of the DMN (Moraczewski et al., 2018). These findings provide evidence for a developmental trajectory of the DMN that may be closely linked to the development of social cognition in childhood.

In line with observations on the DMN, we observed a fragmented architecture in other networks supporting higher-order cognitive functions in our 5-year-old group. Frontal and parietal networks appeared as separate components, possibly representing patterns of frontoparietal networks. Additionally, we identified an anterior cingulate component and temporal/anterior insula components, which may represent parts of the salience network. A previous longitudinal seed-based fMRI-study covering the first year of life suggested that the salience and frontoparietal networks showed limited maturation of network topology and remained far from adult-like at the end of the first year (Gao et al., 2015). A cross-sectional rs-fMRI study with a small sample size of 24 children aged 1–3 years also identified the salience network and right frontoparietal network; however, the clusters were small, and the left frontoparietal network was not detected (Chen et al., 2021a). In contrast, de Bie et al. (2012), also with a small sample (N=18), found the left but not the right frontoparietal network. The salience network (also referred to as the cingulo-opercular network) was identified in two separate components. In 6–8-year-olds (N=84) scanned awake with eyes closed, using an ICA dimensionality of 16, both left and right frontoparietal networks, as well as the salience network, were detected (White et al., 2014). The same study also examined network stability across acquisition times. Interestingly, the sensorimotor network showed the least stability, whereas the salience and auditory networks demonstrated the greatest stability, with all networks stabilizing after 5½ minutes. In conclusion, studies covering age ranges both younger and older than our 5-year-old sample have reported variability in the organization of higher-order networks during childhood. Some of these differences are likely related to variations in scanning procedures and analysis methods, including ICA component dimensionality, as discussed above. However, this possible immaturity of higher-order functional networks at the age of 5 years aligns with child cognitive development, as higher-level cognitive skills, such as executive function and self-regulation, continue to mature well into adolescence (Anderson, 2002; Luna et al., 2004). Characterizing the brain circuitry underlying these developmental immaturities can provide insight into the neural basis of protractedly developing skills such as cognitive control (Luna et al., 2010).

We conclude that fMRI during movie-watching can be successfully applied in children at the age of 5 years, in line with previous studies (Vanderwal et al., 2015, 2019). However, it remains unclear how movie-watching paradigms affect brain functional connectivity and, in turn, the organization of intrinsic connectivity networks across development. As most previous child studies have been conducted at rest (during natural sleep or while awake with eyes open or closed), our results cannot be directly comparable with those. Moreover, a child's "rest" while awake may differ significantly from an adult's rest in terms of functional connectivity, due to the greater demand for inhibitory control, as children are expected to wait for the next meaningful stimulus (Camacho et al., 2020). In 6-year-olds, watching an age-appropriate movie of the child's choice elicits significant changes in functional connectivity between the visual system and the dorsal attention network compared to rest (Emerson et al., 2015). In late childhood (9–12 years), network configuration has been shown to vary both by age and by cognitive state when compared with adults (Le et al., 2020). In adolescence and young adulthood, movie watching (*Despicable Me)* elicited varying levels of functional stability across networks when compared with rest (Li et al., 2020). In a small adult sample (N = 22), *Inscapes* evoked an intermediate level of intersubject correlations, both widespread and stronger than rest, yet spatially more limited and weaker than a narrative movie (*Ocean's Eleven*) (Vanderwal et al., 2015). Moreover, functional connectivity differences across these three conditions were observed within the somatomotor, visual, ventral attention, frontoparietal, and default networks. In the future, shifting the standard resting stimulus or narrative movies to a low stimulation video may improve comparability across samples and ages and be especially useful in longitudinal studies.

It is also worthwhile to consider the possible impact of motion when scanning this challenging age group, as even subtle head movements can introduce systematic bias in measures of network connectivity (Power et al., 2014). While there are various motion denoising pipelines (Ciric et al., 2017), there is currently no consensus on the best approach, especially in children. We applied ICA-based methods (manual, non-aggressive, and aggressive AROMA) for denoising and used group-ICA to capture the components. We found that all these techniques were generally comparable in their ability to capture the networks, especially in the occipital networks and DMN subcomponents. However, the frontal and parietal networks showed more variability in spatial distribution across denoising methods. AROMA (non-aggressive and aggressive) produced more unilateral components than manual denoising, as seen in the sensorimotor and occipital networks. In adults, ICA-AROMA has been shown to be an effective strategy for removing motion-related artefacts (Pruim et al., 2015a). Differences between non-aggressive and aggressive AROMA have been reported, with non-aggressive AROMA showing significantly lower network identifiability than aggressive AROMA in high-motion older adults (Scheel et al., 2022). This same study found aggressive AROMA to provide the highest network reproducibility. Similarly, foetal fMRI work has suggested that ICA denoising at a more stringent threshold is superior to less stringent denoising (Ji et al., 2022). Nevertheless, further research is needed, as the ability to utilize automated denoising algorithms (e.g., ICA-AROMA) is crucial for improving cross-study reliability.

