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Brain Function in Early Childhood: Individual Differences in Age and Attentive Traits

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Brain Function in Early Childhood: Individual Differences in Age and Attentive Traits

by

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ABSTRACT

Children, like adults, are unique individuals with complex interwoven relationships between brain function, behaviour, and phenotypic traits, which further interact with rapid developmental processes. A nuanced description of variability between children will add to our knowledge of how they think and behave, and potentially advance the development of personalized early interventions. With functional magnetic resonance imaging (fMRI), we have gained insight into brain responses – however, due to practical considerations, we have been unable to render a complete understanding of brain-behaviour relationships in young children. The use of naturalistic stimuli in fMRI studies has increased the ecological validity and the retention of developmental neuroimaging data. In this dissertation, I sought to explore the relationships between age, attentive traits, and inter-individual variability of brain function in young children in naturalistic paradigms.

I conducted a scoping review to synthesize the current and historical task- and naturalistic-fMRI literature on the development of visual processing in the brain, through the lens of two influential theories: the interactive specialization and maturational frameworks. I found that while there is generally a consensus of progressive development of visual brain function throughout childhood, there is not enough evidence to fully support other aspects of these theories.

I also conducted two experiments, using naturalistic fMRI and an analysis technique called inter-subject correlation (ISC), which quantifies the spatiotemporal similarity of brain activity between individuals, to explore how age and attentive traits affect inter-individual variability of brain function in children aged 4-8 years. I found that children's brain responses to

movies "homogenized" with increasing age in our sample, with greater variability seen in the younger children. Further, both inattention and hyperactivity were associated with ISC in the sample, though the relationships with these traits were different in widespread regions of the brain. Together, my research advances our understanding of functional brain responses in children and underscores the importance of an individual differences approach to developmental neuroimaging.

DEDICATION

This dissertation is dedicated to the memory of David Morkem, Ross Morkem, and Roswitha Tansey.

PREFACE

Chapters 2 – 4 of this dissertation are comprised of primary research articles that have been published (Chapters 3 & 4), or are under preparation for publication (Chapter 2). All content from the articles were included with permission from the co-authors, which can be found in **Appendix D**. Below are the references of record for the articles:

Chapter 2:

Tansey, R., Graff, K., Rai S., Merrikh, D., Godfrey, K.J., Vanderwal, T., & Bray, S. Development of visual functional neuroanatomy: A scoping review of task- and naturalistic-fMRI studies through the lens of the interactive specialization and maturational frameworks. *In prep*.

Chapter 3:

Tansey, R., Graff, K., Rohr, C.S., Dimond, D., Ip, A., Yin, S., Dewey, D., & Bray, S. (2023). Functional MRI responses to naturalistic stimuli are increasingly typical across early childhood. *Developmental Cognitive Neuroscience, 62,* 101268. https://doi.org/10.1016/j.dcn.2023.101268

Chapter 4:

Tansey, R., Graff, K., Rohr, C.S., Dimond, D., Ip, A., Dewey, D., & Bray, S. (2022). Inattentive and hyperactive traits differentially associate with interindividual functional synchrony during video viewing in young children without ADHD. *Cerebral Cortex Communications, 3*(1), tgac011. https://doi.org/10.1093/texcom/tgac011

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I started graduate school by moving across the country to a city and province that I was almost entirely unfamiliar with. When I moved to Calgary, I believed that I would stay for only as long as I needed to get a Master's degree before moving on to so-called "bigger and better things." Five years later, I'm amused by the thought that I ever expected to breeze through so nonchalantly. The reward for my assumptions was, of course, for the universe to humble me, but thankfully it did so with kindness. Whatever I was chasing, I finally found it here. This change in attitude could only have been brought about by the support and community I've found, both in the academic and personal spheres of my life.

Firstly, I need to extend my deep appreciation to my supervisor, Dr. Signe Bray. When I stumbled into her lab, I couldn't have imagined how lucky I was to study under her vast expertise. As a mentor, Signe is an unparalleled combination of knowledgeable, dedicated, kind, and understanding. Without her patience and willingness to coach me through all aspects of academia, the ups and (very down) downs, I don't think I would be writing this now. I will always remember and try to emulate her deep commitment to her work, students, and science as a whole. Thank you, Signe, and I hope that we have many chances to cross paths again!

I also wish to thank those who have served on my supervisory committee: Dr. Deborah Dewey; Dr. Ashley Harris; and Dr. Giuseppe Iaria. Thank you for your invaluable advice and contributions to my research which have undoubtedly made me a better scientist, and for flexibly adapting through the many changes and iterations this dissertation went through. Thank you to Dr. Iaria for stepping in quite late in the process and taking it all in stride!

It has been an absolute privilege to be a member of both the Bray Lab and the CAIR community at the Alberta Children's Hospital. I have been very lucky to be a part of such a friendly, collaborative group. Thank you to every one of my lab mates throughout the years for collecting data, providing feedback, and creating such a supportive environment to conduct research in. Thank you to the members of "the Forge" in my first year of grad school for making me feel so welcome. Finally, a special thanks to my lab twin, Kirk Graff, who has shared pretty much this entire experience with me, trial and error-ed his way through this thing called "research?" with me, and who has been an amazing collaborator and friend. And no, I will not go home and have a nap, I have work to do!

In September 2019, at a pretty lonely time in my life, I took a chance and signed up for a volunteer orientation at CJSW, the UCalgary campus radio station. With hindsight, I can now say that was one of the best decisions I've ever made. I can fully credit the CJSW community for showing me the weird, wild, and earnest underground heart of Calgary. Somehow I convinced them to let me play whatever strange music I want every week for two hours, which I will always be grateful for. I can definitively say that without the CJSW community and all the friends I have made from (and indirectly because of) being a part of it, I would have skipped town a long time ago. Thank you to all the staff and volunteers I've interacted with over the years for creating a space where I belong!

Acknowledging all the friends who have been there for me through this whole process would be impossible, and I will inevitably leave people out – however just know that you are in my heart. Thank you to Alexa, Elizabeth, and Jade for being there to lean on through grad school and hard times. Thank you to all my friends here in Calgary for giving me support and the much

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LIST OF ABBREVIATIONS

ABCD	Adolescent Brain Cognitive Development® Study
ADHD	attention deficit hyperactivity disorder
AFNI	Analysis of Functional NeuroImages
ANTs	Advanced Normalization Tools
AV	audiovisual
BOLD	blood oxygenation level dependent
CNS	central nervous system
DAN	dorsal attention network
DMN	default mode network
DSC	Dice similarity coefficient
EBA	extrastriate body area
EEG	electroenecephalography
EPI	echo planar imaging
FA	flip angle
FBA	fusiform body area
FC	functional connectivity
FD	framewise displacement
FDR	false discovery rate
FEF	frontal eye fields
FFA	fusiform face area

FWHM	full width half maximum
fMRI	functional magnetic resonance imaging
FSL	FMRIB Software Library
GLM	general linear model
GM	grey matter
HBN	Healthy Brain Network
HCP-D	Human Connectome Project-Development
HICCUP	University of Calgary Healthy Infants and Children's Clinical Research Program
hMT+	human middle temporal complex
HRF	hemodynamic response function
IFG	inferior frontal gyrus
IPS	intraparietal sulcus
ISC	inter-subject correlation
ITC	inferior temporal cortex
ITG	inferior temporal gyrus
LME	linear mixed effects model
LOC	lateral occipital cortex
MFG	middle frontal gyrus
mFus	medial fusiform
MIST	Multiresolution Intrinsic Segmentation Template
MNI	Montreal Neurological Institute
MRI	magnetic resonance imaging

MTG	middle temporal gyrus
MVPA	multivariate pattern analysis
OPA	occipital place area
PCC	posterior cingulate cortex
pFus	posterior fusiform
PPA	parahippocampal place area
PRISMA	preferred reporting items for systematic reviews and meta-analyses
pSTS	posterior superior temporal sulcus
ROI	region of interest
rs-fMRI	resting state-fMRI
RSC	retrospenial cortex
SFG	superior frontal gyrus
SMG	supramarginal gyrus
SNAP-IV	Swanson, Nolan, and Pelham Questionnaire
STG	superior temporal gyrus
STS	superior temporal sulcus
TD	typically developing
TE	echo time
TPJ	temporoparietal junction
TR	repetition time
VWFA	visual word form area
WM	white matter

CHAPTER 1 – Introduction

1.1. Brain Function in Children

Human cognitive abilities are supported by the structural and functional architecture of the brain. Thoughts, feelings, actions, and consciousness arise from the interactions of billions of nerve cells, called neurons, that make up the central nervous system (CNS). Neurons communicate through the release and transfer of electrical signals and neurochemical compounds at junctions known as synapses, and their activity is supported metabolically by a number of support cells and an intricate vascular network. Throughout brain development, neurons and the other cells that make up the CNS arrange themselves into a complex cortical topography, with functionally specialized regions, circuits, and large-scale networks (Kanwisher, 2010) connected by white matter (WM) tracts. Behaviours, both internal and external, arise from the concerted activity of the CNS. While the gross structure, functional organization, and developmental pathways are largely conserved between individuals, slight differences of neuroanatomy and function can be reflective of distinct behaviours, psychology, and disease pathology (Becht & Mills, 2020; Cui et al., 2020; Finn et al., 2020; Kanai & Rees, 2011; Poldrack et al., 2015). A detailed understanding of how human brain function is linked to phenotypic differences between individuals is imperative to clinical, educational, and psychological efforts (Gratton et al., 2020).

Childhood is an exceptionally important developmental period for the brain and cognition. Differences in brain structure and function in children can be linked to behaviours and outcomes (Johnson et al., 2015; Karipidis et al., 2021; Sanders et al., 2022; Sripada et al., 2020) – however, the nature and directionality of associations between functional brain development and behaviour are still a matter of debate (Azhari et al., 2020; Becht & Mills, 2020; Poldrack,

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2010). Children's thoughts and behaviours do not always resemble those of adults, and their brain function is subsequently unique (Durston et al., 2006; Yates et al., 2021). A period of synaptogenesis in early infancy (i.e., a few months postnatal) is followed by a prolonged period of synaptic pruning that extends throughout childhood and adolescence (Huttenlocher & Dabholkar, 1997; Keunen et al., 2017). This is believed to serve as a consolidation process for specialized functional circuits and networks. Brain development is a reciprocal process between inherited genetic information and individual experiential context, and the process can vary greatly depending on individual differences in a number of phenotypes (Stiles, 2017). All of these factors add increasing layers of complexity to the relationships between brain function and behaviour within the child population.

1.2. Functional Brain Development

As the structure of the brain matures across infancy and childhood, so do its coupled physiological mechanisms. A common theme of functional brain development is the heterochronous maturational trajectories of different regions, usually following a cortical hierarchy that runs from primary sensory processing areas to more integrative associative regions (Chomiak & Hu, 2017; Guillery, 2005; Sydnor et al., 2021). In newborn infants, early visual and sensorimotor intrinsic networks already resemble their adult counterparts, while networks that support higher order cognitive functions are topographically immature (W. Gao et al., 2015; Gilmore et al., 2018). While primary visual processing areas such as retinotopic parts of the visual system are relatively matured at a few months of age (Ellis et al., 2021), category-specific higher order visual responses in the ventral temporal cortex are not yet fully specialized in infancy (Deen et al., 2017). Preschool children show responses to to perceptual listening tasks in

frontal areas related to cognitive control and attention, which are subserved by sensory auditory areas in older children (Brown & Jernigan, 2012). As children mature, sensory networks become more integrated with other functional networks, while higher order association networks become more segregated, a process which supports the development of executive functioning (Keller et al., 2023; Pines et al., 2021). Category-specific visual responses also mature and become more specialized through the school-age and adolescent years (Nordt et al., 2021). Children's brain responses to complex, dynamic movie stimuli become increasingly adult-like between the ages of 3-12 years in higher-order visual areas, such as the precuneus (which is also part of the default mode network [DMN]), the lateral occipital cortex, as well as in the inferior frontal cortex, while adult-like functioning can be seen in early occipital cortex as early as 3.5 years of age (Yates et al., 2021).

1.2.1. Potential Mechanisms of Functional Development

There have been a number of theories posited to explain the developmental mechanisms driving specialization in the brain. Multiple potential pathways could result in the maturation of adult-like neural and cognitive function. Traditionally, developmental cognitive neuroscience approached this question in terms of specialized brain regions that "came online" in concurrence with the development of the related skill or ability (Johnson, 2011). This is referred to as the "maturational" framework of functional brain development. It implies that there should be no BOLD signal change in a nascent specialized region of the brain before its corresponding cognitive ability has emerged. For example, the neural signature for integrating multimodal cues to determine depth in the occipital cortex is not present until children are able to behaviourally perform tasks that rely on this skill, at around the age of 10 years (Dekker et al., 2015). There is

also evidence that the visual word form area (VWFA) in the ventral temporal cortex emerges during the first year of schooling as children are formally taught to read, and it "superimposes" itself in a mosaic-like fashion on the pre-existing functional architecture without altering the topography of other category-specific regions (Dehaene-Lambertz et al., 2018).

Another developmental framework that has been suggested is that of "interactive specialization." Interactive specialization differs from the maturational framework as it posits that during processing and cognition, young children employ spatially diffuse and functionally un-specific brain regions, rather than displaying a total lack of activity in the emerging specialized areas. It suggests that these diffuse responses are eventually reduced and pruned through competitive interactions with other regions to the specialized topography seen in adulthood (Durston et al., 2006; Johnson, 2011). There is evidence for an interactive specialization framework for the development of face processing (de Haan et al., 2002; Joseph et al., 2011), numerical skills (Battista et al., 2018), theory of mind (Richardson et al., 2018) and naturalistic processing of movies (Kamps et al., 2022; Moraczewski et al., 2018). While the piecemeal evidence for the interactive specialization framework is compelling, it is not yet clear if functional brain development broadly follows this pattern.

1.3. Sources of Individual Variation of Brain Function in Young Children

There is substantial heterogeneity in children's brain function, depending on a number of factors, including (but not limited to) developmental stage, early life experiences, personality, and psychopathological traits. Unfortunately, compared to adults, research describing brain function and inter-individual variability in children is relatively limited. This is likely related to a

number of unique practical issues that arise when collecting neuroimaging data from children (Poldrack et al., 2002; Raschle et al., 2012).

In children and adolescents, variability in brain function has been linked to a number of out-of-scanner outcomes and behaviours. Differences in cognitive abilities such as theory of mind (Richardson et al., 2018), arithmetic (Battista et al., 2018; Cantlon & Li, 2013; Kersey et al., 2019), reading (Church et al., 2008; Kersey et al., 2019), and visual integration (Dekker et al., 2015) are reflected in brain function as recorded with fMRI. Psychopathological traits such as depression (Gruskin et al., 2020), anxiety (Ashworth et al., 2021; Gold et al., 2020), and behaviours related to attention deficit hyperactivity disorder (ADHD) (Rohr et al., 2019; Wang et al., 2013) also have been shown to have links to differences in brain function in children. It is imperative that more research is conducted in this area to optimize our understanding and support of children's unique individual needs.

1.3.1. Age

As development plays an important role in functional brain responses, age is a measurable source of inter-individual variability between children. However, children of different ages are often grouped together in studies and compared to older children or adults in order to make a developmental claim. This practice buries the meaningful variability between children, even if otherwise they are considered relatively homogeneous (i.e. they would be sorted into a "typically developing" [TD] or "healthy control" group). Children of different ages can recruit different parts of the brain for the same task, and these age-specific responses can be relatively granular; for example, Hao et al. (2021) delineated unique activity related to an attentional alerting task between children who were only a year apart. Further, brain

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development is often a non-linear process (Bethlehem et al., 2022; Lenroot & Giedd, 2006), which can affect the amount of variability within an age group, even if the range is relatively narrow (i.e. one year). If the pace of change is more rapid in the younger group, that would result in greater variability between the younger children than older children. Differences in inter-individual variability with age have been seen in a number of functional responses, such as those to movies (Cantlon & Li, 2013; Moraczewski et al., 2018, 2020), face processing (Tian et al., 2021), and the topographical localization category-specific visual responses (Scherf et al., 2007).

The literature exploring the relationship between age and between-person variability underscores the need to consider individual differences in developmental cognitive neuroscience research, as group-based analysis methods may obscure an important source of inter-individual variability. Brain function is complex, and we currently have an inadequate understanding of how variation between individuals meaningfully manifests in terms of cognition and phenotypes, such as psychological traits and cognitive abilities. The consequence of this fact, combined with the low signal to noise ratio of fMRI and typically small samples, is that group findings are often insufficiently reproducible and do not generalize well to individuals. This hinders the potential practical applications of fMRI. Clinical advancements will require the ability to identify alterations in brain function that are associated with psychopathology independent of normative variation in age, sex, and other traits.

1.3.2. Attentive Traits

ADHD is a neurodevelopmental disorder with a childhood presentation that often includes age-inappropriate levels of inattention, hyperactivity, impulsivity, and/or distractibility (Cabray, 2018). ADHD is a common condition, with some estimated child and young adult

prevalence rates as high as 8.6% in Canada (Espinet et al., 2022; Morkem et al., 2020).

Researchers conceptualize ADHD as a spectrum disorder, with the dimensional traits of

inattention and hyperactivity/impulsivity lying on a continuum across the general population

(Haslam et al., 2006; Marcus & Barry, 2011; Neuman et al., 1999). There is considerable

heterogeneity in the presentation of ADHD in children, in both the domains of neurocognitive

impairments (sustained attention, working memory, and self-regulation) (Y. Luo et al., 2019) and

developmental symptom trajectories. Generally, hyperactive/impulsive symptoms tend to decline

with age, while inattention symptoms decline only slightly or stay relatively stable (Biederman et

al., 2000; Larsson et al., 2006; Monuteaux et al., 2010; Vergunst et al., 2019).

Due to the dimensional nature of ADHD, symptoms related to inattention and

hyperactivity have impact not only in children with a clinical diagnosis, but also in children who

do not meet current diagnositic criteria, but display elevated subclinical levels of inattention and

/ or hyperactivity. For this reason, it is very important to take a dimensional perspective on

research into attentive traits. Children with subclinical attention problems often experience social

problems in their peer groups (Rielly et al., 2006) and have worse outcomes later in adolescence

and adulthood, such as increased risk of graduation failure (Bussing et al., 2010), and increased

rates physical health, financial, crime, and substance abuse issues (Moffitt et al., 2011).

There are a number of studies that have also linked dimensional levels of inattention and

hyperactivity, in both ADHD and non-ADHD individuals, to variation in brain function. While

these dimensional relationships between attentive traits and brain function in children have yet to

be concretely established, it appears there may be an association between inattentive/hyperactive

behaviours and the DMN). In non-ADHD adults, differences in impulsivity between participants

was reflected in brain responses to movies within the frontal pole, precuneus, posterior cingulate

cortex (PCC), and lateral occipital cortex (LOC), while inattention showed association with brain function during movies in the precuneus only (Salmi et al., 2020). Dynamic functional connectivity (FC) within the DMN and with the somatomotor network is associated with inattention and hyperactivity scores in children aged 6-16 years old, both with and without ADHD (L. Luo et al., 2023), and static FC between the cerebellum and DMN (as well as the dorsal attention network [DAN]) is associated with inattentive and hyperactive traits in non-ADHD girls aged 4-7 years (Rohr et al., 2019). Due to the prevalence and variability of inattentive and hyperactive behaviours in young children, and their potential links to brain function and outcomes even in children without ADHD, attentive traits are a compelling potential source of individual differences that should be explored.

1.4. Functional Magnetic Resonance Imaging (fMRI)

Our understanding of cognitive development in the brain has been accelerated by the advancement of neuroimaging technologies. MRI allows for *in vivo* characterization of the structure, neurochemistry, and function of the human brain. Functional neuroimaging can predict out-of-scanner cognition and behaviour (S. Gao et al., 2019; Ooi et al., 2022), positioning fMRI methods as a powerful technique for understanding psychological development in children.

fMRI harnesses MRI principles in order to give insight into the spatiotemporal nature of activity and processing in the brain. All matter contains subatomic particles called protons that spin (or precess) along an axis. Under regular conditions, the spins of these protons are randomly aligned, with little homogeneity. An MRI scanner subjects an object to a strong, external magnetic field, which aligns proton spins within the same plane, parallel to that of the field. A quick radiofrequency pulse is then applied to the object in the scanner, causing the protons to tilt

into an orthogonal plane. Following the pulse, the protons will naturally relax back to the plane of the magnetic field, letting off energy that can be captured by the scanner as they do so, which is translated into the MR signal. Protons in different tissues relax at varying rates, allowing for the scanner to pick up contrasts between different parts of the body. In the brain, WM, grey matter (GM), and cerebrospinal fluid (CSF) all have distinct properties that allow for their visualisation with MRI (Huettel et al., 2009).

Neuronal activity causes a metabolic demand that is met by increasing the flow of oxygenated blood to the corresponding area of the brain. The oxygenation state of hemoglobin causes a change in its electromagnetic characteristics, allowing blood flow in the brain to be imaged with MRI. There is a 20% increase in the magnetic susceptibility of completely deoxygenated blood when compared to oxygenated blood (Huettel et al., 2009). A specific MR contrast, called T_2*, is sensitive to the levels of deoxygenated blood in the brain. In active regions, oxygenated blood rushes in to meet metabolic demands, which causes a decrease in the concentration of deoxygenated blood in the active area. The resulting signal, referred to as the blood-oxygenation-level dependent (BOLD) signal, gives us an indirect measure of neural activity, and a powerful way to elucidate how the brain processes stimuli (both external and internal). Positive BOLD signals are reflective of this decrease in the concentration of deoxygenated hemoglobin (Hillman, 2014).

fMRI can be conducted under a number of experimental conditions. Typical task-based fMRI studies involve presenting participants with a stimulus and measuring the brain response. In contrast, resting state fMRI (rs-fMRI) is conducted with the subject simply lying in the scanner, without the presentation of any stimulus. The goal of rs-fMRI is often to elucidate the intrinsic activity and connections between areas of the brain that occur spontaneously by

studying functional connectivity (FC) (Van Den Heuvel & Pol, 2011). A middle ground between traditional, highly controlled tasks, and resting-state, are passive viewing or listening paradigms, where the participant freely and naturally experiences the stimulus, which is often rich, dynamic, and can be multimodal, such as movies (Sonkusare et al., 2019).

Due to its relatively high spatial resolution, fMRI one of the best tools for investigating the functional organization of the brain. However, there are a number of reasons why it is difficult to conduct fMRI studies in children, which contributes to the paucity of literature in the developmental neuroimaging field. Participants must lie very still in a supine position for several minutes (length of time is variable depending on the nature of the experiment) in a narrow bore. Additionally, the machine makes loud noises as it completes the scan, adding to the participant's discomfort. fMRI is highly sensitive to head motion, and children exhibit much higher levels of motion in the scanner than adults (Dosenbach et al., 2017). Other potential barriers include the necessity of child-appropriate equipment for the MRI scanner, analytical considerations during data pre-processing such as child brain atlases, and suitability of in-scanner tasks for younger individuals in terms of both skill and interest (Fonov et al., 2011; Luna et al., 2010; Raschle et al., 2012). Recent methodological innovations have improved the retention and success rate of fMRI scanning in young children (Dosenbach et al., 2017; Greene et al., 2018; Horien et al., 2020; Vanderwal et al., 2018), but our knowledge surrounding the development and variability of brain function in children remains limited.

1.5. Naturalistic fMRI and Inter-subject Correlation

1.5.1. Naturalistic Viewing Paradigms

A technique that has gained recent popularity, and can mitigate some of the challenges in developmental fMRI, is the use of naturalistic stimuli within the scanner (Bartels & Zeki, 2004; Hasson et al., 2004). In these experiments, participants are presented with a dynamic stimulus that more closely resembles real-life interactions than typical controlled psychological tasks. Often, a film will be used as the naturalistic stimulus (Sonkusare et al., 2019; Vanderwal et al., 2018); however, other modalities have been implemented (Kauppi et al., 2017; Simony et al., 2016; Wild et al., 2017). Naturalistic stimuli elicit BOLD signal change in widespread networks involved in visual, auditory, language, and emotion processing, as well as spatial navigation and attention (Bottenhorn et al., 2018). There are several advantages to using naturalistic paradigms, including increased ecological validity (Sonkusare et al., 2019). A stimulus that better approximates the real world could allow for greater generalizability of results outside of the laboratory. On the other end of the spectrum, unlike the resting state, which is entirely unconstrained, the stimulus is expected to induce a change in brain activity from the baseline, allowing for the ability to make hypotheses and draw inferences about the relationship between cognition, perception, and brain activity (Finn, 2021). Additionally, movie-watching in the scanner offers unique advantages for developmental neuroimaging. Movies have been shown to reduce head motion in young children when compared to rest (Greene et al., 2018; Vanderwal et al., 2015), and watching a film is an uncomplicated task that is easy for child participants to complete. Several studies have already employed this kind of stimulus to uncover insights into the functioning and development of children's brains (Benear et al., 2022; Cantlon & Li, 2013; Cohen et al., 2022; Di & Biswal, 2022; Kamps et al., 2022; Kersey et al., 2019; Moraczewski et

al., 2018, 2020; Richardson et al., 2018; Richardson & Saxe, 2020; Rohr et al., 2017, 2018, 2019; Vanderwal et al., 2018, 2021; Yates et al., 2021, 2022).