6.3 Early Life Factors Affecting Functional Brain Development

6.3.1 Maternal Perinatal Depressive Symptoms

In Study III, our main finding was that higher maternal depressive symptoms, especially when measured at 3 months postnatally, were associated with higher ReHo in the offspring's left amygdala. This is notable given the relatively strong and localized association observed in the whole-brain statistical models. In SCA, we did not find any significant associations in the functional connectivity between the amygdala and the rest of the brain.

We found that greater maternal perinatal depressive symptoms were positively associated with left amygdala ReHo values in offspring at the age of 5 years. A higher ReHo value represents higher coherence and centrality at the millimetre scale, reflecting greater local synchrony of brain activity. A previous study of participants aged 11–35 years showed that overall ReHo values decrease with age throughout the grey matter (Lopez-Larson et al., 2011). However, this study did not cover early childhood, and the normative developmental trajectory of local connectivity measured with ReHo is unclear. Nevertheless, a wide range of findings from other methods support the idea of functional connectivity maturation from local to distal, with local connectivity decreasing and distal connectivity increasing with age. This pattern possibly reflects an increase in pruning in the developing brain and thus a decrease in the strength of local connectivity. Studies covering the infancy period suggest that local connectivity changes from birth to adulthood follow an inverted U-shaped developmental course (Ouyang et al., 2017). However, it remains to be seen what our finding of greater amygdala coherence in children exposed to maternal depressive symptoms might reveal about the amygdala's developmental stage and how it could reflect offspring exposure to early life stress.

Research investigating associations between perinatal maternal depression and functional brain development in children has typically focused on the amygdala and its widespread connectivity across the brain. In Study III, the SCA analysis using the amygdala as a ROI did not reveal significant associations between maternal depressive symptoms and amygdala seed-based connectivity. Previously, preterm neonates of mothers diagnosed with prenatal anxiety and/or depression showed reduced functional connectivity between the left amygdala and the thalamus, hypothalamus, insula, and brainstem (Scheinost et al., 2016a). Depressive symptoms in the second trimester have been associated with increased functional connectivity between the amygdala and the temporal cortex, insula, anterior cingulate cortex, and prefrontal cortices in infants at 6 months of age (Qiu et al., 2015). In line with this, increasing or peak stress late in pregnancy has been shown to be associated with increased amygdala functional connectivity with the anterior insula and ventromedial PFC in offspring at 1 month of age (Marr et al., 2023). In contrast, in 4-year-old girls, mothers' second-trimester depressive symptoms were linked to decreased right amygdala functional connectivity with the orbitofrontal cortex and temporal pole, as well as reduced left amygdala connectivity with the anterior cingulate cortex, putamen, insula, and caudate (Soe et al., 2018). Finally, in 6-year-olds, postnatal maternal anxiety and depressive symptoms were negatively associated with amygdala-PFC and frontal pole functional connectivity (Uy et al., 2023).

In previous resting-state studies, altered amygdala functional connectivity has been linked to anxiety disorders (Hamm et al., 2014), depression (Cullen et al., 2014), and aggressive behaviours during childhood and adolescence (Sukhodolsky et al., 2021). In addition, neurodevelopmental disorders like ASD and ADHD often show atypical amygdala connectivity (Ma et al., 2023; Yang et al., 2021). Previous task fMRI studies have shown elevated amygdala reactivity in response to fearful faces in groups of children exposed to maternal deprivation in early life (Gee et al., 2013a; Tottenham et al., 2011). Strong amygdala responses have been associated with a more mature response (Thomas et al., 2001). Furthermore, it has been suggested that amygdala hyperactivation may indicate accelerated development of the amygdala's functionality early in life (Guadagno et al., 2021). Considering these findings, our results raise the possibility that amygdala connectivity may serve as a neural marker of intergenerational transmission of risk for depression, other psychiatric disorders, and emotion regulation problems. However, future studies are required to further investigate whether the amygdala connectivity changes observed in exposed children are later manifested as psychiatric or neurodevelopmental disorders, or as variations in psychological development, such as emotion regulation and social skills.

Interestingly, our study highlighted the importance of the left, but not the right, amygdala in whole-brain statistical models. Similarly, Qiu et al. (2015) found that prenatal depressive symptoms were associated with left, but not right, amygdala functional connectivity. Another study focusing on maternal perinatal anxiety found a relationship between maternal second-trimester anxiety symptoms and left, but not right, amygdala connectivity (Donnici et al., 2021). The left amygdala has been implicated in more cognitive and intentional control of mood (Dyck et al., 2011), and across studies is more often activated than the right amygdala, suggesting different roles in emotional processing (Baas et al., 2004). Additionally, it has been demonstrated that top-down mechanisms influence activity in the left amygdala rather than the right, suggesting that the left amygdala may be more sensitive to top-down regulation in the context of emotion and anxiety (Ochsner et al., 2009). However, fMRI research on the lateralization of emotional processing in the brain has yielded mixed findings, and further studies are needed.

The timing of exposure to maternal depressive symptoms was found to be essential. In Study III, whole-brain voxel-wise associations were found when EPDS scores were measured at 3 and 12 months postnatally. There were no associations between ReHo values and EPDS scores measured at gw 24 or 6 months postnatally. In linear regression analyses, associations were found for EPDS measured at gw 24, 3 months, 6 months and 12 months postnatally, with the largest effect size observed at 3 months postnatally. Previous studies have reported associations between perinatal maternal depression and offspring amygdala functional connectivity (see

Table 1 in the literature review). However, most of these scans were conducted during the first few months after birth, which very likely reflects an important timing effect. It is also worth noting that the timeframes covered by the questionnaires vary, typically ranging from a week to a month, although some assess shorter periods or ask participants to evaluate overall symptom levels over longer durations. The onset and timing of prenatal depression may have variable impacts on the developing brain in utero, and these effects may be moderated by factors such as child age, sex, and the presence of postnatal depression (Manning et al., 2025). Moreover, evidence suggests that stress-symptom trajectories may influence symptom severity differently and independently of effects on the offspring's brain and behavioural development (Korja et al., 2024; Marr et al., 2023). Future longitudinal studies using trajectory analyses of depressive symptoms are needed to better capture the effects of timing, intensity, and persistence of maternal perinatal stress on offspring brain development.

Finally, it is suggested that postnatal maternal depression likely acts through a psycho-social pathway via mother–child interaction. In a meta-analysis of studies on the early mother–child interactions, mothers with postpartum depression were found to be more irritable and hostile, less engaged, less emotionally expressive and warm, and to play less with their infants (Lovejoy et al., 2000). Moreover, infants of depressed mothers also differ in their interaction patterns, showing more gaze avoidance, reduced vocalizations, and fewer positive expressions compared to infants of non-depressed mothers (Mäntymaa, 2006), potentially affecting dyadic interaction independently. By around 2 to 3 months of age, infants undergo a key socioemotional developmental shift, marked by the emergence of the social smile, recognition of familiar faces and expressions, and early communicative vocalization. At this stage, socioemotional development begins to emerge, and the child is highly dependent on the caregiver's emotional support. These early developmental steps could be especially sensitive to changes in maternal mood, and, based on our findings, such changes could have implications for later brain development. Finally, increasing evidence suggests that supportive postnatal environments (e.g., parental sensitivity) may buffer the effects of prenatal depression on offspring development (Nolvi et al., 2023). Further research examining both mediating and moderating pathways is needed to better understand the mechanisms underlying these associations.

6.3.2 Maternal Sensitivity

It is well established that early caregiving plays a critical role in offspring psychosocial development. However, evidence on how this is reflected in brain development remains limited, especially within the normative range. In Study IV, our main finding was an association between maternal sensitivity during infancy and local functional connectivity in the offspring's PFC. Specifically, children of more sensitive mothers at the age of 8 months showed higher ReHo values in the PFC at the age of 5 years. In addition, these prefrontal regions showed widespread connectivity across the brain, but the strength of the longer-range connectivity was not significantly associated with maternal sensitivity. Further, there was no association between maternal sensitivity in toddlerhood (30 months of age) and child brain local connectivity at the age of 5 years. Our small sample size limits our results; however, the findings provide preliminary evidence for the importance of maternal sensitivity during infancy.

We used ReHo as a first-stage analysis method, which enabled us to examine whole-brain associations without preselecting a region of interest. This choice was motivated by the limited knowledge of how early maternal sensitivity in infancy and toddlerhood relates to offspring brain functional connectivity at preschool age. From whole brain voxel-wise analysis, we found a significant association between maternal sensitivity and functional connectivity in the offspring's PFC. As previously described, the PFC is one of the key brain regions for emotional regulation and executive functions, and its protracted maturation across childhood makes it especially susceptible to environmental influences. Considering that that sensitivity has been linked to a range of developmental outcomes in children, including cognitive, behavioural, and social domains, our finding in the PFC seems highly plausible.