1.5.2. Inter-subject Correlation (ISC)

One way to leverage the advantages of naturalistic movie stimuli during the analysis stage is a technique called inter-subject correlation, or ISC, which was introduced by Hasson et al. (2004). ISC is a way to quantify the spatiotemporal similarity (or "synchrony") of brain responses between individuals exposed to the same naturalistic stimulus. To calculate ISC, the time-course of the response in an area of the brain (voxel, region of interest [ROI], etc.) of one individual is correlated to the time-course in a corresponding area of the brain of another individual (Nastase et al., 2019). ISC is a data-driven, model-free technique that does not rely on *a priori* knowledge regarding functional localization to determine similarities or differences in responses between individuals.

ISC is especially useful when exploring the effect of individual differences of certain characteristics on brain functioning. ISC can be used to describe differences in brain synchronization between groups (Cantlon & Li, 2013; Finn et al., 2018; Kersey et al., 2019; Moraczewski et al., 2018; Salmi et al., 2020), but it can also be used to determine how continuous traits and dimensions are related to differences in brain activity between individuals (Camacho et al., 2023; Finn et al., 2020; Van Baar et al., 2021). Significant differences in neural synchronization based on traits can be detected using a linear mixed-effects model with crossed random effects (LME w/ CRE) (Chen et al., 2017; Finn et al., 2018), which accounts for the high level of interdependence in the data while still allowing for a flexible model design.

1.6. Overview of Thesis Chapters and Hypotheses

Children's brain function is variable and heterogeneous, depending on a vast number of traits and factors. Behaviour and cognition have reciprocal relationships with brain activity that are important to disentangle in order advance our understanding of psychology, mental health, learning, and neurodevelopmental disorders. Methodological and analytical innovations like ISC allow the study of individual differences in brain function and phenotypes. In order to make more nuanced claims about brain function in children, we must understand the role that age and behaviour play in the complexity of brain responses.

In this dissertation, I investigated the associations between brain function and characteristics such as age and attentive behaviours in childhood. Chapters 2 and 3 examined the links between brain function and age, while Chapter 4 explored the relationship between inter-individual variability of brain function and attentive traits. In Chapter 2, I conducted a scoping review of the fMRI literature to synthesize what is currently known about the development of visual processing in the brain. Specifically, I focused on whether the interactive specialization and maturational frameworks of functional development were generally supported in the literature. In Chapter 3, I used ISC to test whether brain responses to movies "homogenize" with age, or whether there are stereotypical age-specific responses across the age range of 4-8 years. I also investigated whether variability in responses between young children is related to more topographically diffuse processing in the brain at younger ages. In Chapter 4, I used ISC in the same sample of children to investigate whether inter-individual variability of brain response was associated with attentive behavioural traits (inattention and hyperactivity). In Chapter 5, I discuss the implications of my findings and outline potential directions of future research. Together, the

aim of this thesis is to shed light on the sources of between-person variability of brain function in young children.

1.6.1. Chapter 2

In Chapter 2 of this thesis, entitled "Development of visual functional neuroanatomy: A scoping review of task- and naturalistic-fMRI studies through the lens of the interactive specialization and maturational frameworks," I conducted a scoping review of the fMRI literature on visual development following the PRISMA-ScR guidelines (Tricco et al., 2018). The final review included 89 articles. From those 89 articles, I collected data on their findings, support for (or against) the developmental theories, sample sizes and demographics, methodologies. I conducted descriptive statistical analyses and visualization of my findings, synthesized the literature, and made recommendations for future research and for the refinement of developmental theories.

1.6.2. Chapter 3

In Chapter 3, entitled "Functional responses during naturalistic fMRI are increasingly typical across early childhood," I used a cross-sectional dataset of $n = 81$ children aged 4-8 years to investigate the associations between inter-individual variability of brain function and age in a early childhood sample. I used pairwise ISC (Hasson et al., 2004; Nastase et al., 2019) in a LME with CRE (Chen et al., 2017) to model whether the association between brain similarity and age was better described by a "homogenization" of brain function, or age-specific responses. We then conducted analyses to determine whether more variability among younger children could be attributed to greater spatial diffusivity of brain response. I hypothesized that we would see a

decrease with age in the volume of the cortex that was associated with the shared component of the brain response with age from the fusiform face area (FFA) and the superior temporal sulcus (STS). We also investigated whether the spatial topography of the response in the same regions of interest (ROIs) showed homogenization or age-specific activity, using the Dice coefficient (Dice, 1945).

1.6.3. Chapter 4

Chapter 4 is entitled "Inattentive and hyperactive traits differentially associate with interindividual functional synchrony during video viewing in young children without ADHD." Again, I used pairwise ISC and a LME with CRE to determine whether inter-individual similarity of brain response was linked to levels of inattention and hyperactivity in children without an ADHD diagnosis aged 4-8 years ($n = 81$). I hypothesized that children with higher levels of inattentive and hyperactive behaviours would have more dis-similar brain responses to one another than children with low levels of those behaviours.

1.7. Statement of contributions

1.7.1. Chapter 2

Chapter 2 has not been published, but will be submitted for publication shortly after defending this dissertation. The authors contributing to the manuscript are Tansey, R., Graff, K., Rai, S., Merrikh, D., Godfrey, K.J., Vanderwal, T., and Bray, S.

Author contributions: <u>Ryann Tansey</u> – Conceptualization, Methodology, Software, Validation, Formal analysis, Investigation, Data curation, Writing – original draft, Writing – review & editing, Visualization; <u>Kirk Graff</u> – Investigation, Writing – editing & review; <u>Shefali</u>

Rai – Investigation, Validation, Writing – editing & review; <u>Daria Merrikh</u> – Investigation, Writing – editing & review; <u>Kate J. Godfrey</u> – Investigation, Writing – editing & review; <u>Tamara Vanderwal</u> – Conceptualization, Writing – editing & review; <u>Signe Bray</u> – Conceptualization, Methodology, Resources, Writing – original draft, Writing – editing & review, Supervision, Funding acquisition.

1.7.2. Chapter 3

Article: Tansey, R., Graff, K., Rohr, C.S., Dimond, D., Ip, A., Yin, S., Dewey, D., and Bray, S. 2023. Functional MRI responses to naturalistic stimuli are increasingly typical across early childhood. *Developmental Cognitive Neuroscience*, 62, 101268.

https://doi.org/10.1016/j.dcn.2023.101268

Author contributions: <u>Ryann Tansey</u> – Conceptualization, Methodology, Software, Validation, Formal analysis, Investigation, Data curation, Writing – original draft, Writing – review & editing, Visualization; <u>Kirk Graff</u> – Methodology, Software, Investigation, Writing – review & editing; <u>Christiane S. Rohr</u> – Investigation, Writing – review & editing; <u>Dennis Dimond</u> – Investigation, Writing – review & editing; <u>Amanda Ip</u> – Investigation, Resources, Writing – review & editing; <u>Shelly Yin</u> – Investigation, Resources, Writing – review & editing; <u>Deborah Dewey</u> – Conceptualization, Resources, Writing – review & editing, Funding acquisition; <u>Signe Bray</u> – Conceptualization, Methodology, Validation, Resources, Writing – original draft, Writing – review & editing, Supervision, Project administration, Funding acquisition

1.7.3. Chapter 4

Article: Tansey, R., Graff, K., Rohr, C.S., Dimond, D., Ip, A., Dewey, D., and Bray, S. 2022. Inattentive and hyperactive traits differentially associate with interindividual functional synchrony during video viewing in young children without ADHD. *Cerebral Cortex Communications*, 3(1), tgac011. https://doi.org/10.1093/texcom/tgac011

Author contributions: <u>Ryann Tansey</u> – Conceptualization, Methodology, Software, Validation, Formal analysis, Investigation, Data curation, Writing – original draft, Writing – review & editing, Visualization; <u>Kirk Graff</u> – Methodology, Software, Investigation, Writing – review & editing; <u>Christiane S. Rohr</u> – Investigation, Writing – review & editing; <u>Dennis Dimond</u> – Investigation, Writing – review & editing; <u>Amanda Ip</u> – Investigation, Resources, Writing – review & editing; <u>Deborah Dewey</u> – Conceptualization, Resources, Writing – review & editing, Funding acquisition; <u>Signe Bray</u> – Conceptualization, Methodology, Validation, Resources, Writing – original draft, Writing – review & editing, Supervision, Project administration, Funding acquisition

CHAPTER 2 – Development of Visual Functional Neuroanatomy: A Scoping Review of Task- and Naturalistic-fMRI Studies Through the Lens of the Interactive Specialization and Maturational Frameworks

2.0. Abstract

Objective: To assess support for the interactive specialization and maturational frameworks of development in task- and naturalistic-fMRI literature across childhood.

Introduction: Overarching theories such as the interactive specialization and maturational frameworks have been proposed to describe human functional brain development. One of the domains with the longest and deepest history of study is visual processing, including early vision and functional representation of higher-order visual categories and features (e.g., faces, places and motion). Studies in this area have recently expanded to include naturalistic paradigms that facilitate study in younger age ranges. Here, we synthesize studies of visual functional development to assess support for these developmental frameworks.

Inclusion criteria: fMRI studies that employ a visual task or naturalistic visual paradigm, that investigate associations between age and functional responses.

Methods: A scoping review of MEDLINE, PsycINFO, Scopus, and Web of Science was conducted. Records were screened and data regarding the methodology, sample, and results were extracted. We determined whether the results supported the interactive specialization or maturational frameworks by determining whether they showed evidence of "progressive" (increases in the magnitude, extent, or specificity of BOLD response in a brain region with age), "regressive" (decreases of the same with age), or "emergent" development (no BOLD response prior to a certain age/in the younger group, with change present after that age/in the older group).

Results: A total of 89 papers were included. We found that across domains many studies reported progressive development, but few studies describe regressive or emergent changes necessary for maturational or interactive specialization frameworks.

Conclusions: Studies were broadly supportive of progressive developmental changes towards more adult-like patterns of responding. However, our findings suggest a need for refinement of models of functional development and clearer reporting of both progressive and regressive changes, along with well-powered, longitudinal studies.

2.1. Introduction

Cognition undergoes rapid and substantial changes across childhood and adolescence, believed to be supported by underlying development of the brain's structure and function (Brown & Jernigan, 2012; Johnson, 2001; Keunen et al., 2017). Neuroimaging techniques have shed light on the developing neural correlates of cognitive and perceptual abilities. fMRI is a non-invasive brain imaging method with relatively high spatial resolution, which has allowed the characterization of the brain's functional organization and how it changes with age. Vision is one of the most studied aspects of human perception and cognition (Himmelberg et al., 2022; Sereno et al., 1995; Tootell et al., 1998; Zaretskaya, 2021), including from the perspective of functional brain development. Indeed, the development of the extended visual system has been studied using fMRI from early functions such as retinotopic organization (Conner et al., 2004; Ellis et al., 2021) to higher-order category-selective visual representations in the ventral (Nordt et al., 2021; Scherf et al., 2007) and dorsal (T. Dekker et al., 2011) streams, and under more dynamic, "naturalistic" visual conditions (Kamps et al., 2022; Yates et al., 2022).

As the field of developmental neuroimaging has emerged and evolved, theories to both account for findings and motivate further study have been advanced. Two important frameworks, the "interactive specialization" framework and its opposing "maturational" framework (Johnson, 2000, 2011), have been important for developmental research. While the maturational framework posits that brain regions are specialized for particular functions and "come online" at certain ages, corresponding with the emergence of their function, the interactive specialization framework hypothesizes that much of the functional architecture of the brain is initially involved in a broad number of behaviours and processes, eventually gaining specificity through competitive, activity-dependent interactions between brain regions (Johnson, 2011). While both

theories require evidence of some kind of "progressive" development, (i.e., increases in BOLD signal magnitude, extent, or specificity with age), the maturational framework suggests that these progressive changes should be evident as the "emergence" of the function (i.e., no change in signal to a stimulus in children before a certain age, but change in response to stimulus apparent in older participants), while the interactive specialization framework necessitates that "progressive" developments are paired also with "regressive" development (decreases in BOLD magnitude, extent, or specificity with age, either to the category of interest in regions that are not typically associated with that function, or to other categories in the region typically associated with the function being studied; e.g. decreased BOLD signal to houses across childhood in a region associated predominantly with faces in adults (Joseph et al., 2011)).

Recently, developmental functional neuroimaging has seen an increase in the use of naturalistic fMRI tasks, which hold many advantages for scanning young children (D. J. Greene et al., 2018; Vanderwal et al., 2015, 2018), and have the potential to complement traditional task designs to probe developing visual functions (Cantlon, 2020). In addition to increasing ecological validity and potentially generalizability of findings (Nastase et al., 2020; Sonkusare et al., 2019), naturalistic fMRI has opened up the study of children as young as pre-school aged (Richardson et al., 2018), as well as infants (Cusack et al., 2018; Ellis et al., 2020; Yates et al., 2021). Given the opportunity for using movie paradigms in studying visual functions and the growth in this literature, it is important to synthesize findings across traditional and naturalistic tasks to identify points of convergence and divergence.

An important consideration in reviewing literature in this field is the advancement of methods over time towards increasing reliability and validity (Gratton et al., 2022; A. S. Greene et al., 2022; Marek et al., 2022; Noble et al., 2022). Problems that have contributed to the

"reproducibility crisis" (Munafò et al., 2017; Poldrack et al., 2017) in neuroimaging include the low study power, due in part to the confluence of inherently low effect sizes (Marek et al., 2022), poor signal to noise ratio (Bianciardi et al., 2009), and small samples (Button et al., 2013; Turner et al., 2018); and the lack of participant diversity, which leads to inaccurate predictions and low generalizability of findings to underrepresented individuals (Ge et al., 2023; A. S. Greene et al., 2022). A number of mitigating strategies have been increasingly used to enhance reproducibility in developmental neuroimaging (Klapwijk et al., 2021), including (but not limited to) increasing sample sizes, stringently controlling for motion, and recruitment of underrepresented populations.

While the interactive specialization and maturational frameworks have been important motivators for investigating visual development (both in task- and movie-fMRI; Joseph et al., 2011; Moraczewski et al., 2018), it is not currently clear whether the literature broadly supports these frameworks, as there has been no systematic synthesis of the currently available research. Further, with a recent focus on improving the methodological quality and reliability of fMRI studies (Elliott et al., 2021; Marek et al., 2022), it is important to assess historical trends of experimental characteristics that could affect data quality in developmental neuroimaging. Finally, with the increasing popularity of naturalistic tasks, it is worthwhile to assess whether there is a consensus between recent work using movie paradigms in younger samples and the findings from more traditional fMRI task-based studies. There are three main objectives to this scoping review:

1. To determine whether the interactive specialization and the maturational frameworks of visual functional brain development have support in the fMRI literature, across different

visual domains (early visual processing, category-specific visual processing, and naturalistic visual processing).

2. To assess the quality of fMRI studies of visual development (sample sizes, sample demographics, and strategies to control for motion contamination of data).

3. To synthesize the findings from traditional task- and movie-fMRI studies and determine whether there is complimentary support across experimental paradigms for models of functional brain development.

2.2. Methods & Materials

This scoping review followed methodological recommendations from the PRISMA-ScR (Preferred Reporting Items for Systematic Reviews and Meta-Analyses extension for scoping reviews) guidelines (Tricco et al., 2018) and the Joanna Briggs Institute Manual for Evidence Synthesis (Peters et al., 2020), based on the framework proposed by Arksey and O'Malley, 2005, and Levac et al., 2010. A protocol for this scoping review was pre-registered and can be found online (https://osf.io/yjck4/).

We note that while the gold-standard for developmental studies remains longitudinal designs that can detect individual trajectories (Lindenberger et al., 2011; Louis et al., 1986), a high number of neuroimaging studies are designed to find associations with age in a cross-sectional sample, due mostly to cost and other practical issues that arise in fMRI studies. While we acknowledge that truly "developmental" studies collect data longitudinally, for the sake of communication, in this review, we refer to both studies and findings from longitudinal and age-association cross-sectional studies as "developmental."

2.2.1. Deviations from Pre-registered Protocol

The original intention for the scoping review was to investigate the development of both visual and auditory functions, and the database searches formulated for the review reflect this aim. However, partway through the screening process, it became clear that the scope of the project was too large, and it was decided that the scoping review would focus on development of visual functions only. The inclusion and exclusion criteria were revised at the full-text screening stage to reflect this decision. Further, the reference lists of the final included studies were not examined for potential related studies, as was originally outlined in the protocol, due to the large number of studies included in the final review.

2.2.2. Inclusion Criteria

The inclusion criteria was developed using the "Participant, Concept, Context" (PCC) framework as outlined by the Joanna Briggs Institute (Peters et al., 2020). Because of the decision to limit the scoping review to only visual studies, the inclusion criteria at the search stage were different than the inclusion criteria used at the full text screening stage. The "Concept" part of the inclusion criteria was revised following the change in protocol; the original "Concept" is listed below in italicized text.

Participants: We will include any peer-reviewed primary studies that focus on children and adolescents (ages of 0-18 years). Longitudinal studies where the baseline age is 15 years or younger and the upper age limit is 18 years or younger will be included. Studies that compare children to adults will be accepted if the child group is younger than 18 years of age.

Concept (original): The scoping review will focus on peer-reviewed studies that investigate higher-order (i.e., category-specific) visual function and language function. Both longitudinal and cross-sectional studies will be included.

Concept (revised): The development of visual function (early visual function, category-selective visual function, and naturalistic visual function) in human infants, children, and adolescents. Both longitudinal and cross-sectional studies will be included.

Context: We will only include papers that use fMRI to investigate the aforementioned participants and concepts.

Types of sources: We will include only primary sources in this scoping review.

2.2.3. Exclusion Criteria

Similarly to the inclusion criteria, the exclusion criteria used at the search and initial screening stage were different than the final exclusion criteria used in the full text screening stage.

Following the modification of the protocol, a fifth point was added to the exclusion criteria (along with some wording clarifications to the original exclusion criteria in points 2 and 3):

1. Secondary sources (i.e. narrative, systematic, and scoping reviews and meta-analyses)

2. Studies that did not use task-based stimulation of some kind (i.e., resting-state fMRI studies)

3. Studies where functional connectivity is the only functional brain metric analysed (i.e., no "task" effects reported)

4. Case-control clinical studies that do not include an association with age in the control group

5. Studies that did not look at the visual domain (i.e., studies that focused on auditory or language development, or other cognitive domains)

2.2.4. Search Strategy

We searched the following databases for relevant articles: Ovid MEDLINE, Ovid PsycINFO, Web of Science, and Scopus. An academic health sciences librarian at the University of Calgary was consulted to develop the search terms and search strategy. Specific searches and search terms are included in the **Appendix A1-A4**. The databases were accessed on November 8, 2022.

2.2.5. Source Selection

We used Covidence review management software to conduct this scoping review. The abstract screening team was made up of four independent reviewers (R.T., D.M., K.G., and K.J.G.). R.T. screened all abstracts, and D.M. and K.G. provided a second vote on half of the abstracts each. In the case of a disagreement regarding an abstract, a third reviewer broke the tie (this reviewer was K.G. for abstracts that had initially been voted on by R.T. and D.M., and K.J.G. for abstracts that had initially been voted on by R.T. and K.G.). Screeners reviewed the abstract, title, and keywords to determine whether the article should advance further in the screening process.

Articles that passed initial abstract screening moved forward to full-text review. Full-text review was conducted by R.T. and K.G. In this stage of the source selection, the reviewers

examined the entire text of the articles to determine whether they fit the inclusion criteria. In the case of disagreements, the conflict was discussed by R.T. and K.G. and a consensus was reached as to whether the article was included or excluded.

2.2.6. Data Extraction

The data extraction form is included in **Appendix A5**. The data extraction was conducted by R.T., and the data extraction was checked for accuracy by S.R. in Covidence, by going through all the data extraction forms filled out by R.T., checking them against the original articles, and correcting where necessary. The final, verified versions of the data extraction forms were used in analysis and presentation of the results. In brief, data was extracted from the sources summarizing the participant demographics, the visual domain studied, the paradigm/task-design, the pre-processing and statistical analysis methods of the neuroimaging data, the key findings, the brain regions with significant findings, and whether interactive specialization and/or the maturational framework were explicitly tested or discussed ("developmental theories tested" and "developmental theories supported by findings").

2.2.6.1. Demographics. Both total sample size and the number of child participants and adult participants per sample were recorded. Sample country of origin, ethnicity distribution, and socioeconomic characteristics were recorded if listed. It was also noted if a study did not report the ethnicity or socioeconomic characteristics of their sample.

2.2.6.2. Visual Domain. Visual function has been studied through different categories of stimuli, designed to elicit processing in early visual regions, and downstream motion-sensitive or category-specific regions. Naturalistic visual stimuli (i.e., movies) can engage many of these regions by nature of the movie content. In the data extraction stage, R.T. categorized each study

by nine stimulus categories based on the description of the stimuli and contrasts. This categorization was included in the verification step of the data extraction conducted by S.R. A study was counted towards each domain if the authors reported using stimuli and an associated statistical contrast; studies that included multiple categories in separate contrasts could count towards more than one domain.

2.2.6.2.1. Early visual processing. Studies included in this category used stimuli such as flickering lights or checkerboards designed to evoke activity in early visual regions (i.e. V1, the calcarine sulcus), or looked at the processing of low-level visual properties, such as luminance.

2.2.6.2.2. Visual motion. Studies included in this category included stimuli and contrasts to measure response to visual motion (e.g., random dots in motion > static dots), motion coherence (e.g.., the detection of forms from systematic motion) or biological and/or social motion.

2.2.6.2.3. Non-affective faces. Studies included pictures or short dynamic video clips of isolated faces that included only neutral expressions.

2.2.6.2.4. Affective faces. Studies included pictures (or videos?) of isolated faces that varied in emotional expressions. These studies contrasted different emotional expressions.

2.2.6.2.5. Objects. Studies included pictures of manmade objects (e.g. shoes, toys, cars), abstract objects, or tools.

2.2.6.2.6. Scenes. Studies included pictures of outdoor and indoor scenes, and houses.

2.2.6.2.7. Bodies/limbs. Studies included stimuli that depicted images of headless bodies or isolated limbs.

2.2.6.2.8. Characters/symbols. Studies included stimuli that represented characters and symbols such as letters, numbers, or abstract symbols.

2.2.6.2.9. Naturalistic/movies. Studies were included in this category that employed a passive viewing paradigm and dynamic, continuous clips from narrative stories (both clips from longer narratives, such a features films, as well as short films in their entirety). It should be noted that some of the traditional task studies also employed videos or moving images (i.e. stimuli with moving facial expressions rather that static images). However, to be considered a naturalistic/movie task, the clips had to have a larger context, such as a narrative and include more features (background or otherwise) than isolated stimuli in traditional tasks would.

2.2.6.3. Experimental Methodology. In order to minimize the spurious effects of motion, it is considered best practice to statistically control for movement during the pre-processing stages using regression of motion parameters (Engelhardt et al., 2017) and censoring of high-motion volumes, and excluding participants with unacceptably high levels of motion (Ciric et al., 2017, 2018; Graff et al., 2022; Parkes et al., 2018). Use (or omission) of head motion controls at the participant level (i.e. exclusion) and/or at the statistical level were noted, along with the preprocessing steps reported in the studies.

2.2.7. Analysis and Presentation of Results

A screening flowchart was created using the *PRISMA2020* toolbox (Haddaway et al., 2022). Descriptive statistical analyses of the data (as seen in **Tables 2.1 & 2.2** and **Figures 2.2-2.4**) were conducted using custom scripts in Python, using the *Pandas*, *Matplotlib*, and *Seaborn* packages. Each visual sub-domain was investigated separately, to account for the potential scenario where certain sub-domains had a maturational framework of development, whereas others had evidence of an interactive specialization framework. Main findings and

methodological characteristics of each study within each visual domain were summarized following data extraction.