Altered PFC functional connectivity has been linked to neurodevelopmental disorders like ADHD (Leisman & Melillo, 2022; Zang et al., 2007) and ASD (Doyle-Thomas et al., 2015; Odriozola et al., 2019; Zheng et al., 2025), both of which often involve problems in emotion regulation. The development of amygdala–PFC connectivity is a crucial aspect of emotion regulation and cognitive control (Kim et al., 2011). Task-evoked studies of amygdala–PFC functional connectivity have reported age-related decreases from childhood to young adulthood (Gee et al., 2013b), whereas others have observed age-related increases (Vink et al., 2014). Findings from resting-state studies are mixed: some report increased connectivity (Gabard-Durnam et al., 2014), while others report decreased connectivity with age (Skyberg et al., 2023). In addition, evidence suggests that stimulus-elicited connectivity can shape the later nature of resting-state connectivity in the amygdala–PFC circuit during childhood (Gabard-Durnam et al., 2016). However, during this maturation phase across infancy and childhood, external agents (e.g., caregivers) can serve as social regulators of affect and amygdala activity (Gee et al., 2014). When parenting quality is low, it may be beneficial for the child to switch from parent-regulated to self-regulated emotion control. This may lead to accelerated development of the amygdala–PFC circuit (Herzberg et al., 2021), possibly even when variation in parental care falls within the normative range (Thijssen et al., 2017). However, evidence for accelerated development of this circuit has been more consistent in task-based studies than in resting-state studies (McLaughlin et al., 2019). Although somewhat speculative due to our small sample, our finding that ReHo values in the mPFC were higher in children with higher maternal sensitivity suggests amplified local, but still immature distal, connectivity of the mPFC in preschool-aged children. Future studies are needed to further investigate whether these PFC connectivity changes are associated with child psychological development, especially executive functions and emotion regulation skills, which are closely linked to PFC functionality.

We found an association between maternal sensitivity and offspring PFC functional connectivity during infancy, but not during toddlerhood, even though the sample size was larger. This finding may reflect shifts in the role of different parenting dimensions during child development. Infants are more dependent on their caregivers, making infancy a period when parenting is especially demanding and requires the highest level of parental interaction. In toddlerhood, the need for autonomy grows and behaviours become increasingly complex (Ballarotto et al., 2023). In contrast to changes in the role of parenting, the elements of early mother–child interaction, especially maternal sensitivity, are suggested to be moderately stable across early childhood (Holmberg et al., 2022). A previous study with a small sample size (N=17) found associations between maternal sensitivity during infancy and offspring hippocampal functional connectivity at 6 months of age (Rifkin-Graboi et al., 2015). Another later study by Wang et al. (2019b), also focusing on hippocampal functional connectivity, found associations between maternal sensitivity assessed at 6 months postpartum and functional connectivity of the right anterior hippocampus and regions of sensorimotor, visual, and top-down cognitive networks at the ages of 4 and 6 years. This study closely matches the age range of our sample, and both findings suggest that maternal sensitivity in infancy has a long-term impact on brain functional connectivity in preschool-aged children. However, studies combining normative-range parenting quality during toddlerhood with neuroimaging data in childhood remain lacking.

6.4 Strengths and Limitations of the Studies

A strength of this study is the use of task-free fMRI data from typically developing children within a narrow age range of 5 years, a largely unstudied group due to scanning challenges. We used the *Inscapes* movie during acquisition and carefully standardized scanning conditions. We were able to use prospectively collected maternal depression and anxiety symptom scores across multiple time points spanning the pre- and postnatal periods, allowing us to better identify the timing effects of maternal perinatal distress. Maternal sensitivity was evaluated through direct observation, which is considered more reliable than self-report measures.

The studies presented in this thesis also have limitations. In Study I, these are primarily related to the literature search and our selection criteria. First, we may have missed articles not captured by our chosen keywords. Second, because our focus was on scanning during the first 2 years of life, the review does not fully reflect scanning approaches used with older children, such as mock-scanner training. Finally, due to the heterogeneity in how scanning success rates were reported, we were unable to provide a reliable synthesis of the effectiveness of different preparation methods.

In Studies II–IV, the study population consisted of participants from the FinnBrain Birth Cohort Study, which is broadly representative of the Finnish population, though with a lower prevalence of younger, multiparous, and smoking women (Karlsson et al., 2018). Additionally, the study children were drawn from a geographically restricted region (Southwest Finland), so caution is warranted when extrapolating the results to other ethnicities.

In fMRI data acquisition in 5-year-olds (Study II–IV), limitations are related to scanning conditions, preprocessing, and analysis methods. First, we used a movie-watching paradigm, specifically the *Inscapes* movie, during functional scanning (also considered a strength). The decision was made based on current evidence about the advantages of naturalistic paradigms in paediatric fMRI scanning. However, it is not entirely clear how naturalistic paradigms affect intrinsic functional connectivity compared to other conditions, especially in children undergoing rapid developmental changes in brain functional connections (Emerson et al., 2015). Some evidence suggests that there is a ‘core’ functional connectivity pattern associated with naturalistic viewing, which also changes with age (Sanchez-Alonso et al., 2021). Similar potential concerns arise when considering other variables related to the scanning environment, especially the presence of a parent in the imaging room, which can modulate brain functional connectivity during childhood (Gee et al., 2014). Nevertheless, we believe that it is crucial to standardize circumstances and report all factors possibly affecting scanning conditions and, in turn, functional connectivity.