Next, it was determined whether the findings from each study were supportive of the maturational and/or interactive specialization frameworks (as seen in **Appendix A6**). Three features were considered, which in specific combinations could show evidence for one of these frameworks. These features were based on the sub-hypotheses as outlined in Joseph et al. (2011). We assessed evidence for "progressive" development (i.e., increasing BOLD contrast amplitude/volume of significant clusters for a function with age; an underlying hypothesis common to both the theories); evidence for "regressive" development (i.e., a decrease of BOLD contrast amplitude/extent of significant clusters with age, or loss of statistically significant response in brain regions that are not typically associated with the domain in adults with age); and evidence of "emergence" of a function (i.e., no suprathreshold BOLD contrast in participants before a certain age, or presence of a significant cluster in an adult group that was not present in the child group). If a study had both "progressive" and "regressive" findings, it was classified as supporting the interactive specialization framework; if it had "progressive" and "emergent" findings, it was classified as supporting the maturational framework; if it showed only "progressive" findings, it was classified as "progressive development"; and if findings did not show any of these patterns or there were no significant associations with age, it was categorized as "insufficient evidence" (Joseph et al., 2011).

2.3. Results

2.3.1. Search Results

The search results are summarized in the PRISMA-style flow chart in **Figure 2.1**, created

with the _PRISMA2020_ tool (Haddaway et al., 2022). The initial search yielded 9267 abstracts

after the removal of duplicates. Following the abstract screening, 8891 abstracts were excluded,

leaving 376 articles for full-text screening. Of these articles, 2 were unable to be retrieved due

unavailability of an English version of the document, and following full-text screening, a further

285 were excluded. After updating of the inclusion/exclusion criteria, 75 of these were excluded

because they focused on studying auditory and/or language development. For the remaining

excluded studies, the main reason for exclusion was use of a task designed to study a non-visual

function (e.g., executive function; $n = 91$), followed by not investigating the effect of age within

non-clinical participants (i.e., the study compared a clinical group to a control group, and did not

examine the effects of age within the "healthy control" group; $n = 66$). "Wrong study design"

referred to studies that were focused on non-relevant experimental paradigms, brain metrics,

and/or acquisitions states, such as functional connectivity, resting state, or structural studies. The

final number of studies included in the review after full-text screening was 89.
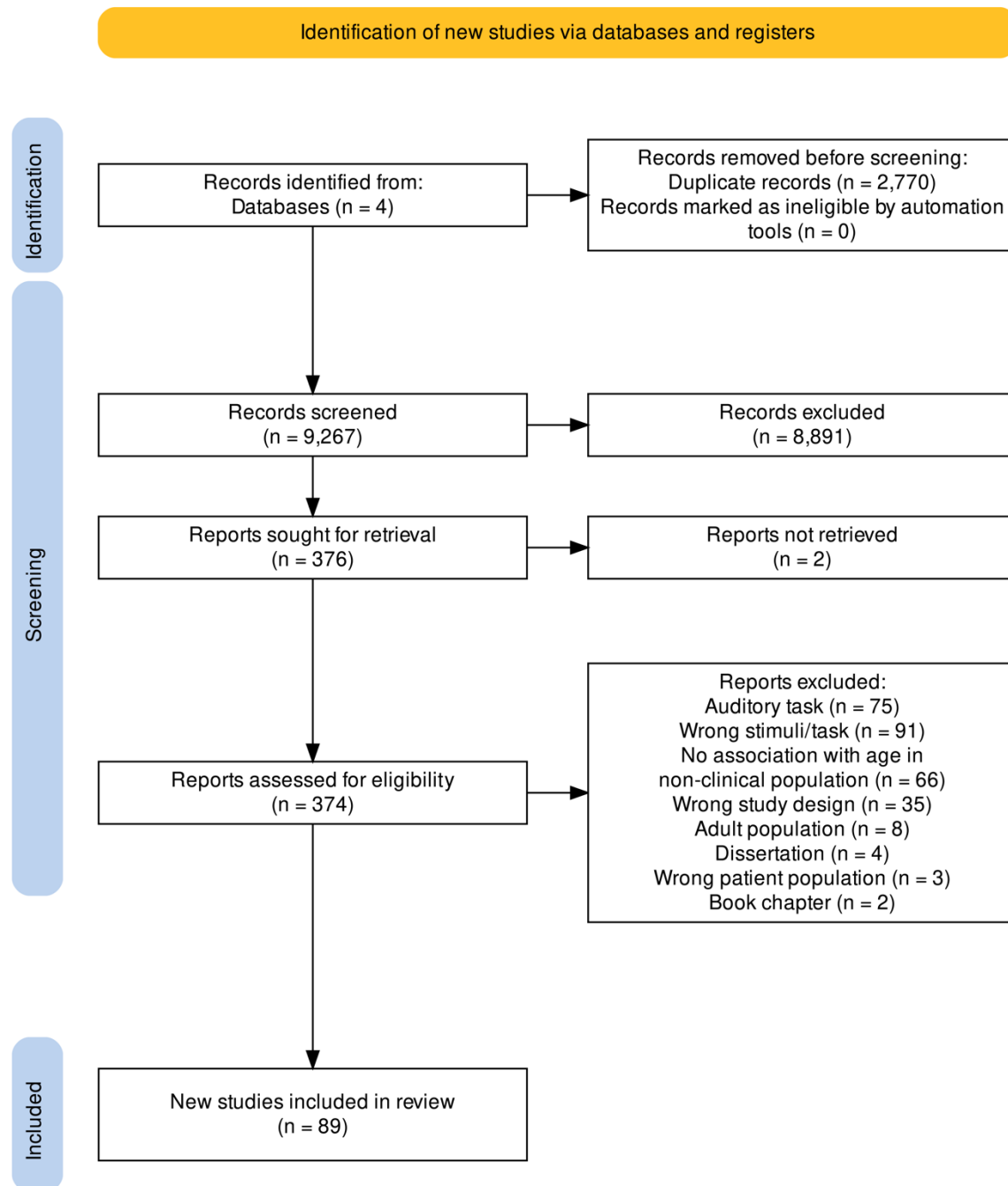
Figure 2.1. PRISMA flow chart of study identification and screening procedure.

Created with the *PRISMA2020* tool (Haddaway et al., 2022).

2.3.2. Study Characteristics

A table outlining the experimental characteristics of the studies included in the review can be found in **Table 2.1**. As most studies included stimuli from multiple visual categories, the frequency counts of the studies in each category do not add up to 89. Most of the studies investigated face processing (59.6%), followed by objects (29.2%). In terms of paradigm, the vast majority of studies employed traditional task paradigms (83.1%), of which, a block design was the most popular. Only 11 studies (12.5%) employed a naturalistic paradigm, and 7 (7.9%) used a hybrid task / naturalistic paradigm (i.e., a block design with video clips in each experimental block). Two studies engaged participants in both a traditional task paradigm and a naturalistic paradigm. Most studies were cross-sectional (95.5%).

The studies were assessed for whether they supported the underlying hypotheses of the interactive specialization and the maturational frameworks. The summary of all the studies' findings in relation to these two theories can be found in **Appendix A6**. For a more detailed summary of the specific findings of each study, refer to **Appendices A7-A15**, which are grouped by sub-domain, as is **Appendix A6**.

Table 2.1. Experimental characteristics of studies included in the final review.

Study characteristic	Number of studies (%)
Domain studied	
Early visual processing	12 (13.5%)
Faces	53 (59.6%)
Non-emotional	24 (27.0%)
Emotional	29 (32.6%)
Objects	26 (29.2%)
Scenes	19 (21.3%)

Bodies	6 (6.7%)
Characters/symbols	8 (9.0%)
Motion	11 (12.4%)
Naturalistic visual processing (movies)	11 (12.4%)
Other	17 (19.1%)
Paradigm	
Traditional task	74 (83.1%)
Block design	58 (65.2%)
Event-related design	13 (14.6%)
Hybrid block/event-related design	2 (2.3%)
Not specified	1 (1.1%)
Naturalistic	11 (12%)
Hybrid	7 (7.9%)
Cross-sectional or longitudinal design	
Cross-sectional	85 (95.5%)
Longitudinal	4 (4.5%)
Participant state	
Awake	88 (99.0%)
Asleep (no sedation)	1 (1.1%)
Sedated	3 (3.4%)

2.3.2.1. Sample Size & Demographics. In terms of sample demographics, the majority of samples were drawn from North America (69.7%), followed by Europe (28.1%). Only 2 studies included samples from Asia (one from Japan and one from China), and no studies included samples from Africa, Oceania, or South America. Only 9 studies (10.1%) reported the ethnicity of their samples, and only 2 studies (2.3%) reported the socioeconomic status.

Demographic characteristics of all studies included in this review are summarized in **Table 2.2**.

The median total sample size (the number of participants, across all age groups, included in a

study) was $n = 32$ (**Figure 2.2**), and the sample sizes increased significantly in size over the time

period between the earliest and the most recent studies (1998-2022; Pearson's $r = 0.34$; $p =$

0.001; **Figure 2.3**). All studies with over 100 participants ($n = 4$) were published in 2020 or later.

Table 2.2. Demographic characteristics of the studies included in the review.

Sample characteristic	Number of studies (%)
Location of sample	
Africa	0 (0.0%)
Asia	2 (2.3%)
Europe	25 (28.1%)
Oceania	0 (0.0%)
North America	62 (69.7%)
South America	0 (0.0%)
Ethnicity	
Recorded	9 (10.1%)
Not recorded	80 (89.9%)
Socioeconomic status	
Recorded	2 (2.3%)
Not recorded	87 (97.8%)
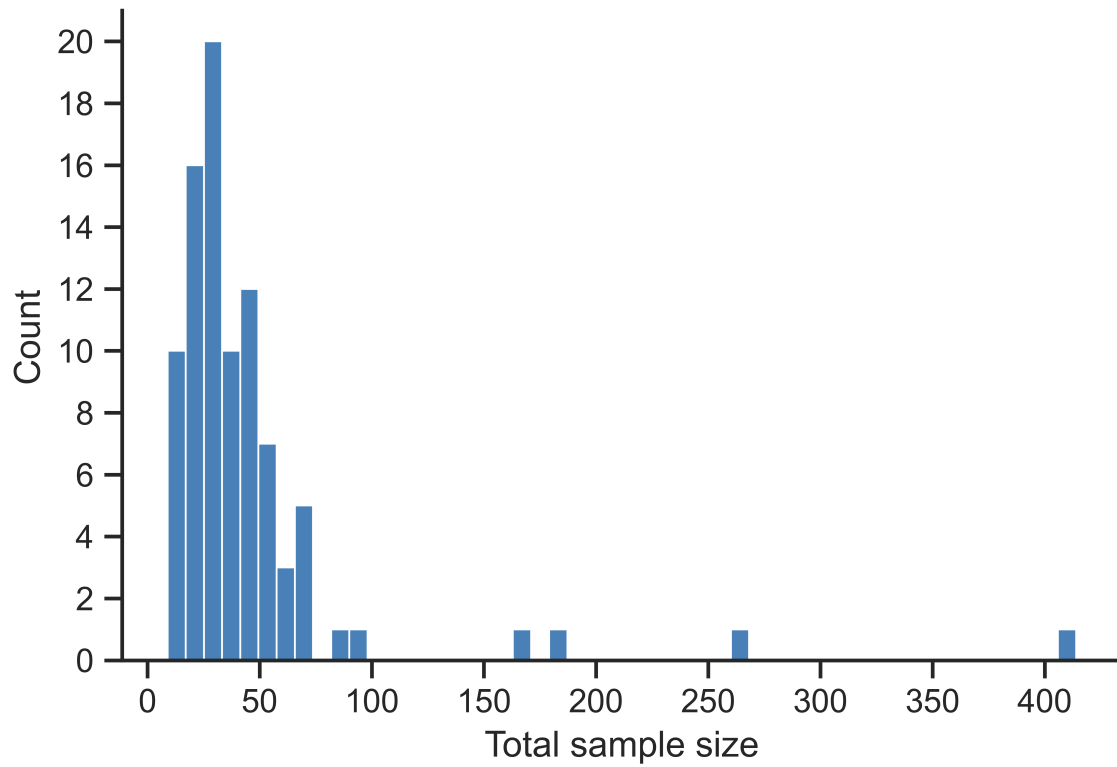
Figure 2.2. Histogram of the total sample size of the included studies.

The median sample size of the studies included in the review is $n = 32$.
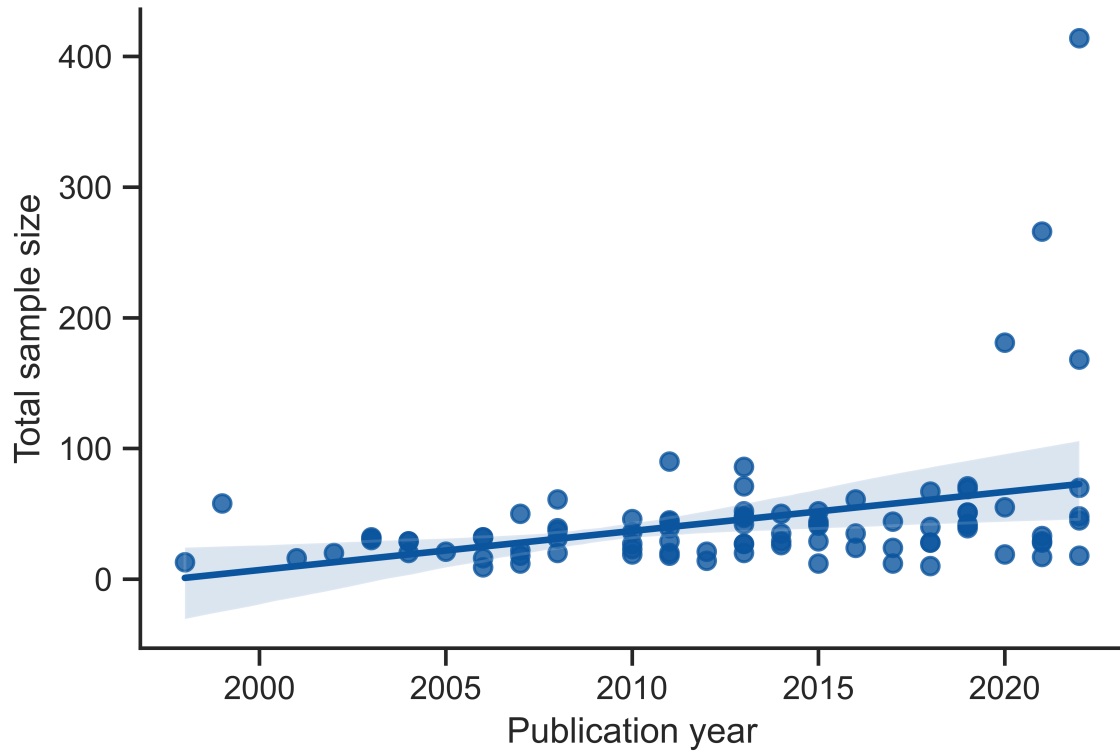
Figure 2.3. Scatterplot of total sample size by publication year.

Regression line is included for visualization purposes. Publication year and total sample size are correlated at a Pearson's *r* of 0.34 ($p = 0.001$).

2.3.2.2. Head Motion Mitigation. The majority of studies ($n = 76$) implemented at least one head-motion mitigation strategy, though a non-negligible number did not implement (or at least, report) either ($n = 13$). Of the studies that only reported implementing one kind of motion mitigation strategy, exclusion-based strategies ($n = 42$) were more popular that statistical control strategies ($n = 5$); 29 studies utilized both. Motion control strategies are visualized in **Figure 2.4**.
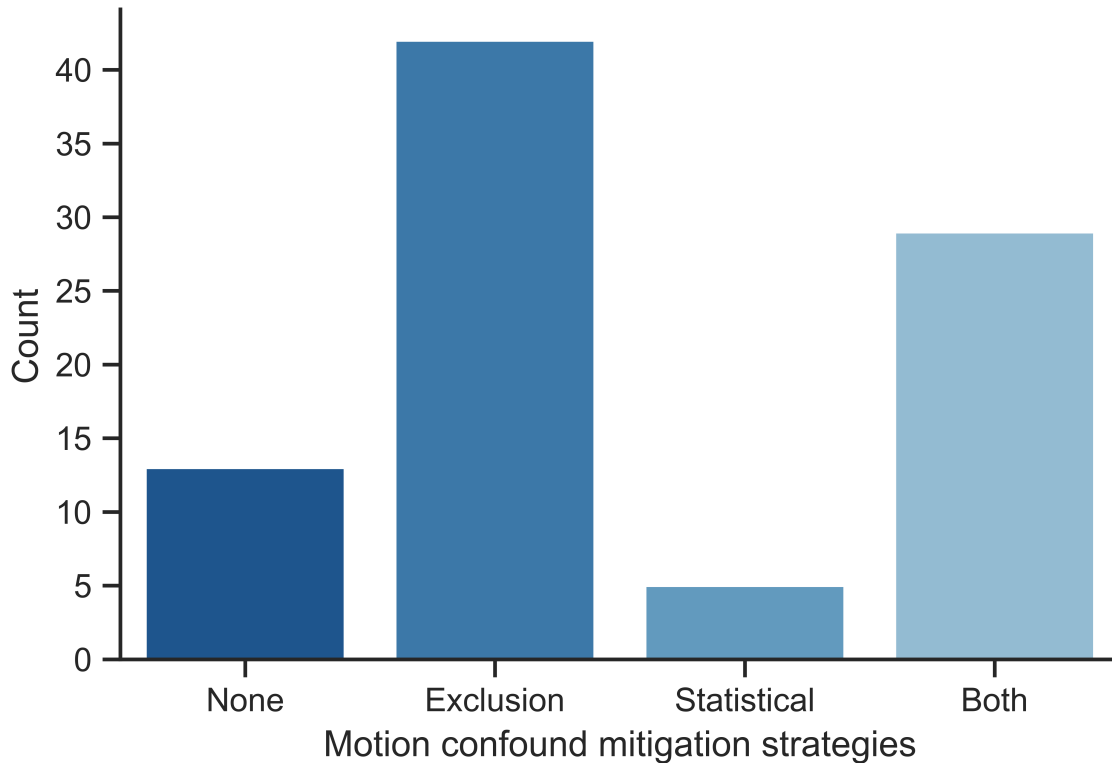
Figure 2.4. Bar chart of motion control strategies.

"Statistical" control strategies include motion censoring, interpolation, and/or including head

motion parameters in a general linear model (GLM) or confound regression. "Exclusion" refers

to whether the authors set a threshold for motion (i.e., average framewise displacement), and

excluded participants with motion above this threshold. "Both" refers to studies that

implemented both exclusion-based and statistical control-based motion mitigation strategies,

while "None" refers to studies that had neither.

2.3.3. Support for Developmental Models

2.3.3.1 Early Visual Processing. Studies of early visual processing were generally

concerned with responding in retinotopic primary and secondary visual cortices, i.e. areas V1,

V2, and V3 (Wandell et al., 2007). Twelve studies focused on early visual processing

(summarized in **Appendix A7**). Of these, half investigated responses to photic stimulation, either in the form of a flickering light or a flickering checkerboard (Born et al., 1998; Kang et al., 2003; Martin et al., 1999; Muramoto et al., 2002; Richter & Richter, 2003; Wenger et al., 2004). Three studies employed retinotopic mapping tasks (Ellis et al., 2021; Gomez et al., 2019; Kim et al., 2021). The 2 remaining studies focused on BOLD response to luminance forms (Bucher et al., 2006) or depth cue integration (T. M. Dekker et al., 2015), respectively. The sample sizes of the studies ranged from $n = 13$ to $n = 58$. All studies were cross-sectional. Collectively, the child samples in the 12 studies covered an age range from 1 day old (Martin et al., 1999) to 17 years of age (Bucher et al., 2006) with no gaps in age coverage.

Generally, these studies found that the coarse functional organization of the occipital cortex supporting early visual processing was in place early in infancy (Born et al., 1998; Ellis et al., 2021), with little to no difference between young children (i.e., 6-9 years of age) and adults (Kang et al., 2003; Richter & Richter, 2003; Wenger et al., 2004). Any continuing developments that occurred throughout infancy and childhood were described as subtle processes of progressive fine-tuning (Ellis et al., 2021; Gomez et al., 2019; Kim et al., 2021). A notable exception was the development of depth cue integration; both the perceptual ability to determine depth from different sensory cues and the corresponding neural response pattern in V3b were found not to emerge until around 10.5 years of age (T. M. Dekker et al., 2015), which fits within a maturational framework (Johnson, 2011; Joseph et al., 2011). Unlike the earliest stages of visual perception, which are mostly established in very early life, integrative and associative sensory processes may undergo maturation into middle childhood (T. M. Dekker et al., 2015), though more confirmatory research is needed.

2.3.3.2. Face Processing. Face processing was the most studied visual domain in the literature reviewed. A total of 53 of studies included face stimuli. Over half of these studies (29) were focused on affective face processing, while the remainder were concerned with the functional organization of face-processing. The non-affective studies are summarized in **Appendix A8**, while the studies with a focus on emotional faces are summarized in **Appendix A9**.

2.3.3.2.1. Non-affective Face Processing. Core face processing regions typically include the fusiform face area (FFA) in the lateral fusiform gyrus, the occipital face area (OFA) in the inferior occipital gyrus, and the posterior superior temporal sulcus (pSTS), while areas of the extended face processing system encode information about person knowledge (the anterior temporal cortex and paracingulate cortex, the temporoparietal junction (TPJ), and the precuneus) and emotion (the amygdala, insula, and striatum) (Gobbini & Haxby, 2007; Haxby et al., 2000). Of the 24 studies that looked at non-affective face processing, the sample sizes ranged from $n = 10$ to $n = 266$. Only 2/24 studies looked at longitudinal developmental trajectories (Dehaene-Lambertz et al., 2018; Nordt et al., 2021). Of the studies included in this category, there is one study that looks at children aged 3-8 months (Deen et al., 2017), and collectively, the rest of the studies have overlapping sample age ranges that span from 3 to 18 years, but there are gaps between infancy and 3 years, and before 3 months of age.

Children showed responses selective to faces at ages as young as 3 months (Deen et al., 2017). Only 3 studies did not find any significant associations between age and face processing; one longitudinally over the first year of formal schooling, corresponding to approximately 5-7 years of age (Dehaene-Lambertz et al., 2018), and two that looked at children older than 10 through to the end of adolescence (Dalton et al., 2007; Keulers et al., 2019). The majority of

studies that did detect developmental effects found progressive changes in the magnitude, extent, and/or selectivity of BOLD response (Aylward et al., 2005; Cantlon et al., 2011; Deen et al., 2017; Gathers et al., 2004; Golarai et al., 2007, 2017; Jiang et al., 2014; Joseph et al., 2006, 2011, 2015; Natu et al., 2016; Nordt et al., 2018, 2021; O'Hearn et al., 2011; Passarotti et al., 2003; Scherf et al., 2007, 2014; Vuontela et al., 2013). Of these studies, 8 also found evidence of regressive associations (Deen et al., 2017; Gathers et al., 2004; Joseph et al., 2011; Kamps et al., 2022; Nordt et al., 2021; Passarotti et al., 2003; Scherf et al., 2007; Vuontela et al., 2013), indicative of an interactive specialization framework, while only one found an "emergence" of preferential face processing in the fusiform face area (FFA) at around 9 years of age, which is evidence for the maturational framework (Joseph et al., 2015). Based on the collective evidence, the maturational framework of functional development does not appear to be the mechanism driving changes in face-processing across childhood. There is not a consensus on the interactive specialization framework, either, although most studies in this domain did find evidence for at least progressive development. Face-processing also became more "adult-like" (a progressive change) and more similarity between individuals with increasing age, both under naturalistic conditions (Kamps et al., 2022) and when using a more traditional task paradigm with dynamic face stimuli (Tian et al., 2021).

  2.3.3.2.2. Affective (Emotional) Face Processing. The emotional aspects of face processing involve the extended face network in the amygdala and insula (Gobbini & Haxby, 2007; Haxby et al., 2000). There were a total of 29 studies that investigated emotional face processing, with sample sizes from $n = 12$ to $n = 181$. Only 1 of the studies in this category was longitudinal (van den Bulk et al., 2013). Combined, the studies in this category covered an age range of 3-18 years, with no coverage earlier than 3 years of age.

A prominent trend amongst the developmental neuroimaging literature in affective facial processing were regressive findings, specifically, a decrease in BOLD signal to emotional faces with age, with children and adolescents often showing greater change in BOLD signal than adults, especially in areas of the extended face network (Gobbini & Haxby, 2007; Haxby et al., 2000), such as the amygdala (Gee et al., 2012; Guyer et al., 2008; Hoehl et al., 2010; Killgore & Yurgelun-Todd, 2007, 2010; Sahraei et al., 2022) and the insula (Pagliaccio et al., 2013; Sahraei et al., 2022). Regressive relationships were also found in areas of the prefrontal cortex when viewing emotional faces (Pagliaccio et al., 2013; Wu et al., 2016), as well as in the fusiform gyrus (Guyer et al., 2008), and the lingual gyrus and the temporoparietal junction (Kryza-Lacombe et al., 2019). While some studies did show progressive changes in BOLD response (Blair et al., 2011; Cohen Kadosh, Johnson, Dick, et al., 2013; Cohen Kadosh, Johnson, Henson, et al., 2013; Garrett et al., 2012; Gee et al., 2012; Killgore & Yurgelun-Todd, 2007; Todd et al., 2011; Yurgelun-Todd & Killgore, 2006), a substantial number of studies also found no significant associations with age (Hildesheim et al., 2020; Maheu et al., 2010; Monk et al., 2008; Perlman et al., 2013; Rahko et al., 2010; Scherf et al., 2015; van den Bulk et al., 2013; Weng et al., 2011). In summary, none of the affective face processing studies showed evidence of an "emergence" of this function; however, a few did show both progressive and regressive associations that suggest an interactive specialization framework (Cohen Kadosh, Johnson, Henson, et al., 2013; Gee et al., 2012; Killgore & Yurgelun-Todd, 2007), and there is some evidence to generally support progressive changes, though this is not ubiquitous (Blair et al., 2011; Cohen Kadosh, Johnson, Dick, et al., 2013; Cohen Kadosh, Johnson, Henson, et al., 2013; Garrett et al., 2012; Gee et al., 2012; Killgore & Yurgelun-Todd, 2007; Todd et al., 2011; Yurgelun-Todd & Killgore, 2006).

2.3.3.3. Object Processing. Object-specific processing has been localized to the posterior fusiform/occipitotemporal sulcus (Grill-Spector & Weiner, 2014), as well as the lateral occipital cortex (LOC) (Grill-Spector et al., 1998). While a substantial number of studies ($n = 26$) included objects as stimuli in their paradigms, many ($n = 10$) of those only used objects as a contrast for faces or other categories, and did not analyze object-specific BOLD responses (Cantlon et al., 2011; Haist et al., 2013; Joseph et al., 2006, 2011, 2015; Nordt et al., 2018; Ross et al., 2014, 2019; Scherf et al., 2014). The remaining 16 studies (summarized in **Appendix A10**) that did specific analyses on object processing had sample sizes ranging from $n = 10$ (for a longitudinal study) to $n = 266$. Two studies were longitudinal (Dehaene-Lambertz et al., 2018; Nordt et al., 2021) while the remainder ($n = 14$) had cross-sectional designs. The studies covered age ranges from infancy (3-8 months) (Deen et al., 2017) through childhood (Dehaene-Lambertz et al., 2018; T. Dekker et al., 2011; Gathers et al., 2004; Golarai et al., 2007, 2017; Kamps et al., 2022; Meissner et al., 2019; Nishimura et al., 2015; Nordt et al., 2021; O'Hearn et al., 2011; Scherf et al., 2007; Tian et al., 2021; Turkeltaub et al., 2008) and later adolescence (Golarai et al., 2007; Keulers et al., 2019; Nishimura et al., 2015; Nordt et al., 2021; O'Hearn et al., 2011; Scherf et al., 2015); however, there were gaps in coverage between 8 months and 3 years and no studies that looked at object processing in infants younger than 3 months of age.

Temporoparietal regions sensitive to objects over faces were observed in children as young as 3-8 months (Deen et al. 2017), suggesting that there is some form of object-specific processing in the postnatal period. However, the findings for studies conducted in childhood and adolescence are contradictory. Of the 16 studies that looked at object-related BOLD signal change, 8 studies found no significant associations with age at all, progressive or regressive

(Dehaene-Lambertz et al., 2018; T. Dekker et al., 2011; Golarai et al., 2007; Keulers et al., 2019; Scherf et al., 2007, 2015; Tian et al., 2021; Turkeltaub et al., 2008). Golarai et al. (2017) found regressive change as a decrease in the extent of the mid fusiform gyrus that significantly responded to objects, but not progressive change. However, Nishimura et al. (2015) and Scherf et al. (2007) found no significant differences in the extent of object-preferential BOLD signal response in the lateral occipital cortex (LOC) between children, adolescents, and adults, which may suggest that there are different developmental processes occurring in different object-preferential regions of the cortex. Object-related signal change in areas that would eventually be specialized for other categories decreased with age in 2 studies (Deen et al., 2017; Meissner et al., 2019), though Nordt et al. (2021) also saw increases in object-related BOLD signal in the posterior fusiform gyrus (a face area) and the posterior OTS (an emerging word-related area) to string instruments, but not any other categories of objects. The only studies that saw an increase in magnitude of BOLD signal change to objects with age were O'Hearn et al. (2011) (in the fusiform gyrus, lingual gyrus, and the inferior occipital gyrus) and Nishimura et al. (2015) (in the LOC). While young children (maybe even infants) show evidence of object-specific processing, given the lack of agreement across studies, more research is needed to describe the development of object-specific visual processing.

      2.3.3.4. Scene Processing. In adults, scene processing has been localized to the parahippocampal place area (PPA), occipital place area (OPA), and the retrosplenial cortex (RSC) (Dilks et al., 2022; Epstein & Baker, 2019). Nineteen studies included scene (often referred to as "place") stimuli in their experimental design. Of these, two studies only used scenes as a control condition to define face regions, and did not conduct any analyses on scene

processing (Hildesheim et al., 2020; Natu et al., 2016). Out of the remaining 17 studies (Aylward et al., 2005; Chai et al., 2010; Deen et al., 2017; Dehaene-Lambertz et al., 2018; Golarai et al., 2007, 2017; Jiang et al., 2014; Kamps et al., 2022; Meissner et al., 2019; Nordt et al., 2021; O'Hearn et al., 2011; Sahraei et al., 2022; Scherf et al., 2007, 2014, 2015; Tian et al., 2021; Vuontela et al., 2013), the sample sizes ranged from $n = 10$ to $n = 266$, with the second largest study having an $n = 168$. Two of these studies (Dehaene-Lambertz et al., 2018; Nordt et al., 2021) had a longitudinal design, while the rest were cross-sectional. The youngest participants included in the studies were infants aged 3 months (Deen et al., 2017), and age ranges from early childhood (i.e., 5 or 6 years) were covered, up to late adolescence (Chai et al., 2010; Nordt et al., 2021; O'Hearn et al., 2011; Scherf et al., 2014, 2015). There was a gap in the age coverage for scene processing studies for ages younger than 3 months, and between ages 8 months and 3 years. The studies that looked at the development of and/or associations with age for scene/place processing are summarized in **Appendix A11.**

A significant category-specific response to scenes was evident in infants 3-8 months of age in the parahippocampal gyrus and the LOC, though these areas do not appear to yet be specialized for scene processing, and also had significant BOLD responses to objects and faces (Deen et al., 2017). However, it has been shown that by the age of 5, there are cortical regions that respond specifically to houses over other categories (Dehaene-Lambertz et al., 2018). There is a fair amount of evidence for progressive development of scene processing in the brain over later childhood (i.e., 7 years +) and adolescence, in terms of the magnitude (Aylward et al., 2005; Dehaene-Lambertz et al., 2018; Meissner et al., 2019; O'Hearn et al., 2011), extent (Golarai et al., 2007; Meissner et al., 2019; Nordt et al., 2021; Scherf et al., 2014), and selectivity (Meissner et al., 2019; Nordt et al., 2021) of BOLD response, though there are some inconsistencies in the

literature, and two studies found no evidence of developmental change (Sahraei et al., 2022; Scherf et al., 2015). There is also some evidence of regressive change: Meissner et al. (2019) found that increased selectivity to scenes in the PPA and OPA in adults was driven by both increases in BOLD signal to scenes and decreases in response to objects, while O'Hearn et al. (2011) found that areas that responses to faces in the older group were responsive to scenes in the younger children, which was not present in their older group. No studies included in this review find an apparent "emergence" of scene-related responses, as there are regions that show significant BOLD responses to scenes as early as 3 months of age (Deen et al., 2017); though it must be noted that, for this category, there are no studies that represent the age range between infancy and 5 years, so a full picture of the developmental timeline is not available. While there seems to be no evidence supporting a maturational framework of scene-specific visual processing, and the interactive specialization framework is not universally confirmed either, most of the studies do find evidence of at least progressive development of scene-processing in the cortex from infancy through to adulthood. It will be important to conduct studies that explicitly test for both progressive and regressive development to confirm whether the interactive specialization framework is supported for scene processing development.

2.3.3.5. Visual Body / Limb Processing. There are two typical body-selective visual areas localized in adults: the fusiform body area (FBA) and the extrastriate body area (EBA). (Downing et al., 2001; Downing & Peelen, 2011). There were 6 studies that looked at the development of visual category-selective processing of bodies (summarized in **Appendix A12**) (Deen et al., 2017; Dehaene-Lambertz et al., 2018; Nordt et al., 2021; Ross et al., 2014, 2019). These studies cover the development of visual processing of bodies from infancy (Deen et al.,

2017), and early and middle childhood (Dehaene-Lambertz et al., 2018; Nordt et al., 2021; Ross et al., 2014), through to adolescence (Nordt et al., 2021; Ross et al., 2019). Other than one study that had a sample with an age range of 3-8 months, the studies covered an age range from 5-17 years, with a gap in coverage between the ages of 8 months and 5 years, and no coverage of children younger than 3 months old. The sample sizes of the studies ranged from $n = 10$ to $n = 69$. Two of the studies were longitudinal (Dehaene-Lambertz et al., 2018; Nordt et al., 2021). One other study included bodies as a stimulus category in a localizer experiment, but did not specifically look at the development of the body-selective cortex (Natu et al., 2016). While the sample sizes for the existing literature on visual body-selective development are in the lower range (n ranging from $10 - 69$), this is partly mitigated by the inclusion of two longitudinal studies, both with an impressive number of scans per participant (6–7 scans per participant over the course of a year for Dehaene-Lambertz et al. (2018), and an average of 4.41 scans with a range of 2–10 scans per participant over the course of 1–5 years in Nordt et al. (2021)).

The findings for visual body/limb-selective processing are interesting and slightly contradictory. Though it is not clear if explicitly body-selective areas are present in infancy, face-selective areas in the ventral temporal and lateral occipital cortices initially show a response to bodies as well, which eventually decreases over time as face-selectivity increases, suggestive of early interactive specialization (Deen et al., 2017). The overall trend within visual body-selective regions appears to be an increase in magnitude of BOLD signal change and volume across both childhood and adolescence (Ross et al., 2014, 2019). That being said, the change may be gradual, as it does not appear that there is much alteration in body-selective cortical responses between the ages of 6–7 years (Dehaene-Lambertz et al., 2018). Further, there may be a dissociation between general body-selective responding and that of limbs, as Nordt et al.

(2021) identified separate body-selective and limb-selective regions and found a clear diminishment of response in limb-selective regions in the occipitotemporal sulcus to the advantage of expanding word- and face-selective cortex, that was not reflected in general body-selective regions. Further, Dehaene-Lambertz et al. (2018) found that the emergence of the VWFA at around ages 6 and 7 years did not appear to alter the functional organization of existing category-selective visual regions (including body-selective cortex).

2.3.3.6. Character / Symbol Processing. Visual word recognition is often attributed to the VWFA, which is left lateralized and located in adults in the occipitotemporal sulcus adjacent to the fusiform gyrus (McCandliss et al., 2003). Eight studies (9.0%) included character or symbol (letters, numbers, words, or pseudowords) stimuli in their task protocol. Of these 8 studies, 2 did not report any developmental analyses for the symbol stimuli (Cantlon & Li, 2013; Natu et al., 2016). The remaining 6 studies are summarized in **Appendix A13**. The age range covered by these studies is narrower than other categories, as the minimum sample age was 4 years, and the maximum was 17 years, with no studies covering any ages earlier than 4 years old. Two studies were longitudinal (Dehaene-Lambertz et al., 2018; Nordt et al., 2021), while the remaining four were cross-sectional (Cantlon et al., 2011; T. M. Dekker et al., 2014; Kersey et al., 2019; Turkeltaub et al., 2008). Sample sizes ranged from $n = 10$ to $n = 71$.

The findings from the character / symbol processing studies do not clearly support either the interactive specialization or the maturational frameworks of development. In children, the left lateral mid-fusiform gyrus and the ITG showed similar BOLD response to both letters and numbers, while in adults, the same areas preferred letters (Cantlon et al., 2011). Within the left IFG, children showed responses of trending significance to both numbers and letters, while the

adults only had significant BOLD signal change in response to letters, which may suggest that this area is becoming more specialized for number processing (Kersey et al., 2019). The results from these studies may provide some evidence for the interactive specialization framework. However, the results from remaining studies paint a more complex picture. In their longitudinal study conducted over the first year of schooling (between the ages of roughly 6-7 years), Dehaene-Lambertz et al. (2018) suggests that the VWFA does not "come online" until children begin to read, approximately 2-4 months after beginning school, and they suggest that the VWFA "superimposes" itself onto the functional mosaic in the ventral temporal cortex without altering the pre-existing organization, which is supportive of a maturational framework of development. Over a longer period of time (5-17 years), the word-selective area in the ventral temporal cortex appears to double in size at the expense of limb-selective cortex (Nordt et al., 2021), which could be indicative of an interactive specialization framework for this area of the lateral ventral temporal cortex. Their findings also contradict the developmental mechanism suggested by Dehaene-Lambertz et al. (2018), though it is possible that the while the emergence of the VWFA follows their superimposition hypothesis, the later development of the word-selective cortex follows the "cortical recycling" hypothesis put forth by Nordt et al. (2021). The remaining studies do not clearly favour either the interactive specialization or the maturational frameworks (T. M. Dekker et al., 2014; Turkeltaub et al., 2008).

2.3.3.7. Visual Motion. In the occipital cortex, area V5/human middle temporal complex (hMT+) is a key location for motion perception, specifically global motion, motion coherence, and structure from motion (Braddick et al., 2001; Kaderali et al., 2015; Paradis et al., 2000). Biological motion is additionally supported by the superior temporal sulcus (E. Grossman et al.,

2000; E. D. Grossman & Blake, 2002; Saygin, 2007). A total of 11 studies employed tasks that included motion stimuli (summarized in **Appendix A14)** (Anderson et al., 2013; Biagi et al., 2016; Bucher et al., 2006; Carter & Pelphrey, 2006; T. M. Dekker et al., 2015; Keulers et al., 2019; Kirby et al., 2018; Klaver et al., 2008; Lichtensteiger et al., 2008; Sapey-Triomphe et al., 2017; Taylor et al., 2018). Of these studies, one included natural moving scenes along with static object and face stimuli (Keulers et al., 2019) and one focused on the development of depth perception from motion and spatial disparity (T. M. Dekker et al., 2015). The other 9 studies focused on either biological motion/human action perception (Anderson et al., 2013; Biagi et al., 2016; Carter & Pelphrey, 2006; Kirby et al., 2018; Lichtensteiger et al., 2008; Sapey-Triomphe et al., 2017) or motion coherence (Bucher et al., 2006; Klaver et al., 2008; Taylor et al., 2018). Of the 9 that had a main focus on motion perception, sample sizes of these studies ranged from $n = 9$ to $n = 86$. All had a cross-sectional design, and one study included a year-long longitudinal experiment in addition to the cross-sectional analysis (Taylor et al., 2018). Collectively, the studies in this category covered ages 4-17 years, with no studies looking at children younger than 4 years.

Interestingly, several studies support a developmental mechanism of motion perception wherein BOLD responses to motion increases in association and frontoparietal cortex with age, in conjunction with a diminishment of BOLD responses in more ventral, perceptual visual areas, which is in line with the interactive specialization framework. There is evidence for this pattern for both structure-from-motion when compared to random motion when comparing 5-6 year old children to adults (Klaver et al., 2008), and biological motion compared to non-biological motion in 5-7 year old children compared to adults (Lichtensteiger et al., 2008), within children across the ages of 7-10 years (Carter & Pelphrey, 2006), and in children and adolescents aged 8-17

when compared to adults (Sapey-Triomphe et al., 2017). While motion coherence (identifying shapes and structures from motion) and basic motion processing (motion compared to static) appear to be almost fully mature by the late teenage years (Bucher et al., 2006), biological motion may have a more protracted developmental trajectory with either ongoing change across adolescence (Sapey-Triomphe et al., 2017) or a non-linear change between middle/late childhood and adulthood. Indeed, it is unclear when exactly the changes in biological motion processing are occurring, as while Carter & Pelphrey (2006) found evidence of increasing STS activity during biological motion between the ages of 7–10 years, Kirby et al. (2018) found no significant associations between BOLD signal change to biological motion and age in the same age range. It should be noted that the sample size for the Carter and Pelphrey (2006) study was significantly smaller than that of Kirby et al. (2018) – $n = 9$ vs. $n = 40$ – and that while the age ranges overlapped, the range in Kirby et al. (2018) was double that of Carter and Pelphrey (2006). As such, there is a need for future research with a larger sample of children within this age range to clarify the developmental processes and timing.

2.3.3.8. Movies. Naturalistic tasks can engage several functional systems in the brain, including visual, auditory, attentional, emotional, and spatial processing regions (Bottenhorn et al., 2018). The naturalistic studies included in this review were published more recently than most of the traditional task paradigms, as the earliest naturalistic study in this review was published in 2013 (Cantlon & Li, 2013), relative to the task-fMRI studies which were published as early as 1998. In total, there were 11 studies that used movies or movie clips in a naturalistic paradigm (summarized in **Appendix A15)**. These studies also tended to have larger sample sizes than the other categories, with n ranging from 28 to 414; however, none of the studies were

longitudinal. Combined, the age ranges of the studies included were 4-18 years, and there was one other study that looked at infants ages 3-12 months. There was a gap in the age coverage between 1 year and 3 years of age. The analysis methods for these studies often differed from the rest of the task-based studies, with most (Cantlon & Li, 2013; Cohen et al., 2022; Kamps et al., 2022; Kersey et al., 2019; Lerner et al., 2021; Moraczewski et al., 2018, 2020; Yates et al., 2022) using intersubject correlation (Hasson et al., 2004; Nastase et al., 2019). This approach is typically used to capture BOLD signal change associated with similarity or differences between individuals rather than identifying the locus of the response to a specific stimulus. Two of the studies looked at multivariate patterns in response to the movies (Benear et al., 2022; Camacho et al., 2019), while only one used a GLM (Park et al., 2022). Another analysis method used applied a Hidden Markov Model (HMM) to discern the event structure in the fMRI data (Cohen et al., 2022; Yates et al., 2022).

A common finding over a number of naturalistic ISC studies is that the response to movies is still developing across childhood and adolescence in a number of areas of the brain, and that children look more "adult-like" with increasing age in visual areas such as the FFA, pSTS, occipital place area, PPA, RSC, and the LOC (Kamps et al., 2022), large swaths of sensory and association cortex, including visual areas such as the fusiform gyrus and extrastriate cortex (Cantlon & Li, 2013), and visual and multimodal association areas such as the precuneus, supramarginal gyrus (SMG), and temporoparietal junction (TPJ) (Moraczewski et al., 2018, 2020). The event structure derived from the fMRI data of infants also looked more adult-like the older they were, within the infant age range (Yates et al., 2022). Only one naturalistic study found no significant differences with age (Park et al., 2022). Interestingly, two studies found evidence of both progressive and regressive effects of age, suggesting evidence for the

interactive specialization framework – Kersey et al. (2019) found "child-unique" areas of the brain where children showed synchronized responses that adults did not; Kamps et al. (2022) found that in children aged 3 and 4 years, pSTS activity was not yet fully specialized. Cohen et al. (2022) found regressive changes only in visual regions, as ISC decreased with age in higher order associative regions like the TPJ and precuneus. Moraczewski et al. (2018) found that children had weaker and more diffuse ISCs as a group than adults did to one another, and took this as evidence for the interactive specialization framework, though they did not report any areas where children had statistically greater within-group ISC than adults as was reported in Kersey et al. (2019). No studies found clear evidence of any "emerging" regions that would be indicative of the maturational framework of functional development.

2.3.3.9. Findings in the Largest Studies (n > 100). Studies with large sample sizes are worth considering in more detail, as they may reflect more reliable conclusions. There were 4 recent (2020 or later) studies included with samples of $n > 100$ (Cohen et al., 2022; Kamps et al., 2022; Lee et al., 2020; Tian et al., 2021). Cohen et al. (2022) and Kamps et al. (2022) were both movie-fMRI studies, and had sample sizes of $n = 414$ and $n = 168$, respectively, while the remaining studies used tasks to investigate face processing, both affective (Lee et al., 2020; $n = 181$) and non-affective (Tian et al., 2021 $n = 266$). Tian et al. (2021) also looked at scenes and objects. None of these studies used "traditional" task analysis techniques, such as the GLM; instead, Kamps et al. (2022) and Cohen et al. (2022) relied heavily on ISC analysis, while Lee et al. (2020) and Tian et al. (2021) both employed MVPA. It should be noted that none of these studies explicitly tested for interactive specialization or the maturational framework. Kamps et

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al. (2022) supported interactive specialization in the pSTS, as they showed older children had more functionally specialized pSTS responses than younger children.

The other three studies did not show clear evidence for either developmental theory. Lee et al. (2020) found that adolescents have lower emotional discriminability than adults, and were more likely than adults to perceive subtle emotional expressions as neutral. This result does not fit easily into either the "progressive," "regressive," or "emergence" categories, and does not provide evidence for either theory. Similarly mixed results can be seen in Cohen et al. (2022); while technically the authors of the study found both "progressive" and "regressive" findings, the "progressive" findings were in auditory processing areas (as evidenced by increased ISC with age), while the "regressive" associations with age were found in default mode/visual associative areas such as the precuneus and RSC (Alves et al., 2019). As there is only "regressive" change found in areas related to visual processing, the results from this study (which has the highest sample size at $n = 414$, and one of the largest age ranges, spanning 5-18 years) do not clearly support the interactive specialization framework for visual functional development. Finally, Tian et al. (2021) found that for both face- and scene-processing, the multivoxel representations of the stimuli became more similar and "homogenized" with age (i.e., the adults had more similar representations to one another than the children had within the child group). Again, this result does not clearly support either the interactive specialization or maturational frameworks, as it does not show either "regressive" or "emergence" of function, but does reflect progressive developmental change.

2.4. Discussion

Here, we synthesized the fMRI literature related to development of visual functions and did not find a clear consensus on whether the interactive specialization or maturational frameworks are supported, though we did find relatively broad support for 'progressive' developmental changes across childhood and adolescence. This lack of consensus in the literature may be related in part to issues surrounding historical methodological practices in fMRI research, although given the volume of literature, may also warrant refinement of developmental frameworks. Establishing empirically validated developmental frameworks, such as the ones focused on in this review, is extremely important, in order to understand children's changing neural architecture and drive research that is grounded in scientific theory.

2.4.1. Evaluation of the Frameworks

Given the lack of conclusive support in the context of visual functional development, do these frameworks need to be updated? Acknowledging the limitation of only considering visual functions here, this review nonetheless provides an opportunity to consider strengths and limitations of these frameworks, as well as opportunities for ongoing refinement.

2.4.1.1. Maturational Framework

2.4.1.1.1. Support in the literature. This review found very limited support for the maturational framework, and unsurprisingly, evidence in favor was generally in the context of cognitive functions that emerge later in childhood. For example, Dekker et al. (2015) found that the cortical signature of depth cue integration emerged alongside the ability to perform a related task. Dehaene-Lambertz et al. (2018) also found that the VWFA emerged during the first year of schooling, while children were learning to read (though it should be noted that Cantlon et al.

(2011) did show responses to symbols in the occipitotemporal cortex at a slightly younger age).