The designed scanning session was quite long, and fMRI was the last sequence acquired, which may have increased subject attrition and motion during scanning. Additionally, before initiating the fMRI sequence and switching from the participant’s own movie to *Inscapes*, we actively assessed the participant’s willingness to continue and discontinued scanning upon request. This also contributed to the relatively small sample size in our fMRI data, especially in Study IV due to the limited overlap with interaction assessment data. Our overall scanning success profile is similar to previously reported findings, namely that the highest success rates are for structural scans, potentially because these are generally placed at the beginning of the MRI sequence (Hendrix & Thomason, 2022). Moreover, our final data were unbalanced between sexes, with more girls included due to boys being more often excluded because of unusable fMRI data, which aligns with previous findings (Alexander-Bloch et al., 2016; Dosenbach et al., 2017; Frew et al., 2022).

Head motion in fMRI is considered a major factor affecting the fMRI signal, and one must achieve a balance between data cleaning and retaining enough data for statistical analysis. In Study II, we used ICA for denoising the data as well as to analyse the data at group-level models. A limitation of this approach is that it requires an equal time series from all subjects, meaning it cannot be combined with censoring techniques for more robust correction. In Studies III and IV, we used volume censoring approaches to remove volumes affected by high motion. However, denoising methods and choices are diverse, and we did not perform a comprehensive comparison of these approaches. Future studies are needed to address this gap.

In Study II, a possible limitation is that we used a fixed number of components in ICA. We chose a dimensionality of 40 because it generated a set of components similar to those previously reported. However, it has been shown that higher dimensionalities may split components into multiple subnetworks (Pamilo et al., 2012; Ray et al., 2013; Smith et al., 2009). In addition, we focused only on the spatial correspondence of ICA networks, although differences in network connectivity across age-groups may also be relevant.

In Study III, the main variables of interest, EPDS scores and SCL-90 scores, were assessed using self-report questionnaires, which may limit both reliability comparability with studies relying on clinically diagnosed depression or anxiety. In addition, our study population was drawn from the general population, with only a small proportion of mothers showing clinically relevant depressive symptoms (about 13% scoring 10 or above on the EPDS). Therefore, the findings may not be generalizable to clinical or high-risk cohorts. Furthermore, our study did not include longitudinal trajectory analyses of maternal perinatal depressive symptoms, which are suggested to influence offspring brain development in a manner independent of stress severity (Marr et al., 2023). Depression and anxiety are highly comorbid, and we were not able to fully disentangle their effects.

In Study IV, the small sample size reduces statistical power and limits the generalizability of the findings. We also had to adopt a conservative approach in controlling for potential confounders in the SPM models, as adding too many covariates may further reduce statistical power. Additionally, only maternal sensitivity was examined, while paternal sensitivity was not. This represents a limitation, since fathers have also been shown to influence child cognitive and socioemotional outcomes (Rodrigues et al., 2021) as well as brain development (Thijssen et al., 2017). Moreover, our cross-sectional design limits the ability to infer causal impacts of maternal depression and parenting on offspring functional brain development; longitudinal neuroimaging studies are needed.

6.5 Clinical Implications and Future Research

This thesis provides important insights into paediatric neuroimaging, brain functional network organization, and early life exposures associated with brain functional connectivity. Our findings demonstrate that MRI can be successfully performed in young infants during natural sleep and in 5-year-old children while awake, provided that careful, age-appropriate preparations are implemented. In the clinical field, completing MRI scans without anaesthesia offers medical, financial, and psychological benefits (Edwards & Arthurs, 2011). Many institutions currently determine the need for general anaesthesia using a simple age cutoff. However, some children given sedation may be able to complete their MRI scan without anaesthesia if given age-appropriate preparation for awake scanning. The methods described in this thesis can be applied not only in neuroimaging but also in other imaging modalities that require prolonged immobility, such as nuclear medicine and positron emission tomography. Additional approaches to improve data quality, such as real-time motion analytics, could be valuable in both clinical and research settings (Badke D'Andrea et al., 2022; Dosenbach et al., 2017). Still, a better understanding of the factors that predict which children can successfully complete scans while awake is critical for better identifying those who can undergo imaging without anaesthesia (Staab et al., 2024).

In Study II, the findings on functional network organization provide important knowledge on brain development in typically developing 5-year-old children. In addition, our results suggest that video viewing during acquisition represents a condition where intrinsic connectivity networks can be captured in children. Our findings provide significant information for researchers who are planning their scanning conditions and sequences. Adult studies have reported high test-retest reliability during naturalistic fMRI paradigms (Wang et al., 2017; Zhang et al., 2021), but more studies in children are needed to provide evidence supporting the promotion of naturalistic paradigms in functional brain network studies. With improvements in motion prevention and correction as well as large-scale normative datasets, task-free fMRI has the potential to become a valuable tool in paediatric neurology and psychiatry. Potential clinical applications could include studies on neurodevelopmental disorders to identify atypical connectivity patterns.