We did not find any evidence to support the maturational framework in the studies that used

naturalistic movie stimuli, or in the studies with the largest sample sizes, suggesting that power

and ecological validity are not the main contributors to negative findings. Further, of the six

infant studies reviewed here (Born et al., 1998; Deen et al., 2017; Ellis et al., 2021; Martin et al.,

1999; Muramoto et al., 2002; Yates et al., 2022), none showed support for the maturational

framework. These studies examined early visual processing (Born et al., 1998; Ellis et al., 2021;

Martin et al., 1999; Muramoto et al., 2002) as well as higher-order category-specific visual

processing (Deen et al., 2017) and movie processing (Yates et al., 2022). This suggests that a

wide range of visual functions either "emerge" earlier in infancy than the ages these studies

focused on (which was approximately 3-4 months), or they are innate functional properties that

are primed to respond to the visual world prior to birth, and that age range was not a contributor

to lack of support for this framework across domains.

     2.4.1.1.2. Methodological challenges. An important issue to consider when evaluating

the lack of evidence for the maturational framework is the limited ability of commonly used

analysis methods to detect the "emergence" of a function. Traditional inferential statistics can

report whether there is no BOLD signal change that is above a somewhat arbitrary threshold, and

not whether an observed effect is consistent with no response. Alternative statistical

methodologies, such as Bayesian parameter inference (Masharipov et al., 2021), or reporting

techniques that "highlight" significant findings rather than "hiding" insignificant ones (Taylor et

al., 2023), may be more appropriate to assess the maturational framework. However, it should be

noted that many studies were able to detect a response in even their youngest participants, which

may suggest that the issue is more tied to the accuracy of the maturational framework in a visual context rather than methodological limitations.

     2.4.1.1.3. Suggestions for future study and model refinement. Based on the evidence, it appears that the maturational framework may be helpful for understanding very specific and emergent functional domains, but should not be considered a general model for functional development as behaviors undergo progressive refinement. The maturational framework is likely most appropriate for describing patterns of functional change related to late- and relatively abruptly-emerging functions. However, most functions emerge somewhat gradually over repeated exposures and practice, before finally reaching asymptotic performance. Learning about letters as part of learning to read is a process that starts with exposure early in life and continues into late childhood (Schlaggar & McCandliss, 2007). While this seems like a promising candidate domain for a maturational framework (Dehaene-Lambertz et al., 2018) a strict before / after timeline of functional emergence may not be appropriate, and this may underlie mixed findings in the literature. A more nuanced perspective that considers the iterative interplay between exposure, functional response and emergent behaviors may ultimately provide a more useful account of children's functional brain development in most contexts.

     2.4.1.2. Interactive Specialization.

     2.4.1.2.1. Support in the literature. The interactive specialization framework aims to provide a more nuanced perspective and was initially proposed as a domain-general mechanism of functional brain development (Johnson, 2011). In our review, we found some isolated evidence for this framework, but it was not universally supported across visual domains.

2.4.1.2.2. Methodological challenges. While we found substantial evidence for progressive development, we found very limited evidence for accompanying regressive developmental patterns that are presumed to emerge through competitive interactions in this model. Importantly, many studies described here reported analyses related to progressive associations with age, but either did not report, or conduct, analyses related to regressive development. This may be due to a reporting bias against null results, or because these analyses were not conducted, or a combination of these factors. Despite support from a few key studies, especially in terms of category-specific visual processing (Cantlon at al., 2011; Joseph et al., 2011; Nordt et al., 2021), more thorough testing and reporting of regressive developmental patterns is needed to assess the applicability of this model.

2.4.1.2.3. Suggestions for refinement and future work. Despite methodological limitations discussed above, findings in this review suggest a need to refine the interactive specialization model to better account for the current body of literature. Specifically, given the general lack of 'regressive' findings, either improved methods are needed to test for this developmental feature, or models should be refined to reduce the emphasis on regressive activity patterns. We suggest that the term "functional specialization" may better reflect the current evidence for the development of visual processing, given the lack of support for the "interactive" component of this framework.

Indeed, competitive interactions that take place with experience over time are an element of this framework that are particularly difficult to test experimentally. In this review, we looked for regressive patterns in functional data collected across different ages. However, even if we found those patterns, with this approach we cannot directly confirm that these changes arise as a function of 'competitive interactions' between regions. A true test of this model would require

ongoing measurement of activity under naturalistic conditions and the identification of antagonistic interactions between regions. Longitudinal functional connectivity measurements could contribute to bolstering a case for competivite interaction, if there were patterns of initially strong functional connectivity between pairs of regions that declined in parallel with functional responses increasing in one region and declining in another. However, we are not aware of any studies to date that have reported this in the visual domain, and generally found weak evidence for regressive patterns. Other potential scenarios could explore how increasing specialization of top-down circuits (such as the frontoparietal network, or other networks related to attention, executive function and cognitive control) may influence the specialization of responses for more basic sensory processes. It is also possible that interactive specialization intersects with visual development at a more network- or system-level scale (Battista et al., 2018), and searching for evidence in the context of functional connectivity, or across different cognitive constructs, will prove to be more fruitful.

It will also be important to expand the scope and understanding of interactive specialization to reflect non-linear developmental trends. For example, it has been proposed that the development of emotional face processing is non-linear, as there is evidence to suggest that adolescents have greater responses to affective face stimuli than both adults and younger children (Del Piero et al., 2016). If the underlying developmental patterns for other visual functions are also non-linear (Lochy et al., 2019; Shaw et al., 2012), progressive and/or regressive findings may be present only when comparing specific age groups and not seen across the continuum from early childhood across adolescence.

It is also worth considering whether interactive specialization is a domain-general mechanism of functional brain development. Interactive specialization was supported in the

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majority of articles studying motion processing; had limited support in the context of character /

symbol, non-emotional face, early visual, scene, and naturalistic movie processing, and not

supported by any articles for object or body processing. This lack of consistent support may have

implications for the universality of this model. Given some of the evidence for interactive

specialization in other contexts, such as executive function and social behaviours (Johnson,

2011; Johnson et al., 2009), it may be an important mechanism for the development of higher-

order, integrative cognitive functions; but maybe not an accurate model for visual functions or

other unimodal processing.

2.4.2. Methodological Challenges Common to Both Frameworks.

2.4.2.1. Study Power. While there has been growth in sample size over time, study

power is nonetheless a concern that may contribute to divergent findings. Given that more than

50% of studies reported here included fewer than $n = 32$ participants, it is worth considering how

these confounds may influence findings. Studies with low sample sizes increase risk for both

false positives and false negatives (Button et al., 2013; Turner et al., 2018). Under a traditional

whole-brain, univariate analyses, regressive associations in widespread areas of the brain may be

"buried," and unless there is an *a priori* hypothesis about specific areas with regressive change,

this type of association, which is necessary for the interactive specialization framework may go

undetected. Going forward, data sharing and open science efforts are becoming imperative to

combat the historically low power in most developmental neuroimaging studies. Public

consortium datasets (HBN: Alexander et al., 2017; HCP-D: Harms et al., 2018; Somerville et al.,

2018; ABCD: Casey et al., 2018), can add robustness with upwards of thousands of participants

from diverse backgrounds.

2.4.2.2. Demographic Characteristics. A major issue in most of the literature included in this review is the homogeneity of the samples. 69.7% of the studies had samples from North America (of which, only 2 studies included participants from Canada), followed by Europe, which made up 28.1% of the total studies. Only 2 studies analyzed data from participants outside of North America or Europe – one study from China (Tian et al., 2021), and another from Japan (Muramoto et al., 2002). Additionally, only 9 studies reported the ethnicity demographics of their sample, while only 2 reported the socioeconomic status. This is a serious issue, as selection, exclusion, and sampling bias (Green et al., 2022) can lead to homogenous samples that are mostly white and middle- to high-income, which in turn results in model prediction failure in individuals who do not conform to this profile (A. S. Greene et al., 2022). While attention towards this issue specifically in the field of developmental neuroimaging has increased in recent years (Garcini et al., 2022; Green et al., 2022; Nketia et al., 2021), the current findings speak directly to the work that still needs to be done to ensure that research in the field is generalizable, useful, diverse, and equitable.

2.4.2.3. Longitudinal and Cross-sectional Research. Another limitation in this literature is the small number of longitudinal studies. Due to practicalities such as cost and time investment, as well as important statistical and methodological considerations (Herting et al., 2018; King et al., 2018; Telzer et al., 2018), longitudinal fMRI studies are relatively rare, with cross-sectional research comprising the majority of the research upon which current understandings are rooted. Longitudinal studies can help mitigate bias such as the cohort effect, and are able to model within-individual developmental change (Crone & Elzinga, 2015). Crucially, cross-sectional associations with age do not always agree with longitudinal findings (Lindenberger et al., 2011; Louis et al., 1986; McCormick et al., 2017), and it has been suggested

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that cross-sectional studies likely underestimate true developmental change (Di Biase et al., 2023).

2.4.2.4. Head motion. Notably, 67.4% of studies reviewed here reported inadequate motion mitigation strategies (either one of exclusion strategies or statistical control strategies, or neither). High head motion could give the appearance of weaker and/or more diffuse BOLD response patterns relative to data with less head motion. It is therefore important to take findings of progressive development with some caution as it is difficult to disentangle age from head motion in developmental samples. This high head motion, in combination with the lack of explicit support for either framework, suggests that caution should be taken when interpreting findings in the context of the interactive specialization or maturational frameworks. Future studies should focus on reducing motion during scanning (tasks, training, head molds, improvements in protocols) (de Bie et al., 2010; D. J. Greene et al., 2018; Horien et al., 2020; Meissner et al., 2020; Power et al., 2019), developing methods for mitigating head motion during preprocessing (Ciric et al., 2017, 2018; Graff et al., 2022), and collecting larger amounts of data per child to increase reliability and mitigate losses to censoring.

2.4.2.5. Integration of Naturalistic Paradigms. Naturalistic fMRI studies did provide findings that converged with tasks of generally "progressive" developmental associations with age. However, as naturalistic paradigms become more popular, it will be important to consider the implications of the popular analysis techniques used in movie-fMRI paradigms and how they may fare in terms of detecting evidence for the maturational and interactive specialization frameworks. While it is possible to employ a GLM to a movie stimulus (Camacho et al., 2023) many movie studies use other models, such as ISC, HMMs, or MVPA, as reflected in the movie studies included in this scoping review. ISC, for example, would likely be an inappropriate

analytical tool for investigating the maturational hypothesis. Since ISC reflects the level of synchronization between individuals, a lack of significant ISC in a brain region is indicative of an inconsistent response between individuals, rather than no response at all.

Movies present a unique opportunity to investigate developmental patterns at the network- and system-level scale that would be difficult to conduct in traditional tasks. Since they engage many different modalities and have complex cognitive and attentional demands, the functional interactions between different regions and networks can easily be assessed. On the other hand, if one is interested in studying the applicability of these frameworks within specific regions or system (as was the case in this review), it may be difficult to detect or disentangle the developmental effects of that specific system from the influence of the other networks that are engaged. Studies that test these frameworks in both traditional controlled tasks and free-viewing movie contexts that find consensus between their results will be important in robustly determining their validity across different contexts (Cantlon, 2020).

2.5. Conclusions

In this scoping review, we did not find clear support for either the maturational or interactive specialization frameworks of functional development in the context of visual processing in the brain, though there was more support for interactive specialization, and broad support for progressive developmental change, which is an element of both frameworks. To support the understanding of functional brain development through the lens of developmental frameworks, future research should prioritize formulating clear, testable hypotheses from a strongly motivated theoretical basis (Cantlon 2020; Crone & Ridderinkhof, 2011), implementing statistical methods to directly test these frameworks, and increasing the number of high-quality

longitudinal study designs. A strong base of mechanistic theory that underlies the rationale and hypotheses of future studies is imperative to advance our understanding of childhood functional brain development.

2.6. Acknowledgements

CHAPTER 3 – Functional Responses During Naturalistic fMRI are Increasingly Typical Across Early Childhood

3.0. Abstract

While findings show that throughout development, there are child- and age-specific patterns of brain functioning, there is also evidence for significantly greater inter-individual response variability in young children relative to adults. It is currently unclear whether this increase in functional "typicality" (i.e., inter-individual similarity) is a developmental process that occurs across early childhood, and what changes in BOLD response may be driving changes in typicality. We collected fMRI data from 81 typically developing 4-8-year-old children during passive viewing of age-appropriate television clips and asked whether there is increasing typicality of brain response across this age range. We found that the "increasing typicality" hypothesis was supported across many regions engaged by passive viewing. Post hoc analyses showed that in a priori ROIs related to language and face processing, the strength of the group-average shared component of activity increased with age, with no concomitant decline in residual signal or change in spatial extent or variability. Together, this suggests that increasing inter-individual similarity of functional responses to audiovisual stimuli is an important feature of early childhood functional brain development.

3.1. Introduction

Functional brain responses during sensory and cognitive processing are refined across childhood and adolescence (T. T. Brown & Jernigan, 2012; Johnson, 2001; Keunen et al., 2017). While the period around school entry (i.e., 4-8 years) is one of the most pivotal for child development (Morrison et al., 2019) and important for the diagnosis of neurodevelopmental conditions (Daniels & Mandell, 2014; Visser et al., 2014), relatively little is known about brain function in this age range, due to practical limitations in the collection of neuroimaging data from young children (Dosenbach et al., 2017a; Frew et al., 2022; Greene et al., 2018b; Horien et al., 2020; Poldrack et al., 2002; Raschle et al., 2012). Describing the normative patterns of brain function and their association with age across early childhood can support the early identification of atypical patterns, and inform our understanding of the reciprocal relationships between brain and cognitive/behavioral development (Geng et al., 2021).

A general assumption underlying much of the developmental cognitive neuroscience literature is that of stereotypical age-appropriate functional responses. In support of this assumption, it has been shown that children and adults engage different brain regions during the same task (Kersey et al., 2019; Yates et al., 2021), and that there are differences in functional responses between children at distinct developmental stages (Hao et al., 2021). Children tend to have more topographically diffuse and less functionally specific responses to stimuli than adults (Durston et al., 2006; Johnson, 2011). Evidence for child- or age-specific processing has been found for faces (Deen et al., 2017; Golarai et al., 2017), language (Olulade et al., 2020), attention tasks (Hao et al., 2021) and audiovisual stimuli (Cohen et al., 2022; Kersey et al., 2019; Yates et al., 2021), including in the supramarginal gyrus (Di & Biswal, 2022) and the posterior temporal sulcus (Kamps et al., 2022). With age-specific responding, children should look more like other

similar-aged peers than adults, following normative trajectories through these different age-specific responses as they develop.

However, there is also evidence for substantial inter-individual variability between children. For example, children show less inter-individual spatial consistency of visual ventral stream functional topography than adults (Scherf et al., 2007). Studies using "naturalistic" (Nastase et al., 2020; Sonkusare et al., 2019b) movie-watching paradigms have shown that children have less synchronized responses to movies relative to adults (Cantlon & Li, 2013; Moraczewski et al., 2018), and in category-specific face, scene, and object areas, there does not appear to be a "child-specific" response to movie stimuli (Kamps et al., 2022). For face- and scene-processing in the ventral visual cortex, it has been shown that neural representations "homogenize" with age to a common adult template, rather than showing qualitatively different child- and adult-specific templates (Tian et al., 2021), in contrast to much of the previous evidence for age-specific patterns of facial processing development. This line of evidence implies that rather than functional brain responses being highly similar between age-matched peers, children have relatively individualistic and idiosyncratic ways of responding to stimuli, that converge to a more stereotyped response as they develop into adulthood. This increasing "typicality" (Gruskin et al., 2020a) between individuals may be an important feature of functional brain development.

Evidence for more idiosyncratic responses in younger children has generally come from studies contrasting groups of children with adults rather than considering children relative to one another (Cantlon & Li, 2013; Moraczewski et al., 2018). It is therefore unclear whether increasing inter-individual consistency occurs across early childhood or at an intermediate

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developmental stage, and how this developmental shift from more idiosyncratic to more typical function interacts with the age-specific responses that have been identified in the literature.

In the present study, we used a naturalistic video-viewing task to investigate the presence of increasingly typical patterns of functional responses across an early childhood sample (aged 4-8 years). Passive viewing tasks have a number of advantages for studying individual differences in brain function in early childhood (Cantlon, 2020): they engage distributed responses in numerous sensory (i.e., early visual and higher visual face-processing) and association (i.e., language) areas simultaneously (Bottenhorn et al., 2018) in a manner more similar to the cognitive demands of real life than traditional task paradigms (Sonkusare et al., 2019b); increase compliance and reduce head-motion in the MRI scanner (Greene et al., 2018b; Vanderwal et al., 2015, 2018); and have been shown to be useful for delineating functionally-defined regions in young children for whom conventional localizer tasks are challenging (Kamps et al., 2022). Further, naturalistic tasks can be harnessed for studying individual differences in functions of the brain between individuals (Finn et al., 2020a).

We tested the hypothesis that inter-individual similarity of brain responses to a movie stimulus would increase across the age range of 4-8 years. Our results largely confirmed this hypothesis, showing an increasingly typical brain response from 4-8 years of age throughout regions of the brain engaged in the movie-watching task. To better understand the changes driving this effect, we undertook several *post hoc* analyses in specific bilateral ROIs that are functionally relevant to the video stimulus (Bottenhorn et al., 2018) and have been extensively studied in a developmental context as they are related to maturing face/social and language processing: the FFA (Rosenke et al., 2021; Tian et al., 2021) and the STS (Labache et al., 2019; Masson & Isik, 2021). The FFA was selected because of functional relevance to video-viewing,

relative functional specificity, as well as the fact that there has been evidence for both age-specific (Deen et al., 2017; Golarai et al., 2017) and increasingly typical (Scherf et al., 2007; Tian et al., 2021) patterns of development in this region. We selected the STS for functional relevance to language processing (i.e., in Wernicke's area) (Labache et al., 2019) and multimodal social interaction (Masson & Isik, 2021; Watson et al., 2014). The ROI analyses were conducted to determine whether greater idiosyncrasy of functional responses in younger children could be explained by more spatially diffuse BOLD responses (Durston et al., 2006), weaker stimulus-related responses, or greater variability in individual-unique signal components of the responses in ROIs. Together, our findings add to the understanding of normative functional development across the early childhood period.

3.2. Methods & Materials

3.2.1. Participants

This study was approved by the University of Calgary Conjoint Health Research Ethics Board. Child participants aged 4-8 years were recruited from Calgary and the surrounding area through the University of Calgary Healthy Infants and Children's Clinical Research Program (HICCUP), as well as through posters distributed throughout the community. In total, 135 children participated in the scan (F = 79, M = 56). Children were excluded if they had a history of neurological or neurodevelopmental disorders or had any contraindications to an MRI scan. Parental consent and child assent were obtained from all participating families. Following data collection, participants were excluded if > 2 minutes of their functional data was deemed to contain high motion (defined as as > 0.2 mm framewise displacement [FD]) (Jenkinson et al., 2002), resulting in a final sample size of $n = 81$ (sample age range: 4.14-7.89 years; mean age =

5.88 years; F = 51, M = 30; average relative FD range: 0.035-0.17 mm; mean average relative FD = 0.076 mm). Data from overlapping samples have been previously published (Dimond, Heo, et al., 2020; Dimond, Rohr, et al., 2020; Graff, Tansey, Ip, et al., 2022; Graff, Tansey, Rai, et al., 2022; Rohr et al., 2017b, 2018b, 2019b; Samson et al., 2021; Tansey et al., 2022).

3.2.2. Code and Data Availability

Data from this study can be made available upon reasonable request. Python scripts for processing and analysis are shared publicly on the lab's GitHub at https://github.com/BrayNeuroimagingLab/BNL_open.

3.2.3. Study Procedure and Stimuli

All children participated in a mock scanner session (de Bie et al., 2010) to familiarize themselves with the MRI scanning environment and procedure. During the mock scan and the MRI scan, participants watched an 18-minute series of clips from the children's television show *Elmo's World*. Participants watched the same clips during the mock scan and MRI scan to minimize novelty effects of the video stimulus. Clips were presented continuously with no breaks in between. This stimulus was chosen because it is educational, relatively gender neutral, and similar to stimuli used in a related study (Cantlon & Li, 2013). Clips were approximately 1 minute long and included content related to early numeracy and literacy and social interaction, with every clip including some spoken language and 16/18 clips including human and/or animated or puppet faces. Cognitive, intelligence, and parent-report behavioural data were also collected, though they were not included in the current study.

3.2.4. MRI Data Acquisition

Structural and functional MRI data were collected at the Alberta Children's Hospital on a 3.0 T GE MR750w (Waukesha, WI) scanner, using a 32-channel head coil. T1 structural images were collected with a 3D BRAVO sequence with the following parameters: voxel size 0.8 x 0.8 x 0.8 mm, matrix size 300 x 300, repetition time (TR) = 6.764 ms, echo time (TE) = 2.908 ms, flip angle (FA) = 10°. Approximately 18 minutes of movie-watching T2*-weighted fMRI data was acquired with a gradient-echo echo planar imaging sequence with the following parameters: voxel size 3.5 x 3.5 x 3.5 mm, matrix size 64 x 64, TR = 2500 ms, TE = 30 ms, FA = 70°, 34 axial slices.

3.2.5. fMRI Data Preprocessing

Structural and functional data preprocessing was completed using in-house Nipype scripts (K. Gorgolewski et al., 2011) that combined functions from Advanced Normalization Tools (ANTs) (Tustison et al., 2014), Analysis of Functional NeuroImages (AFNI) (Cox, 1996), and FMRIB Software Library (FSL) (Jenkinson et al., 2012). Structural images underwent bias field correction, brain extraction, normalization to the Montreal Neurological Institute (MNI)-space NIHPD 4.5- to 8.5-year-old atlas (Fonov et al., 2011), and tissue segmentation using ANTs (Tustison et al., 2014). The functional image pipeline includes confound mitigation steps as recommended in functional connectivity studies, and was shown to maximize signal recovery in ISC in a dataset that overlapped with the present study (Graff, Tansey, Ip, et al., 2022). Head motion parameters were estimated prior to any other steps (Power et al., 2017). The functional data then underwent the following: slice time correction, rigid body alignment, and brain extraction using FSL (Jenkinson et al., 2002, 2012); normalization to a study-specific echo-

planar imaging (EPI) template (Huang et al., 2010) in MNI space with ANTs (Tustison et al., 2014); removal of linear and quadratic trends; high-pass filtering at 0.01 Hz; and regression of 6 head motion parameters, WM, CSF, and global signal, along with each regressor's derivatives, quadratic terms, and quadratic term derivatives. Volumes with a framewise displacement over 0.2 mm (Jenkinson et al., 2002) were censored. Smoothing with a 8.0-mm full width half maximum (FWHM) Gaussian kernel (slightly larger than twice the size of the voxels (Nastase et al., 2019b; Pajula & Tohka, 2014)) was applied.

3.2.6. ISC Analysis

In order to test whether typicality (inter-individual similarity) of response increases with age, we conducted an ISC analysis in AFNI (Chen et al., 2017; Cox, 1996). We hypothesized that if typicality increases with age, we should see higher synchrony between pairs of children that are older compared to pairs of children that are younger. To this end, we created a group-level LME with crossed random effects (Chen et al., 2017; Finn et al., 2020a) that included the average age of the pair as a variable of interest. To test whether participants with wider age gaps would show greater functional response differences than pairs who are close in age, we also included the absolute difference in age between the pairs in our model. This could also potentially account for the possibility that there are areas that show an age-specfic response pattern to the movie, as under that hypothesis, we would expect that children close in age to one another would be more synchronized than children with a larger age difference. The pairwise total number of censored volumes and the sex of each pair (M-M, F-F, or M-F) were included as nuisance covariates. Inferences were drawn using a voxelwise cluster-forming threshold of $p <$

0.0001 and a cluster size of 156 voxels, which controlled for a family-wise error rate equivalent to a corrected cluster *p*-threshold of 0.01 (Cox, 1996).

3.2.7. ROI Selection

To better understand the factors driving age-associated idiosyncrasy, we selected two bilateral ROIs for follow-up analyses. These ROIs (a face processing and a language/social ROI) were chosen because they are engaged by naturalistic tasks (Bottenhorn et al., 2018) and have been extensively studied in development (Enge et al., 2020; Golarai et al., 2017; Gomez et al., 2018; Olulade et al., 2020).

3.2.7.1. Fusiform face area (FFA). For the face ROI, we used the FFA ROIs (which we created by combining the mFus and pFus ROIs) from a visual cortex atlas (Rosenke et al., 2021). In this atlas, the right medal fusiform (mFus) and posterior fusiform (pFus) ROIs were defined using a category-selective functional localizer task. Evidence suggests that the core facial processing network has not yet been lateralized to the right side before adolescence (Dundas et al., 2013, 2014; Hildesheim et al., 2020; Lochy et al., 2019). We therefore analyzed both the right and left FFA separately. We defined a left FFA ROI by flipping the right-hemisphere mFus and pFus ROIs over the *x*-axis and combining them.

3.2.7.2. Superior temporal sulcus (STS). The STS ROI was defined using an open atlas of auditory and visual sentence-comprehension ROIs (Labache et al., 2019). We selected ROIs from this atlas that roughly corresponded to Wernicke's area in the posterior STS (labelled in the atlas as STS 3 and STS 4), an area well characterized for its involvement in auditory and visual language comprehension (DeWitt & Rauschecker, 2013). Similar to facial processing, previous research has shown language lateralization increases across childhood (Olulade et al., 2020). We

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therefore created a right hemisphere STS ROI by flipping the left-hemisphere ROI over the x-axis.

3.2.8. Group Average Signal Regression Analysis

The fMRI blood oxygenation level dependent (BOLD) signal acquired during movie-watching can be described in terms of a combination of sources: (1) the stimulus-driven response (common across individuals); (2) individual-specific processing, i.e., idiosyncratic responses related to off-task thought, or specific/unique interpretations of the stimulus (individual- and session-specific variation); and (3) measurement noise, which is not temporally consistent within or across participants (i.e., session-specific variation) (Di & Biswal, 2022; Finn et al., 2020a; Nastase et al., 2019b). An increase in 'functional typicality' (Gruskin et al., 2020a) with age between children could be due to either an increased contribution of the common stimulus-driven component of the signal, a decrease in the contribution of the idiosyncratic component of the signal (made up of the individual-specific processing and noise), or both.

To investigate which of these effects may be driving an increased synchronization between pairs children with increasing age, we used a regression analysis technique similar to those outlined in previous research studies on naturalistic processing in infants (Wild et al., 2017) and children (Gruskin et al., 2020a; Kamps et al., 2022). In each individual and ROI, we estimated (i) the strength of the shared 'stimulus-driven' response's contribution to the individual's signal, and (ii) the standard deviation of the residuals of the BOLD signal after the shared response was accounted for, to represent the variability of the "idiosyncratic" component of the signal. The shared response for each ROI was derived by calculating the group-average of the z-scored time courses of all participants (Gruskin et al., 2020a; Kamps et al., 2022; Wild et

al., 2017), ignoring censored volumes. The group-average was calculated iteratively, holding out one participant on each iteration. The leave-one-out shared response was then used as a regressor in a linear model to predict the average ROI time course for the left out individual (Wild et al., 2017). We included the left-out individual's censored volumes as nuisance covariates in the regression. From each participant's first-level ROI model, we extracted two values of interest: (i) the β coefficient for the group average time course regressor and (ii) the standard deviation of the residuals after regressing out the group average time course, to represent the variability of the unique component of the individual's response. We chose to use regression, rather than correlation, for this analysis as it enables separation of these components of the signal as beta-weights and residual time series. We tested the hypotheses that (i) the strength of the shared response (the β coefficient) increases with age and (ii) the standard deviation (SD) of the residual component decreases with age. The SD of the residuals was chosen because a greater SD would be reflective of larger fluctuations away from the shared common response. At the group level, we calculated partial Spearman correlations between age and the brain imaging metrics of interest (controlling for sex and head motion), and to assess significance we used a non-parametric approach with 10,000 permutations (similar to Gruskin et al., 2020) to assess the our one-tailed hypotheses (i.e., a positive association between age and the β coefficient, and a negative association between age and the SD of the residuals). This analysis will give evidence as to what is driving the increase in inter-individual similarity over this age range – whether it is due to an increase of the shared stimulus-driven common response with age, a decrease in the idiosyncratic component of the functioning, or both.

3.2.9. Diffuse to Localized Analysis

We explored whether lower inter-individual similarity of brain function in younger children could be in part due to a transition from spatially diffuse to localized functional specificity (Durston et al., 2006). Topographically diffuse responses that lack functional specificity to stimuli could potentially explain why synchronization is lower between younger children. Using the same leave-one-out group average time courses previously calculated in the group average regression analysis, we tested whether the number of voxels associated with the shared group-average response in each individual decreased with age, as the diffuse-to-localized hypothesis suggests. The leave-one-out average group time course was submitted as a regressor (Wild et al., 2017) in a first-level voxel-wise GLM for the corresponding left out participant's non-standardized data within a grey matter mask using FSL's FEAT (Woolrich et al., 2001, 2004). The censored volumes of the left-out individual were included as nuisance regressors in the first-level GLM. The resulting individual voxel-wise z maps were thresholded at $p < 0.05$ (uncorrected), and the percentage of surviving voxels in a cortical grey matter mask derived from the Harvard-Oxford Cortical Atlas (Desikan et al., 2006) was calculated for each participant. To assess associations between age and diffusivity of cortical engagement, we conducted partial Spearman correlations between the percentage of grey matter voxels with a z-score corresponding to $p < 0.05$ and age, controlling for sex and head motion (the total number of censored volumes for the left-out participant). We used the same non-parametric permutation approach in the group average regression analysis to assess the one-tailed hypothesis that the percentage of grey matter voxels associated with the shared signal timecourse would decrease with age.

3.2.10. Dice Coefficient Analysis

Another potential explanation for the relationship of age with spatial patterns of processing is that of decreasing inter-individual variability in the functional topography of the response as age increases. That is, it is possible that while younger children do not use more, or more diffuse, regions of the brain to process a stimulus, they may still use more variable locations compared to older children. To assess this possibility, we used the Dice coefficient to test whether the overlap between areas associated with the shared group-average signals increase between pairs of children with age. We applied the ROI masks to each individual's first-level z-maps obtained from the GLMs described in the diffuse-to-localized analysis. We thresholded the maps at $p < 0.05$ to create binarized spatial maps of the association to the corresponding group-average time courses within each ROI. We then estimated the spatial overlap between pairs of individuals by calculating the Dice similarity coefficient (DSC) (Dice, 1945) of the binarized ROI z-maps for each pair of children. The DSC has a bounded range of [0, 1], and has a highly left-skewed distribution (i.e., skewness < -1 for all our ROIs). For the purpose of drawing statistical inferences, we used a logit function to transform the DSC values into a distribution with a $(-\infty, \infty)$ range. This transformation has been previously utilized for DSC in radiological MRI literature assessing the quality of image segmentations (Anders et al., 2012; Hwee et al., 2011; Stross et al., 2020; Zou et al., 2004).

Similarly to the ISC analyses, we implemented LME models with crossed random effects (Chen et al., 2017) to determine if pairwise DSC was associated with (1) the average age of a pair and (2) the age difference of a pair, using the R package '*lme4*' (Bates et al., 2015). Motion and sex were included as nuisance regressors in all mixed effects models. We repeated this procedure for all four ROIs (left and right FFA, left and right STS). Pairs that have a DSC of 0 or

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1 result in a logit(DSC) that is undefined. As the number of pairs with a DSC of 0 or 1 were low

for each ROI (varying from 0 – 2.5% of all pairs; 0 pairs for the left FFA, 1 pair for the left STS,

24 pairs for the right STS, and 81 pairs for the right FFA, out of a total of 3240 pairs; of these

omitted pairs, 1 pair from the rhFFA and 10 pairs from the right STS were omitted because their

DSC = 1, while the all remaining pairs were omitted because their DSC = 0), we dropped these

pairs before calculating the LME models. In this analysis, positive effects of average age would

suggest that the older a pair, the more similar their functional topography within the ROIs, while

a negative effect of age difference would suggest that children closest in age will be more similar

to one another.

3.3. Results

3.3.1. ISC Analysis

After controlling for motion, ISC across the whole sample was significant throughout

almost all of the brain. A visualization of the areas with strongest ISC can be found in **Figure

3.1**. Average age was associated with ISC throughout widespread areas of the brain, and almost

all significant clusters were positive, save for two in the bilateral occipital pole, located in the

early visual cortex areas (V1-V3) (**Figure 3.2**). Clusters with positive average age were found

bilaterally in the temporal cortex, including the superior, middle, and inferior gyri; the superior

and middle frontal gyri; the ventral fusiform cortex; the precuneus and PCC; and the SMG

(**Appendix B1**). We also considered clusters significantly associated with age difference; only a

few relatively small clusters were found, and all were negative, meaning that ISC decreased with

increasing absolute difference in age of a pair (**Figure 3.3**). Clusters were found in the bilateral

precentral gyri and supramarginal gyri, as well as the superior precuneus near the midline, the

right inferior lateral cortex, and the bilateral cerebellum (**Appendix B2**). All ISC figures were created with BrainNet viewer (Xia et al., 2013a).
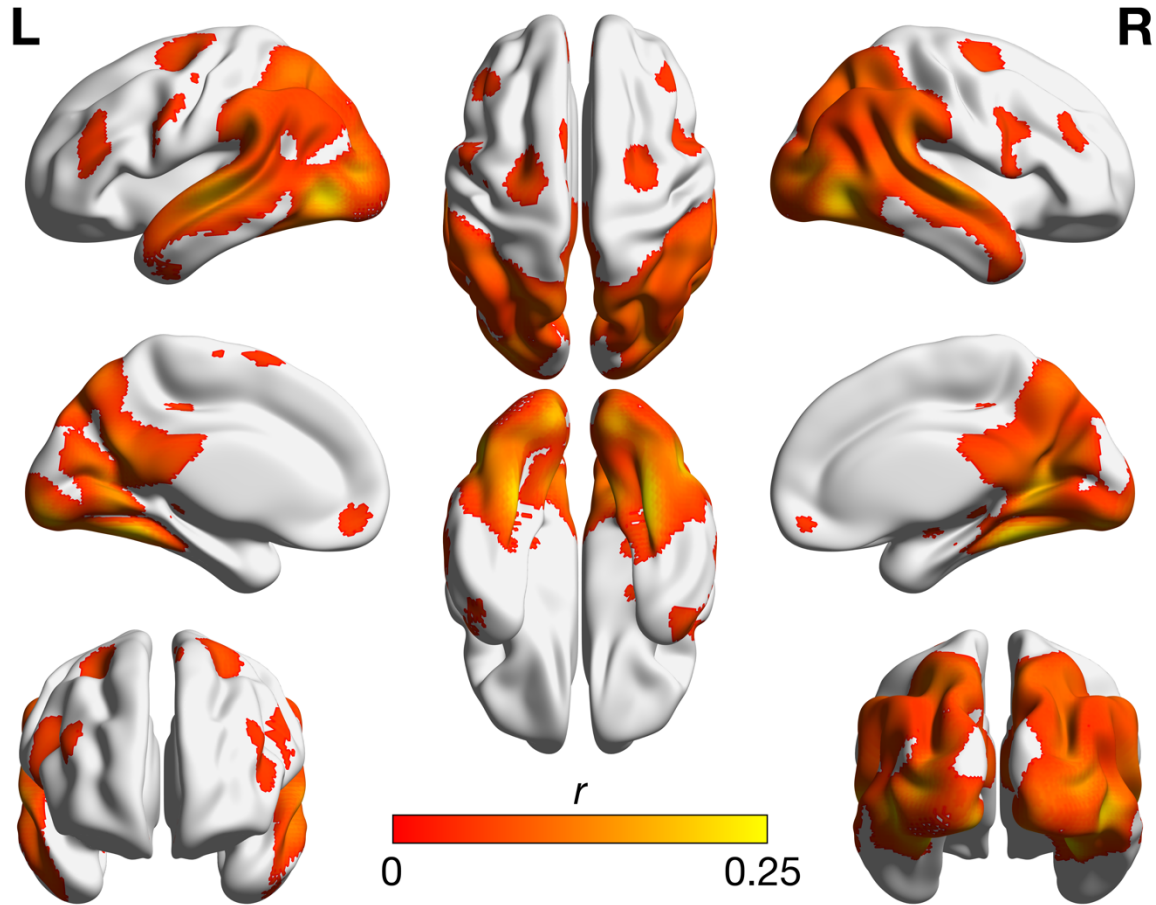
Figure 3.1. Mean inter-subject correlation (ISC) across the group.

Group mean correlation maps were derived from a linear mixed effects model with crossed random effects (Chen et al., 2017), controlling for total number of censored volumes per pair. Colour gradient indicates the ISC value at each voxel in units of Pearson's *r*. Clusters were formed at a voxelwise threshold of $p < 0.0001$ and a cluster forming threshold of $\alpha = 0.01$. As this analysis is sensitive to small effects due to the large number of pairs, for visualization purposes, the map was further thresholded at a voxelwise $r = 0.05$.
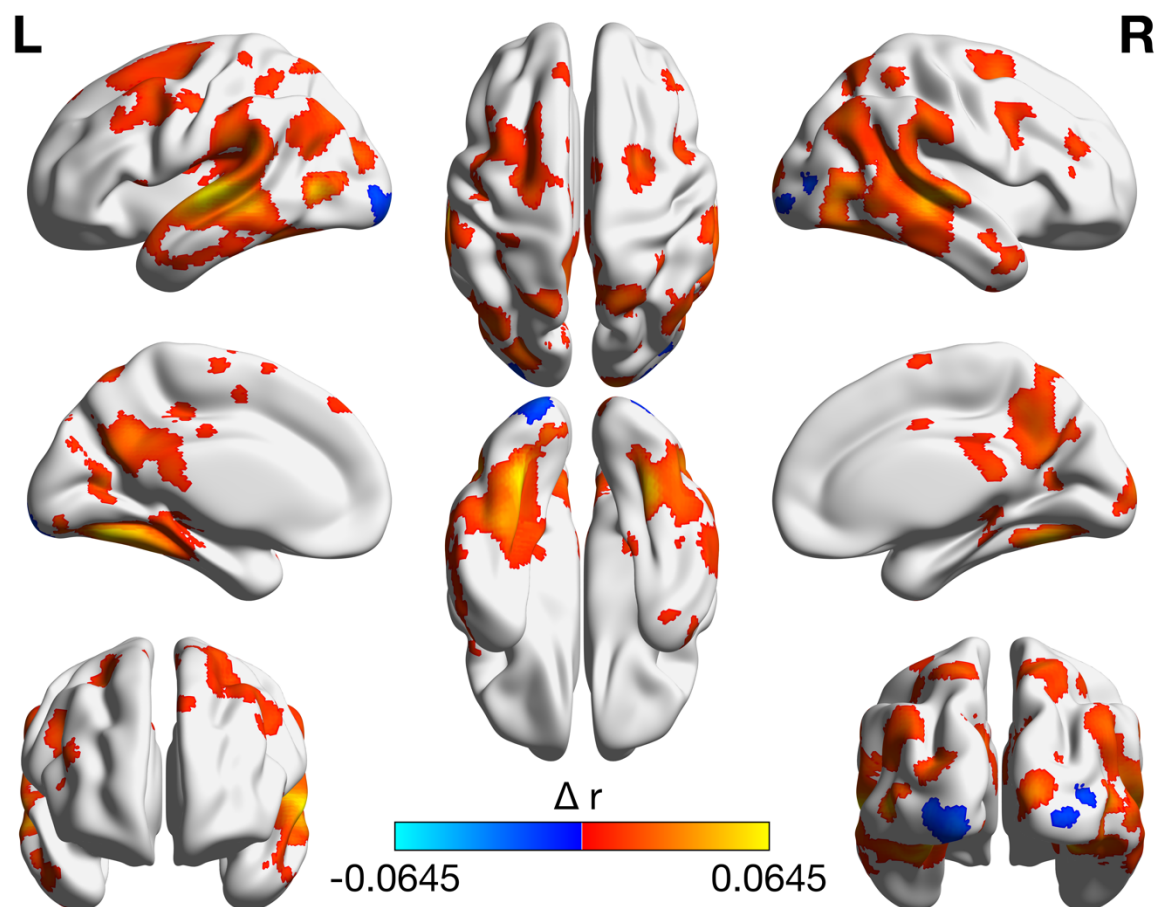
Figure 3.2. The association between ISC and average age of pair.

Colour gradient indicates the β value of average age of pair (in years) at each voxel in units of Pearson's r. Warm colours indicate a positive relationship, where a pair with a greater average age show greater synchrony to one another, and cool colours indicate a negative relationship, where a pair with a younger average age show greater synchrony with one another. Clusters were formed with a voxelwise threshold of $p < 0.0001$ and a corrected cluster p-threshold of 0.01 (Cox, 1996). Significant positive clusters are found throughout much of the parietal, occipital, and temporal lobes, as well as some clusters in the frontal lobes. Negative clusters are found in the very posterior of the bilateral occipital poles.
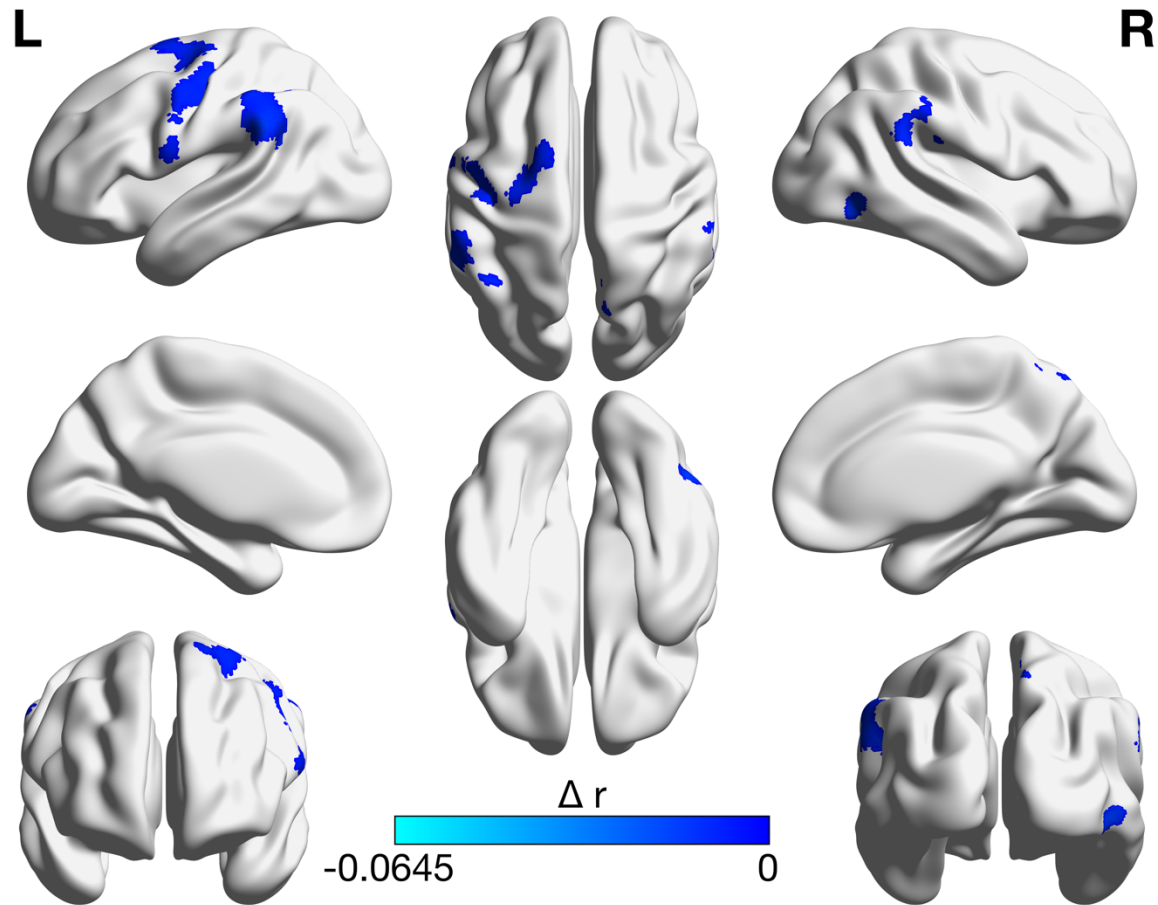
Figure 3.3. The association between ISC and absolute difference in age.

Colour gradient indicates the *β* value of age difference at each voxel in units of Pearson's *r*. Cool colours indicate a negative relationship, where a pair closer in age show greater synchrony with one another compared to pairs farther apart in age. Clusters were formed with a voxelwise threshold of $p < 0.0001$ and a corrected cluster *p*-threshold of 0.01 (Cox, 1996). Significant negative clusters were found in the left precentral gyrus, left supramarginal gyrus, right cerebellum, left cerebellum, right supramarginal gyrus, bilateral superior precuneus, and the right inferior lateral occipital cortex.

3.3.2. Group Average Signal Regression Analysis

There was a significant positive association between the β coefficient of the shared signal response and age in all four ROIs (**Figure 3.4, top row**): the left FFA (Spearman ρ = 0.2524, p = 0.0120); the right FFA (Spearman ρ = 0.1888, p = 0.0479); the left STS (Spearman ρ = 0.2090, p = 0.0338); and the right STS (Spearman ρ = 0.1835, p = 0.0462). When applying false discovery rate (FDR) tests for multiple comparisons, all relationships survived (corrected p-values = 0.0479). For all ROIs, the association of age and standard deviation of the residuals was non-significant under our one-tailed hypothesis (**Figure 3.4**, bottom row; right FFA: Spearman ρ = 0.0622, p = 0.7020; left FFA: Spearman ρ = 0.1754, p = 0.9494; left STS: Spearman ρ = 0.0300, p = 0.6043; right STS: Spearman ρ = -0.0129, p = 0.4563).
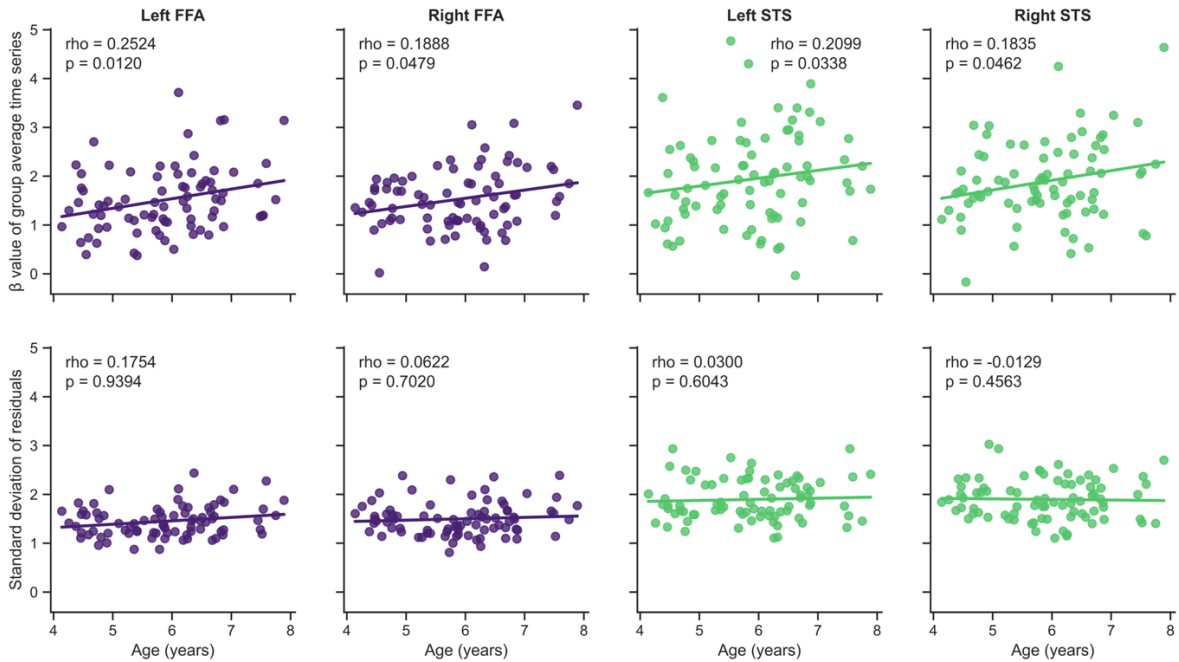
Figure 3.4. Age associations for temporal response properties in ROIs.

The top row shows the scatter plots for each ROI between age and the strength of the β value of the group average time series in predicting the time series of a left out individual. The bottom

row shows the scatter plots for each ROI between age and the standard deviation of the residuals after regressing out the group average time series from each individual. The rho on the plots indicates the partial Spearman correlation between age and the metric of interest, controlling for sex and head motion, p-values are one-tailed based on directional hypotheses. Trend lines are included for visualization purposes.