As mothers' self-reported depressive and anxiety scores were used instead of clinical diagnoses, and only a limited number of mothers had clinically significant levels of depression or anxiety, the results in Study III suggest that even subclinical symptoms of psychological distress in mothers can influence the developing brain of their offspring. Considering these findings, perinatal detection of depressive symptoms and intervention are hugely important in preventing later problems in offspring. Prevention of maternal perinatal depression is the ideal goal, and efforts to increase screening and access to timely and effective support for pregnant women are essential. Early interventions may also need to focus on mother–infant interactions as a key factor in later child development. There is evidence that parents can change their behaviour based on advice or teaching to improve the outcomes of their children (Sanders et al., 2014). Further investigations should examine how interventions, such as parental support programmes or stress-reduction strategies during the perinatal period, can mitigate the effects of maternal stress on child brain development (Gunnar, 2023; Sullivan et al., 2024). Finally, it is important to link the findings regarding associations between parenting and children's brain function with children's cognitive and behavioural outcomes to better understand the role of the identified associations in child development. Longitudinal data covering childhood and adolescence are needed to clarify whether the effects of early experiences become stronger or more consistent across development.

7 Conclusions

The major findings of the studies are as follows:

1. Based on the literature review and our experiences, we conclude that performing MRI in infants and young children without sedation is challenging, but feasible when well prepared. We underline the importance of reporting the used methods and suggest reporting, at minimum, the following procedural details: (1) visit timing, (2) pre-scan preparations at home and in the MRI facility, (3) the subject's state during scanning, (4) motion prevention strategies, (5) sound attenuation methods, (6) monitoring procedures during scanning, (7) total scan duration, (8) the exact number of included and excluded scans, (9) reasons for data loss, and (10) the overall visit duration.
2. Using independent component analysis, we identified intrinsic connectivity networks during video-watching at the age of 5 years. Most networks exhibited spatial patterns similar to adults (in previous studies). However, higher-order networks appeared fragmented, indicating more immature characteristics. These findings reinforce existing knowledge of functional network organization in this developmentally significant yet largely understudied age group.
3. Maternal perinatal depressive symptoms were positively associated with offspring left-amygdala local functional connectivity, especially when depressive symptoms were measured at 3 months postnatally. The association remained significant after controlling for multiple covariates. This finding highlights the potentially long-term effects of exposure to maternal perinatal distress.
4. Maternal sensitivity during infancy, but not during toddlerhood, was positively associated with PFC local functional connectivity. Although the study was limited by its small sample size, the findings provide preliminary evidence for the importance of maternal sensitivity in infancy.