3.3.3. Diffuse to Localized Hypothesis

None of the ROIs had a significant association between percentage of GM voxels associated with the shared stimulus-driven response and age under our one-tailed hypotheses. Of the four ROIs, only the right FFA showed a trending negative Spearman correlation (**Figure 3.5**; Spearman ρ = -0.1799, p-value = 0.0571). All other ROIs showed non-significant correlations between age and percentage of GM voxels (left FFA: Spearman ρ = 0.0427, p-value = 0.6518; right STS: Spearman ρ = 0.0341, p-value = 0.6177; left STS: Spearman ρ = -0.0385, p-value = 0.6336).
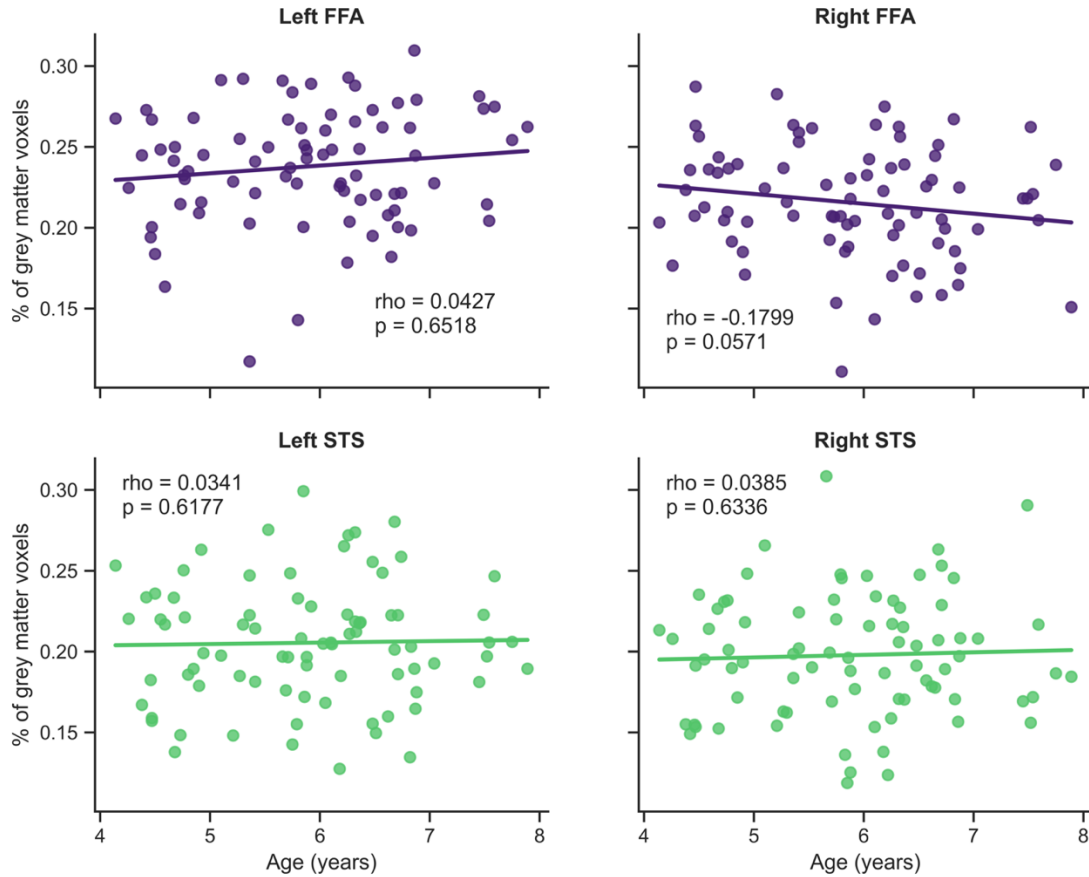
Figure 3.5. The relationship between age and the percentage of stimulus-evoked GM voxels at p ≤ 0.05.

Rho indicates the partial Spearman correlation between age and percentage of GM associated with the group average signal, controlling for sex and head motion, while the *p*-value was determined through permutation tests with a null distribution computed from 10,000 iterations, and are one-tailed based on directional hypotheses. Trend lines on the models are included for visualization purpose.

3.3.4. Dice Coefficient Analysis

The only ROI that showed significant effects of age in the Dice coefficient analysis was the left FFA. All other ROIs had non-significant associations between DSC and average age

(right FFA: β = -0.0751, p-value = 0.464; right STS: β = 0.3789, p-value = 0.136; left STS: β = -0.0836, p-value = 0.5833; all p-values uncorrected) and age difference (right FFA: β = -0.0496, p-value = 0.719; right STS: β = 0.0190, p-value = 0.271; left STS: β = -0.0126, p-value = 0.3127 all uncorrected). In the left FFA, both average age (β = 0.2675, p-value = 0.0112 uncorrected) and age difference (β = -0.2611, p-value = 0.0344 uncorrected) were significant. After adjusting for multiple comparisons over four ROIs using the Benjamini-Hochberg FDR method, neither of the associations remained significant.

3.4. Discussion

This study provides evidence that across early childhood, functional brain responses to naturalistic stimuli generally increase in inter-individual similarity. The ISC analysis found that as the average age of a pair increases, so does the similarity of brain response in broad areas of the brain related to the passive viewing task, while a significant relationship between age difference and ISC was only found in a few localized clusters, notably in the bilateral supramarginal gyrus, precuneus, and left precentral gyrus. The ROI regression analyses showed that in areas of the brain related to visual, language, and social processing, increasing typicality of response with age maybe be associated with an increase in the strength of the shared task-evoked response, rather than a decrease in the individual component of the signal, made up of both individual processing and noise (as represented by the standard deviation of the residual signal). Finally, we also found no evidence to support the diffuse-to-local hypothesis of functional brain development in higher-order visual and language processing regions of the brain. Together, these results suggest an increase in the inter-individual similarity of stimulus

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processing across individuals in regions involved in social, facial, and language functions with increasing age across early childhood.

Generally, associations with average age of the pairs were more widespread than for age difference. Interestingly, the bilateral supramarginal gyri were two areas where age difference was significantly associated with ISC. Combined with previous findings that showed there were qualitatively different child- and adult-specific responses in the supramarginal gyrus during movie watching (Di & Biswal, 2022), this evidence suggests that there may be age-specific patterns of responding in the supramarginal gyri. However, these age-specific patterns are notably focal relative to average age associations. Our result that brain function broadly becomes increasingly consistent or "typical" between children across early childhood builds on findings in previous studies using movie stimuli that suggest that younger children show lower cross-individual consistency in brain function than adults (Cantlon & Li, 2013; Kamps et al., 2022; Moraczewski et al., 2018). This also is supported by literature showing that face- and scene-processing functions in children appear to "homogenize" over time, rather than change from a child-unique to adult-unique response, during task fMRI (Tian et al., 2021). Further, this trend of increasing typicality between individuals may continue across adolescence (Lerner et al., 2021). We will note that while Moraczewski et al. (2018) found that adults had more synchronized responses to one another than children did, they also did not find evidence of significant differences in synchronization between their four- and six-year-old groups. This runs counter to our findings, which show that there is an increase in synchrony / typicality across a similar age range. This may be due to our use of a continuous measure to evaluate age rather than discrete groups, or increased sensitivity related to a wider age range and longer acquisition time.

Considering this work together, it is likely that effect sizes for contrasts between young children and adults are larger than across this smaller early childhood age range.

One well-supported developmental theory is that of 'interactive specialization' (Battista et al., 2018; Johnson, 2000, 2011; Joseph et al., 2011; Moraczewski et al., 2018), which posits that cognitive functions hone their spatial specificity from broadly diffuse, functionally imprecise areas to localized, domain-specific regions (Durston et al., 2006). This refinement of functional topography is achieved via repeated interactions between brain areas as they are exposed to stimuli through experience (Johnson, 2011). While we posited that the greater diffusivity of responses seen at younger ages may be due in part to a greater inter-individual variability in spatial responses that become more similar, localized, and specific over development, generally, findings in our ROIs did not support a diffuse to focal age-related pattern. Similarly, when considering the spatial overlap of responses using Dice coefficients, we only found evidence of decreasing inter-individual variability of spatial response topography with age in the left FFA, though it did not survive multiple comparisons correction. While numerous studies have found evidence supporting the diffuse to localized hypothesis (Bonte et al., 2013; Cohen Kadosh & Johnson, 2007; Golarai et al., 2007; Moraczewski et al., 2018; Scherf et al., 2007), there is further evidence suggesting that as early as infancy, responses to certain stimuli are regionally localized (McKone et al., 2012); for example, the processing of emotional adult human voices compared to other auditory stimuli (Blasi et al., 2011), as well as category-specific visual responses in the occipitotemporal cortex (Deen et al., 2017), with connectivity within early face- and scene-processing networks present as young as 27 days after birth (Kamps et al., 2020); though other evidence suggests that responses in the fusiform gyrus are still being fine-tuned into adolescence (Golarai et al., 2010; Nordt et al., 2021). Our findings in the left FFA suggest that

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there may be some spatial refinement of the response occurring in this area; and indeed, previous research has shown that the face-specificity of the left FFA may occur at a more protracted trajectory than the right FFA (Joseph et al., 2011; Scherf et al., 2007). It is possible that our lack of significant findings in the rest of the ROIs are due to the bulk of the regional localization process in our selected ROIs occurring prior to 4 years of age.

In *post hoc* analyses, we did not find evidence that the increase in inter-individual similarity was due to a decrease of the individual-unique component of the signal. This has interesting implications: it suggests that increasing typicality over early childhood is due to the processing of the stimulus itself becoming stronger, rather than a decrease in individual task-unrelated processes or noise with age. In the case of the left FFA, which was the only ROI that showed significant associations with our age metrics in the Dice coefficient analysis (though they did not survive multiple comparisons correction), this increasing typicality may be due in part to an increasing similarity in the spatial patterns of response to the movie stimulus within the region. Signal variability, typically defined as the standard deviation of the brain signal, changes throughout the lifespan (Nomi et al., 2017) and may underlie cognitive functions such as flexibility (Armbruster-Genç et al., 2016), integration (Garrett et al., 2021), and inhibition (Thompson et al., 2021). While most studies of BOLD signal variability over the lifespan have been conducted during rest (Nomi et al., 2017) or task (Thompson et al., 2021) conditions, one study found that BOLD variability increased longitudinally within subjects between the ages of 2-8 years during movie-watching in the bilateral inferior and superior frontal gyri and the bilateral middle and inferior temporal gyri, and that this increase may be related to white matter development (Wang et al., 2021). In our study, we found that the strength of the shared stimulus-related component of activity increased with age, which could appear as increased overall signal

variability, whereas there was no evidence for a corresponding decrease in residual variability attributed to individual processes and noise.

Our findings of less typicality in the lower end of our age range may be reflective of the fact that younger children may have more unique, idiosyncratic interpretations of, and attentional focus to, the stimulus. There is growing evidence that ISC can encode similarities in interpretation and understanding of external stimuli between individuals (Nguyen et al., 2019; Yeshurun et al., 2017) and attentional engagement. Children are constantly integrating information from the environment in order to construct frameworks with which to understand the world (Cantor et al., 2019; Lucas et al., 2014). Differences in neural processing may therefore be reflective of different conceptual understandings between young children. As we were not able to collect eye-tracking data, we could not ascertain the extent to which ISC is related to differences in attentional focus during the scan. A recent study that combined electroencephalography (EEG), eye-tracking, and physiological recordings found that inter-individual synchrony of both brain signal and eye gaze were related to attentional engagement as well as information retained from a video stimulus (Madsen et al., 2021; Madsen & Parra, 2022). Further, synchrony between children may vary as a function of the content in the different clips – for example, it has been shown that ISC is higher between individuals during moments with high engagement ratings (Song et al., 2021a), though there is also evidence that individual differences in synchrony are preserved for a number of different movie stimuli across approximately a third of the brain, including the superior temporal lobe (Gao et al., 2020). A goal for future research should be to directly investigate stimulus content and attention in relation to idiosyncrasies in functional responses in young children.

This study has several notable strengths. First, our sample represents an age range often overlooked in neuroimaging literature, due to the numerous practical obstacles in collecting data from this population (Poldrack et al., 2002; Raschle et al., 2012). Second, we were able to obtain 18 minutes of movie-watching fMRI data from our participants. Longer scans can improve reliability and decrease signal to noise ratio in fMRI data (Birn et al., 2013; Elliott et al., 2021; Murphy et al., 2007), which is particularly important in young children when high levels of movement in the scanner reduce the usable portion of scans (Dosenbach et al., 2017a). We used a stringent head motion inclusion criterion to control for the potential effects of head motion. There are also several limitations. As noted above, reliable eye-tracking in this age range is challenging to obtain, precluding precisely controlling for eye movements. Another limitation is the use of pre-defined ROIs from group atlases defined from adults. Individual or child-specific ROIs may have yielded different findings (Kamps et al., 2022). Further, our null findings with regards to the relationship between age and the standard deviation of the residuals may be due in part to the individual residual component being made up mostly of measurement noise as head motion is a concern in studies of young chlidren. While we tried to mitigate this by including each participant's censored volumes as a regressor in the first-level linear models, separating measurement noise from systematic individual variation is not possible with the available data (i.e., no stimulus repetition was included in this design). The preprocessing pipeline used here was chosen based on another study conducted in our lab, which used an overlapping sample of data to optimize preprocessing for child movie fMRI data (Graff, Tansey, Ip, et al., 2022), based on maximizing ISC while preserving individual information. As the data from these two studies were not independent, we may have introduced a bias towards higher ISC that could reduce the capacity to detect individual differences. However, we note that preprocessing steps are also

generally in-line with recent relevant literature (Ciric et al., 2018a; Gruskin et al., 2020a; Parkes et al., 2018; Song et al., 2021a). Finally, as data used in this study are cross-sectional, and not longitudinal, we are not able to define developmental trajectories of typicality in brain function; instead, we see cross-sectional associations as age increases. It is possible that longitudinal data may reflect different within-individual patterns of functional typicality.

3.5. Conclusions

While early childhood is a time of rapid development and learning, little is known about the individual differences of brain function in this age range. In this study, we find that over the ages of 4-8 years, the brain responses of young children to dynamic, multimodal video clips become more typical and less idiosyncratic with increasing age. The increasing typicality in key visual and language processing areas may be driven by an increase in stimulus-related activity, rather than a decrease in individualistic activity and noise. The heterogeneity in functional brain responses in young children is especially important to consider when conducting research into cognitive and behavioural development and academic functioning among children in this age range.

CHAPTER 4 - Inattentive and Hyperactive Traits Differentially Associate With Interindividual Functional Synchrony During Video Viewing in Young Children Without ADHD

4.0. Abstract

Inattention and hyperactivity present on a spectrum and may influence the way children perceive and interact with the world. We investigated whether normative variation in inattentive and hyperactive traits was associated with differences in brain function while children watched clips from an age-appropriate television program. fMRI data and parent reports of inattention and hyperactivity traits were collected from 81 children 4-7 years of age with no parent-reported diagnoses. Data were analyzed using inter-subject correlations in mixed effects models to determine if inattentive and hyperactive traits were associated with idiosyncrasy of fMRI response to the video. We hypothesized that pairs of children with higher average inattention and hyperactivity scores would show less inter-individual brain synchrony to one another than pairs with lower average scores on these traits. Video watching engaged widespread visual, auditory, default mode and dorsal prefrontal regions. Inattention and hyperactivity were separably associated with inter-subject correlation in many of these regions. Our findings suggest that the spectrum of inattention and hyperactivity traits in children without ADHD are differentially associated with neural processing of naturalistic video stimuli, which may have implications for understanding how children with different levels of these traits process audiovisual information in unconstrained conditions.

4.1. Introduction

Inattention and hyperactivity are among the most common neurodevelopmental challenges affecting children. In children, non-clinical levels of inattention and hyperactivity have been associated with poorer outcomes such as higher rates of grade retention and graduation failure in adolescence (Bussing et al., 2010), less positive relationships with friends and parents (Rielly et al., 2006), and worse executive functioning (A. J. Brown & Casey, 2016). Population-based studies have further shown that increased inattention symptoms in childhood are associated with lower academic performance in adolescence (Salla et al., 2016; Sayal et al., 2015) and reduced financial earnings in adulthood (Vergunst et al., 2019).

In adults without ADHD, inattentive and hyperactive/impulsive traits have been associated with inter-individual synchrony of BOLD signal during viewing of a naturalistic movie stimuli (Salmi et al., 2020). This suggests that inattention and hyperactivity may impact the way an individual perceives and interacts with their environment. However, the relationships between inattentive and hyperactive traits and brain function in typically developing children remain understudied. Here, we investigate whether inattentive and hyperactive traits in young children without ADHD are associated with neural processing of a complex audiovisual stimulus: clips from an age-appropriate television program.

To capture individual differences in the way the brain processes audiovisual (AV) media, we used inter-subject correlation, or ISC (Hasson et al., 2004). Functional magnetic resonance imaging (fMRI) studies show that naturalistic AV stimuli evoke synchronized brain activity across individuals (Hasson et al., 2004, 2008; Nastase et al., 2019b) in visual, auditory, emotional, navigation, and language processing regions, as well as areas related to attentional control (Bottenhorn et al., 2018). By calculating the ISC (also referred to as "inter-individual

synchrony"; measured as the Pearson correlation between the BOLD time courses from corresponding voxels of individuals watching the same movie), we can quantify whether individuals with similar behavioural traits show synchronized processing of an AV stimulus. Using ISC, researchers have found that individuals with autism and elevated depressive symptoms can show idiosyncratic neural responses to movies (Byrge et al., 2015; Gruskin et al., 2020b). Pairwise ISC measures allow researchers to investigate idiosyncrasy and granular individual differences of both brain function and behaviour, as they can capture the ways in which two individuals may differ in their processing of a stimulus based on their specific continuous traits and phenotypes (Finn et al., 2020b).

Previous work has examined the association between a clinical diagnosis of ADHD and ISC during video viewing. In one adult study (Salmi et al., 2020), controls displayed more synchronized brain activity than ADHD individuals in the lateral and medial occipital cortex, precuneus, temporoparietal junction, superior temporal cortex, and – when speech or music distractors were added to the movie – the posterior parietal cortex. However, they also found that in the control group, similarity of impulsivity scores was associated with greater ISC in the cuneus, dorsomedial prefrontal cortex, and temporoparietal junction, while similarity of inattention was associated with ISC in a small bilateral region of the precuneus. Contrary to these findings, in a case-control study that compared children with ADHD to non-ADHD controls (Tang et al., 2019), the brain activity of the ADHD group was more synchronized than the control group in widespread areas of the occipital and temporal lobes. To our knowledge, the specific dimensional relationships between inattention and hyperactivity in young children without ADHD and ISCs have not yet been investigated.

Video-watching offers attractive benefits in developmental neuroimaging research, as it probes brain function in a dynamic, multimodal, and arguably more "ecologically valid" context than traditional task-based or resting-state paradigms (Sonkusare et al., 2019a), opening up an entirely new realm of unique questions and techniques. It also has the added benefit of reducing head motion of young children during MRI scans (Greene et al., 2018b; Vanderwal et al., 2015). Further, the centrality of screen media in many children's lives warrants investigation into it the ways it is processed by the brain and could offer important nuance regarding the potential benefits and disadvantages of this activity.

In this study, we investigate whether inattentive and hyperactive traits are associated with inter-individual synchrony in young children without ADHD during the presentation of video clips from an educational television show. We hypothesized that greater inattention and hyperactivity scores would be associated with lower pairwise synchrony. Both inattention (Arabaci & Parris, 2018; Jonkman et al., 2017) and hyperactivity traits (Arabaci & Parris, 2018) have been positively linked to mind-wandering in children and adults without ADHD (Frick et al., 2020), which could potentially direct attention away from the shared video stimulus, resulting in decreased synchrony (Nastase et al., 2019b). Specifically, we test the hypothesis that brain function is more idiosyncratic in children with higher inattention and hyperactivity trait levels.

4.2. Materials and Methods

4.2.1. Participants, Study Procedure, & Stimuli

Participants were recruited from Calgary and the surrounding area in Southern Alberta as part of a longitudinal neuroimaging study in early childhood. Study procedures were approved

by the University of Calgary Conjoint Health Research Ethics Board. Parents provided informed consent for their child's participation and children provided assent. All data collection occurred at the Alberta Children's Hospital. Children with a history of psychiatric or neurodevelopmental disorders were excluded, as were any children with a medical condition or other contraindications that prevented participation in an MRI scan. Prior to the scan, all participants underwent a mock scanner training session to prepare them for data collection. A total of 135 children (79 females, 56 males) aged 4-7 years participated. Structural MRI, 18-minutes of video-watching fMRI, and parent-report behavioral data were collected. Following data collection, children were excluded from analysis if they had more than 2 minutes of motion corrupted volumes (motion corruption defined as > 0.2 mm FD, Jenkinson criteria; (Jenkinson et al., 2002)). This exclusion criterion was used to minimize differences in head motion among the participants, as head motion is very high in children in the scanner (Dosenbach et al., 2017b). Further, in ISC analysis, which considers participants as pairs, motion is additive within each pair. In total, 54 of the original sample of 135 children were excluded (F = 28, M = 26), leading to a final sample size of $n = 81$ (F = 51, M = 30). The demographic characteristics of this final sample are presented in **Table 4.1**. The demographics of included vs. excluded children can be found in **Appendix C1**.

During video-watching fMRI, participants passively viewed a selection of clips from the children's television show "Elmo's World." This stimulus was selected as it contains content that is educational and gender neutral, human faces, depicts social interaction, and is similar to the naturalistic stimuli used in other developmental neuroimaging research (e.g., (Cantlon & Li, 2013). The video used in the scanner was also played for each participant during their mock scanner session to minimize between-participant effects of stimulus novelty.

4.2.2. MRI Data Acquisition

All neuroimaging data were acquired at the Alberta Children's Hospital using a 3.0T GE MR750w (Waukesha, WI) scanner with a 32-channel head coil. Structural images were acquired with a T1-weighted 3D BRAVO sequence with the following parameters: TR = 6.764 ms, TE = 2.908 ms, FA = 10°, voxel size 0.8 x 0.8 x 0.8 mm, matrix size of 300 x 300. Functional images were acquired with a T2*-weighted gradient-echo EPI sequence with the following parameters: 34 axial slices, 433 volumes, TR = 2500 ms, TE = 30 ms, FA = 70°, voxel size of 3.5 x 3.5 x 3.5 mm, matrix size of 64 x 64.

4.2.3. Inattention & Hyperactivity Measures

To measure inattention and hyperactivity traits, parents completed the Swanson, Nolan, and Pelham Questionnaire (SNAP-IV), a Likert-type rating scale measuring ADHD behaviors based on DSM-IV criteria (Bussing, Fernandez, Harwood, et al., 2008). We used a shortened version of the SNAP-IV (the MTA SNAP-IV), which has two separate subscales that measure the participant's level of inattention (9 items) or hyperactivity (9 items) (Bussing, Fernandez, Harwood, et al., 2008), and gives a final score for ADHD-hyperactive/impulsive (SNAP-H), ADHD-inattentive (SNAP-I), and ADHD-combined (SNAP-C). Scores can range from 0-3. A higher SNAP score indicates a higher level of ADHD-related behaviors. A parent-report SNAP score of greater than 1.2 is associated with an increased probability of concern, and scores above 1.8 are associated with a higher probability of ADHD diagnosis (Bussing, Fernandez, Hardwood, et al., 2008). This study used the SNAP-I and SNAP-H scores.

4.2.4. fMRI Preprocessing

fMRI data was preprocessed with an in-house, customized Nipype pipeline (K. J. Gorgolewski et al., 2017). Steps in the anatomical image preprocessing include bias correction via ANTs (Tustison et al., 2014) *n4BiasFieldCorrection*, removal of skull and non-brain tissue via ANTs *antsBrainExtraction*, normalization to the NIHPD 4.5-8.5 year-old asymmetrical atlas in MNI space (Fonov et al., 2009, 2011) using ANTs *antsRegistration*, tissue segmentation using ANTs *Atropos*, and AFNI (Cox, 1996)'s *3dmask_tool* to erode the tissue segmentations.

The functional image preprocessing pipeline generally followed recommendations in (Ciric et al., 2018b) and (Graff, Tansey, Ip, et al., 2022). Head motion parameters were first estimated with FSL *MCFLIRT* (Jenkinson et al., 2002) (following recommendations from Power et al. (Power et al., 2017) to estimate head motion parameters for regression prior to slice time correction). Functional data then underwent slice time correction with FSL's *slicetimer*, and rigid body alignment was performed with FSL's *MCFLIRT* (Jenkinson et al., 2002). Next, non-brain tissue and skull stripping were performed with FSL's *BET*. We generated a study-specific EPI template in MNI 2 mm voxel space, following recommendations by Huang et al. (Huang et al., 2010), and used ANTs *antsRegistration* (Tustison et al., 2014) to warp the EPI image to this template. Tissue segmentations from the T1 image were warped to this functional image using FSL's *FLIRT* (Greve & Fischl, 2009; Jenkinson et al., 2002). Linear and quadratic trends were removed, and a high-pass filter at 0.01 Hz was applied. Nuisance regressors included 6 head motion parameters, WM, CSF, and global signal. We also included the derivatives, quadratic terms, and quadratic term derivatives for each of the nuisance regressors into the regression model. Volumes with a framewise displacement exceeding 0.2 mm based on the Jenkinson criteria (Jenkinson et al., 2002) were censored (Power et al., 2012, 2014; Rohr et al., 2019a).