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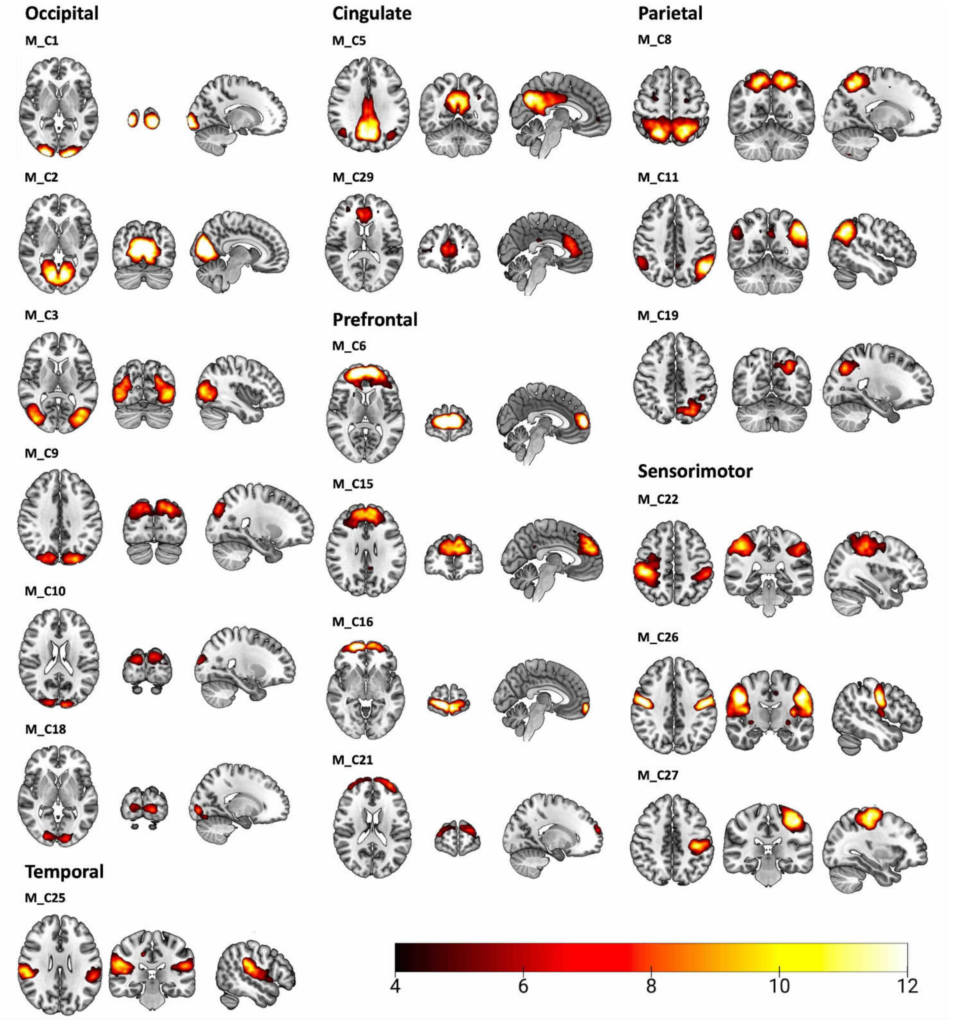
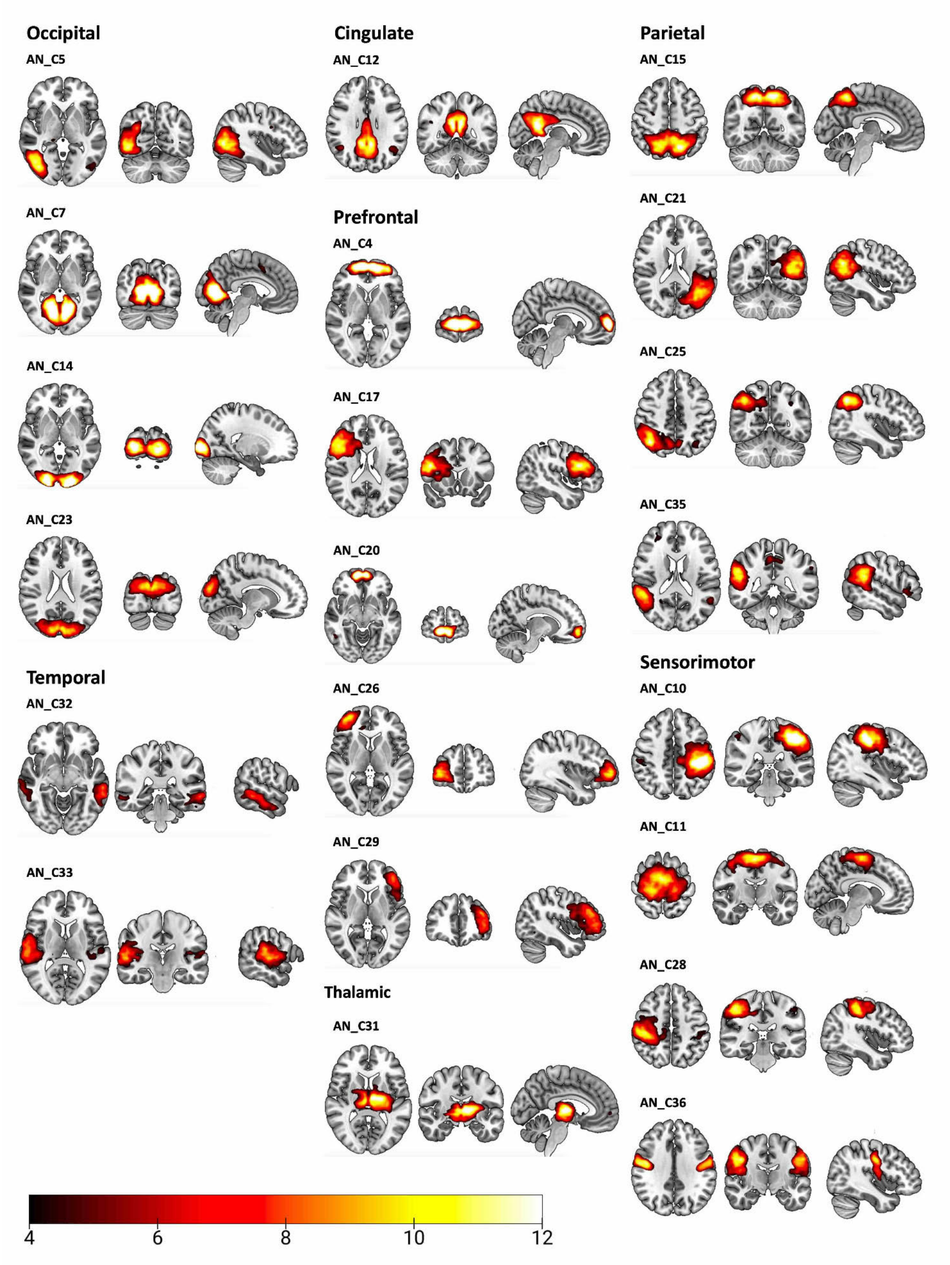
Appendices

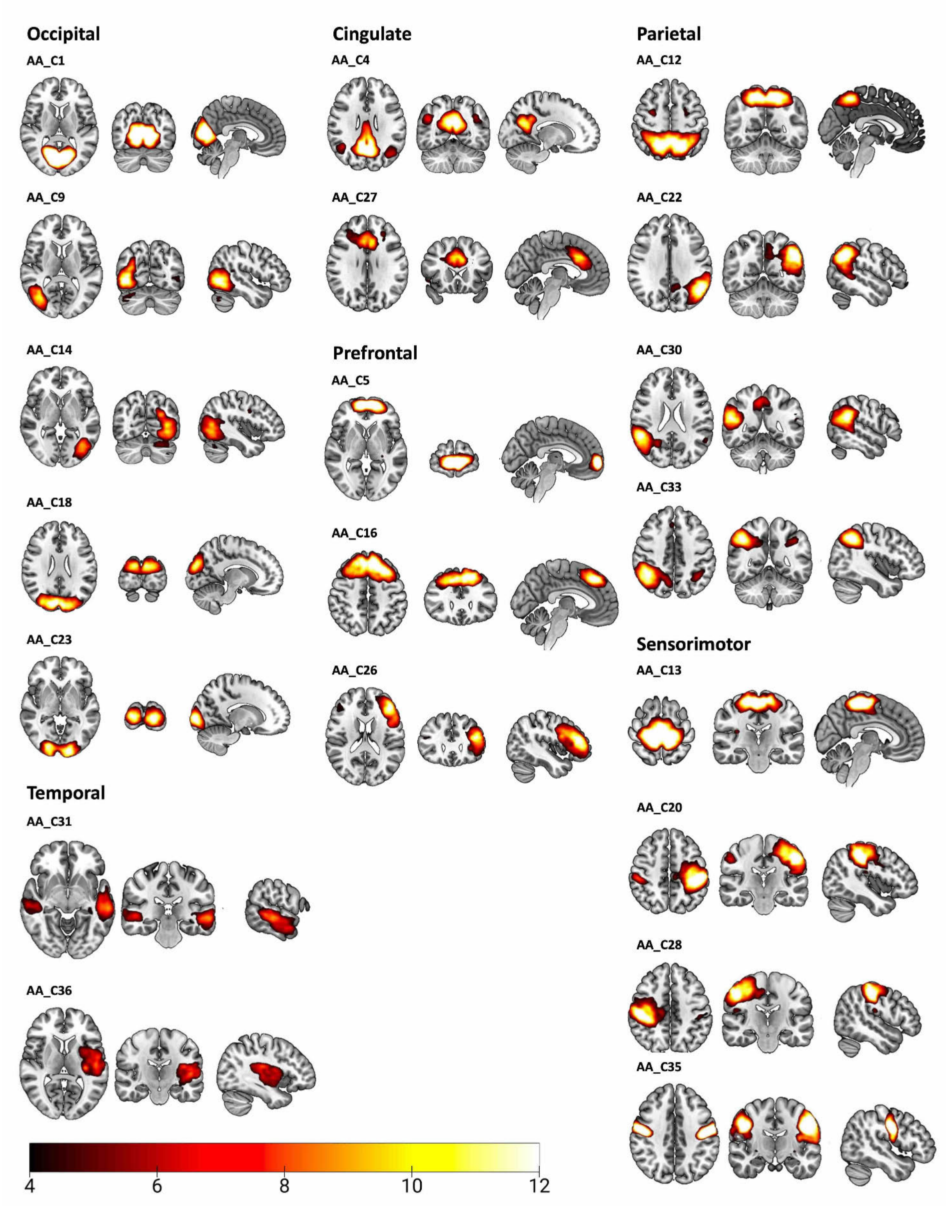
Appendix 1. Components identified by group independent component analysis with manual denoising. Images are shown in the radiological convention on axial, coronal, and sagittal slices, displayed at the most informative levels. The threshold range is 4–12, chosen based on the best visual results. The figure is from Study II (manuscript).



Appendix 2. Components identified by group independent component analysis with non-aggressive AROMA. Images are shown in the radiological convention on axial, coronal, and sagittal slices, displayed at the most informative levels. The threshold range is 4–12, chosen based on the best visual results. The figure is from Study II (manuscript).



Appendix 3. Components identified by group independent component analysis with aggressive AROMA. Images are shown in the radiological convention on axial, coronal, and sagittal slices, and displayed at the most informative levels. The threshold range is 4–12, chosen based on the best visual results. The figure is from Study II (manuscript).



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