Finally, functional data was smoothed using a 8.0 mm FWHM Gaussian kernel, as previous studies have suggested that the optimal smoothing kernel for ISC data is slightly larger than twice the size of the voxels (Nastase et al., 2019b; Pajula & Tohka, 2014).

4.2.5. ISC Analyses

Second-level group analyses were conducted using AFNI. Voxelwise, whole-brain ISCs were computed by calculating the Pearson correlation of the BOLD signal time course at corresponding voxels between each pair of subjects (Hasson et al., 2004). Pairwise *r*-maps were then entered into a LME model with crossed random effects to address the statistical non-independence in ISC data (Chen et al., 2016, 2017).

The pairwise inattention and hyperactivity terms included in models were calculated as the average SNAP-I and SNAP-H scores for each pair. When considering pairwise data for ISC analysis, it is possible to characterize the behavioral distance between individuals in a number of ways; typically, either by averaging the scores of a pair, or calculating the absolute difference in scores between individuals in each pair. We selected the former metric as we are testing the hypothesis that idiosyncrasy of brain response increases with symptom scores (Finn et al., 2020b). In other words, we expected that two children with low scores would show greater ISC to one another than two children with high scores, even if both pairs had the same absolute difference in scores between them. This hypothesis is grounded in the idea that children with high symptom scores will be more distractable and therefore less likely to be attentive to the shared stimulus, and that it is unlikely that individuals will be distracted in a systematic way. Similarly, we included the average age of each pair as a control covariate, as distractibility decreases with age in childhood (Hoyer et al., 2021). To account for head motion, we included

the total number of censored volumes per pair of subjects as a nuisance covariate. Sex was controlled for by including dummy covariates in the model representing sex makeup of each pair (female-female, female-male, and male-male). All continuous variables and covariates were mean-centered.

We created three models in total: 1) one that included inattention, 2) one that included hyperactivity, and 3) one that included both inattention and hyperactivity as variables in the model to account for both simultaneously. This allowed us to calculate a contrast for comparing associations between these measures. Statistical significance was determined through cluster-based thresholding using a voxelwise threshold of $p < 0.001$ and a cluster forming threshold corresponding to an $\alpha = 0.05$ (Cox, 1996). Figures visualizing surface projections of results were created using BrainNet Viewer (Xia et al., 2013b).

To account for potential differences in attention to the stimulus, we calculated versions of all the models that included frontal eye field (FEF) synchrony as a control covariate. FEF signal has been used in previous studies as an approximate for visual attention and gaze behavior (Moraczewski et al., 2018; Redcay et al., 2010). We averaged the ISC values in all voxels within a bilateral FEF region of interest defined from the Multiresolution Intrinsic Segmentation Template (MIST) parcellation (Urchs et al., 2019) for each pair and included this value as a covariate in the models.

4.3. Results

4.3.1. Sample Characteristics

Demographic data for the final sample can be found in **Table 4.1** and SNAP scores in **Figure 4.1**.

Table 4.1. Demographic summary for the entire sample (n = 81).

	Age (years)	Censored volumes	Average relative FD (mm)	FSIQ	SNAP-I	SNAP-H	Sex
Range	4.14 – 7.89	1 – 57	0.035 – 0.17	80 – 139	0 – 2.89	0 – 2.33	
Mean	5.88	21.32	0.076	111.1	0.73	0.76	F = 51
SD	0.94	16.69	0.030	12.77	0.49	0.59	M = 30
Median	5.88	16.00	0.068	112	0.67	0.67	
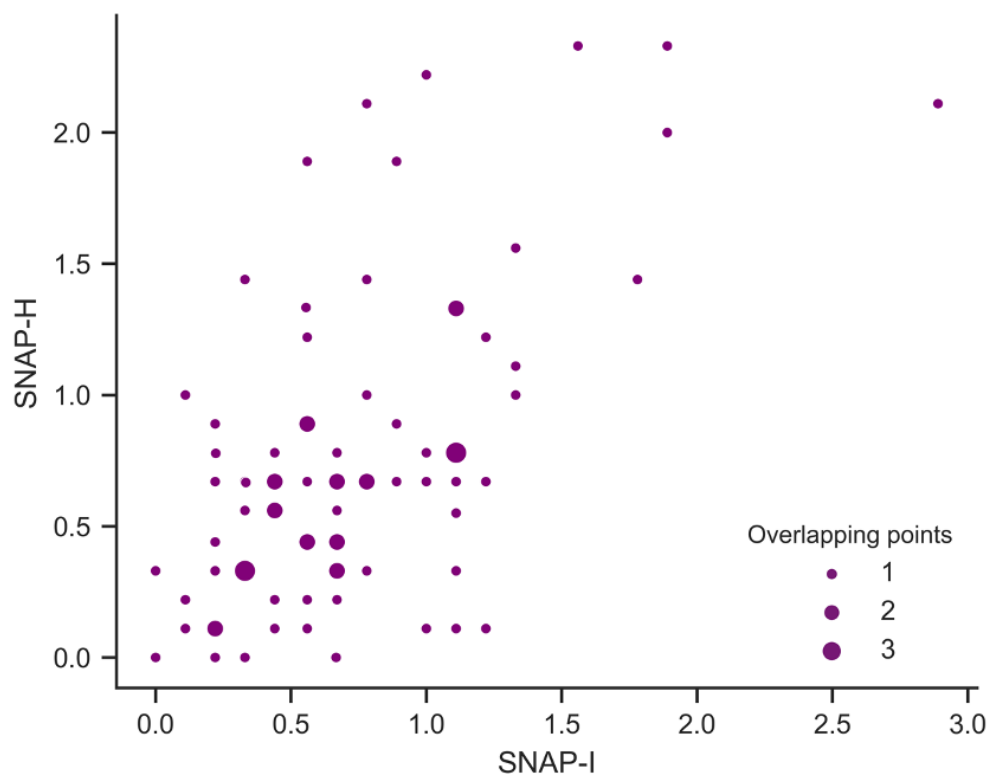
Figure 4.1. Scatterplot of SNAP-I and SNAP-H scores.

The size of points on the graph denotes the number of individuals located at the coordinates to capture overlapping data points. SNAP-I and SNAP-H are correlated at Spearman's $\rho = 0.612$, p < 0.001.

4.3.2. ISCs Across the Whole Sample

Significant ISC is seen in the entire sample across almost all of the brain. Due to high statistical power from the large number of pairs included in the analysis, nearly all grey matter voxels survive cluster thresholding. **Figure 4.2** shows the unthresholded map of group average ISC (Pearson's *r*) of the whole sample.
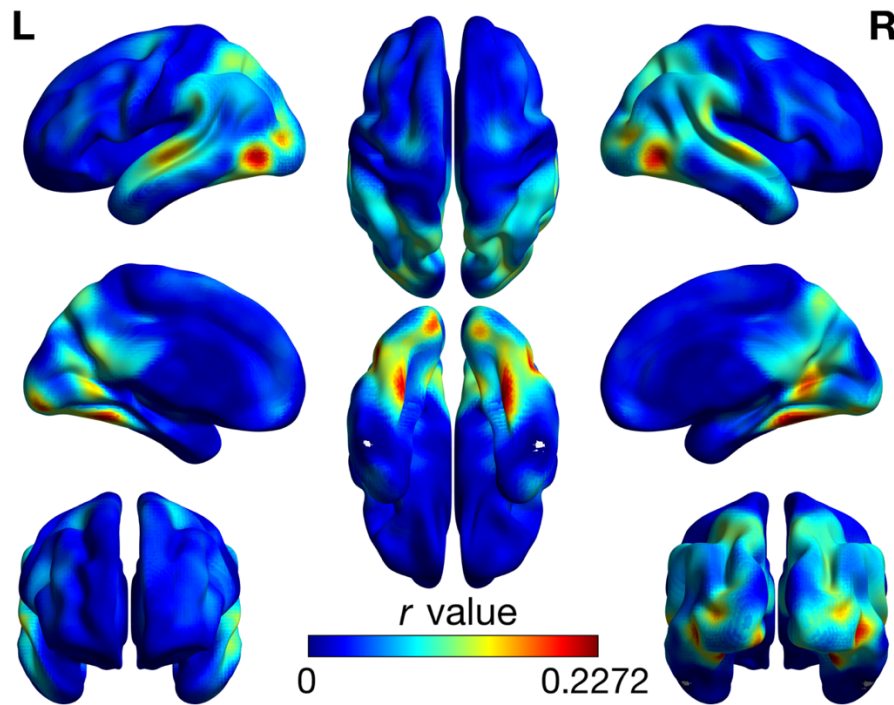
Figure 4.2. Average groupwise ISC for the whole sample.

Figure shows the unthresholded Pearson's *r* values for the whole-sample, average ISC.

4.3.3. Inattention Model Results

Higher ISC was associated with lower pairwise inattention scores in a number of areas in the occipital, temporal, and frontal cortices, including bilateral lateral occipital cortex, occipital

pole, fusiform cortex, lingual gyri, supramarginal gyri, angular gyri, precuneus, precentral gyrus, parietal operculum cortex, and superior cerebellum; the right middle frontal gyrus and posterior cingulate; and the left temporal cortex, including the superior temporal gyrus and the medial temporal cortex (**Figure 4.3a**; detailed cluster information can be found in **Appendix C2**). Most associations were found in areas of the brain where the average group synchrony was relatively high (i.e., greater than $r = 0.05$; see **Figure 4.2**).

Higher ISC was associated with greater pairwise inattention scores in the bilateral middle temporal gyri; the anterior right superior temporal gyrus and frontal pole; the left occipital pole, lateral occipital cortex, supramarginal gyrus, temporal pole, orbital frontal cortex, and precentral gyrus. Models that controlled for FEF synchrony show similar results (**Appendix C3**).

For all models, main findings remain generally unchanged after inclusion of the FEF covariate. Findings from these models are reported in the **Appendices C3, C5, and C7.**

4.3.4. Hyperactivity Model Results

Greater ISC was associated with decreased pairwise hyperactivity scores in bilateral visual occipital cortex, precentral gyri, middle frontal gyri, middle and superior temporal gyri, superior cerebellum; right precuneus, posterior cingulate, intracalcarine cortex, postcentral gyrus, and superior parietal lobule; and left occipital pole, inferior and superior frontal gyri, supramarginal gyrus, frontal orbital cortex, and parietal operculum cortex (**Figure 4.3b**; detailed cluster information can be found in **Appendix C4**).

Greater ISC was associated with elevated pairwise hyperactivity scores in bilateral visual occipital cortex, superior temporal gyrus, fusiform gyri, lingual gyri, and superior cerebellum;

right middle temporal gyrus; and left inferior temporal gyrus. Models controlling for FEF synchrony showed similar results to the original model (**Appendix C5**).
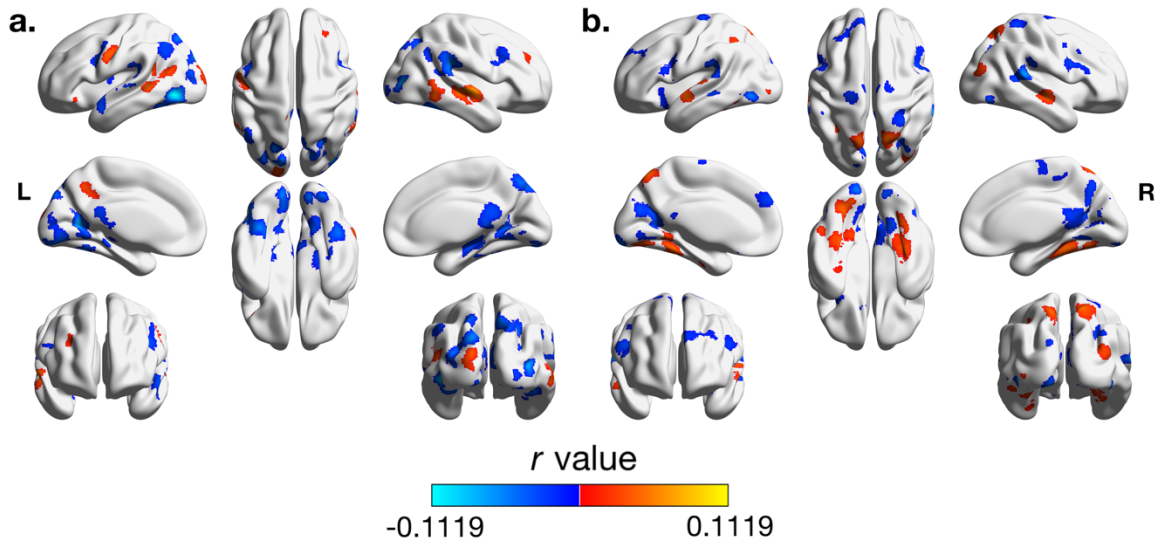
Figure 4.3. Associations between ISC and average pairwise inattentive and hyperactive trait scores.

a) shows the associations between inattention and ISC, and b) shows the associations between hyperactivity and ISC. Colour gradient indicates the β values, in units of Pearson's r. Cool colors denote negative associations (where ISC decreases as average trait score per pair increases) and warm colors denote positive associations (where ISC increases as average trait score per pair increases). For both inattention and hyperactivity, associations were seen in distributed areas of the occipital, temporal, parietal, and frontal lobes. Images are thresholded at a voxelwise threshold of $p < 0.001$ and a cluster-forming threshold of $\alpha = 0.05$.

4.3.5. Differences Between Inattention & Hyperactivity

To determine whether there were dissociable relationships between ISC and inattention relative to hyperactivity, we created a third model that included both pairwise average inattention scores and pairwise average hyperactivity scores as variables. The contrast was calculated as inattention–hyperactivity, so that negative clusters are where the β for inattention scores was more negative than the β for hyperactivity scores, and vice versa for positive clusters (**Figure 4.4**; detailed cluster information can be found in **Appendix C6**). Pairwise inattention score had a more negative/less positive association with ISC in bilateral fusiform cortex and lateral occipital cortex; left inferior and superior gyri and supplementary motor area; and right temporoparietal junction. Hyperactivity score had a more negative/less positive association with ISC in bilateral precuneus, precentral gyrus, middle temporal gyrus, and middle frontal gyrus; right superior gyrus; and left inferior frontal gyrus. Models controlling for FEF synchrony are in **Appendix C7**.
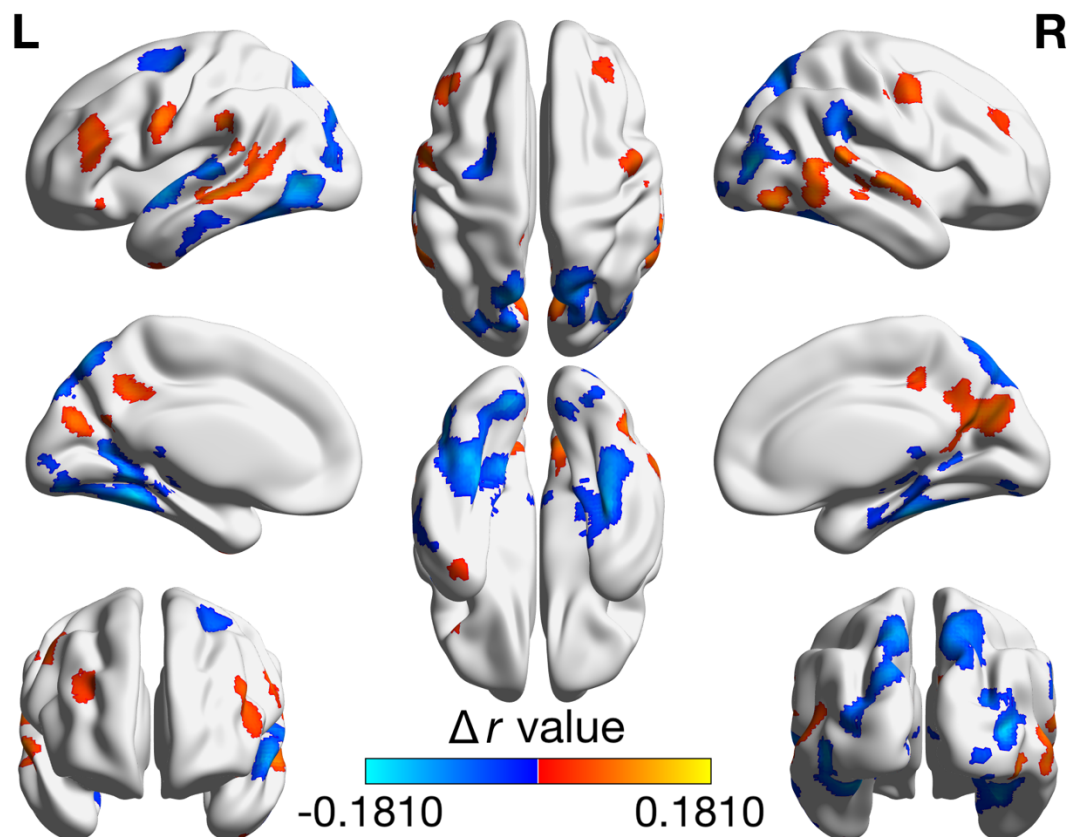
Figure 4.4. Contrast between inattention and hyperactivity.

Figure shows the difference in β values, in units of Pearson's r, corresponding to the inattention–hyperactivity contrast. Negative (cool) clusters indicate that pairwise inattention scores had a more negative/less positive association than pairwise hyperactivity scores, and positive (warm) clusters indicate that pairwise   hyperactivity scores had a more negative/less positive association than pairwise inattention scores. Results are thresholded at a voxelwise threshold of $p < 0.001$ and a cluster-forming threshold of $\alpha = 0.05$.

4.4. Discussion

This study investigated whether normative variation in inattentive and hyperactive traits in young children relates to inter-individual brain synchrony during video viewing. We found that both average pairwise inattention and hyperactivity scores, as measured by the SNAP-IV, show associations with inter-individual synchrony in areas engaged by the video viewing task. For inattention, negative associations—where ISC was lower in pairs with higher average trait scores—were most notably found in both dorsal and ventral visual streams, temporal auditory processing areas, bilateral temporoparietal regions, and precuneus. Hyperactivity scores had a negative association with ISC in several areas including bilateral parietal association cortex, prefrontal cortex, and precuneus. Contrary to our hypothesis of primarily negative associations between ISC and trait scores, we found regions with significant positive associations for both inattention and hyperactivity. Our findings suggest that children's neural processing of complex audiovisual stimuli is associated with inattentive and hyperactive traits and highlight the importance of considering these traits separately and dimensionally in developmental neuroimaging research.

4.4.1. Relationships Between Inattention/Hyperactivity and the Brain in Typically Developing Populations

Population-based studies have shown that across the spectrum of ADHD traits, subclinical symptoms of ADHD in childhood are linked to poorer academic performance at age 12 (Salla et al., 2016) and 16 (Sayal et al., 2015), as well as increased grade retention and failure to graduate (Bussing et al., 2010; Galéra et al., 2009). Higher inattention scores at 6 years old were also associated with a lower annual income three decades later (Vergunst et al., 2019).

Despite the clear implication that subthreshold inattention and hyperactivity traits might affect future outcomes, the literature characterizing the dimensional relationships between trait inattention/hyperactivity and brain measures in undiagnosed individuals (especially in early childhood) has been limited. However, there has been some evidence from both population-based studies, as well as those specifically focusing on control samples with no reported diagnoses, that inattentive and hyperactive symptomology are related to brain structure and function in non-clinical cohorts. Measures such as cortical thinning (Ducharme et al., 2012; Mous et al., 2014; Shaw et al., 2011), putamen (Mous et al., 2015) and prefrontal gray matter volume (Albaugh et al., 2017, 2019), and functional connectivity (Hilger & Fiebach, 2019; Rohr et al., 2019a) have shown associations with inattention and/or hyperactivity in both children and adults in the general population and non-clinical samples. While none of these studies focused specifically on ISC, they are consistent with our finding of a relationship between the brain and normative attentive traits. We have expanded upon this previous work and shown that ISC also has an association with inattention and hyperactivity in the non-clinical population.

4.4.2. Separability of the Inattention and Hyperactivity Trait Dimensions in Typically Developing Populations

In the clinical context, it has been suggested that ADHD is made up of a general underlying ADHD factor and two separable dimensions of inattention and hyperactivity/impulsivity (Smith et al., 2013; Toplak et al., 2009); however, it is unclear whether the separation of the inattention and hyperactivity dimensions extends into the normative spectrum of traits. Studies suggest that in the general population, inattention and hyperactivity have differential associations with cognitive measures (Kuntsi et al., 2014), symptom trajectories

(Larsson et al., 2006, 2011), and educational attainment (Pingault et al., 2011). In terms of brain measures, inattention and hyperactivity have shown associations with gray matter volume in different areas of the brain in a population-based study (Albaugh et al., 2017), and Salmi et al. (2020) found different dimensional associations between ISC and inattention and hyperactivity in their adult control group. In our study, we also found different regional associations between ISC and inattention and hyperactivity in functionally diverse areas. Pairwise inattention scores had more negative/less positive relationships with ISC in areas related to sensory processing, motor planning (Abe & Hanakawa, 2009), and attention/social cognition (Krall et al., 2015; Martin et al., 2019; Wilterson et al., 2021), relative to hyperactivity. This contrasts with the areas where we saw more negative/less positive associations between ISC and hyperactivity, which were found mostly in areas of language processing (Liégeois et al., 2014; Sliwinska et al., 2012; Yen et al., 2019), executive function ((Friedman & Robbins, 2022); and default mode (Li et al., 2019; Utevsky et al., 2014). This suggests that inattention and hyperactivity may preferentially affect different cognitive and processing systems, adding support that they are separable concepts. We note that because our sample did not include any children with an ADHD diagnosis, our findings may not generalize to children with clinically diagnosed ADHD.

4.4.3. Relationships Between Inattention/Hyperactivity Traits and Inter-individual Synchrony

Previous work looking at ADHD and ISC in adults may also offer insight into how inattention and impulsivity relate to inter-individual BOLD synchrony in the non-clinical population. In their study, Salmi et al. (2020) found that in their control group, increasing pairwise similarity in impulsivity scores was associated with greater ISC in the dorsomedial prefrontal cortex, while greater similarity in inattention scores was associated with higher ISC in

a very small cluster in the precuneus. Our results—that there were widespread patterns of association between synchrony and both inattention and hyperactivity in young children without an ADHD diagnosis—reinforce the argument that the heterogeneity in inattention and hyperactivity in what researchers typically refer to as control groups in case-control studies could be reflective of a linked heterogeneity among brain structure, function, and behavioral traits. This has clear implications for conducting categorical studies of ADHD and its neural correlates. Contrary to our hypotheses, we found several areas in both the inattention and hyperactivity analyses where pairs with higher average symptoms levels are more synchronized to one another than pairs with low average scores. For inattention scores, this included temporal auditory processing areas, early visual occipital cortex, default mode network (precuneus), and left temporoparietal junction and precentral gyrus. Pairwise hyperactivity scores showed a positive association with ISC in downstream ventral visual areas, parietal association cortex, and bilateral temporal cortex. While these results were unexpected, we speculate that certain properties of the stimulus may be more salient to specific children depending on their attentive trait scores and capture their attention in a "bottom-up" way, resulting in a more stimulus-driven, synchronized response between individuals who score high on a trait. However, this interpretation will need to be confirmed in further research ideally integrating measures of attention such as eye-tracking.

4.4.4. Implications for Screen Media & Education

Our study has implications for the use of AV media in educational settings. Recent work has suggested that inter-individual synchrony (as measured with EEG) can be used as a marker of "neural engagement" with an educational video stimulus, as an individual's synchrony to the rest of the group was associated with better performance on a test of the video contents.

Supporting the idea that engagement is reflected in inter-individual synchrony, (Song et al., 2021b) found that ISC in the default mode network was higher during scenes in narrative movies that were deemed more "engaging" through participant self-report. Our findings, that both inattention and hyperactivity demonstrated associations with ISC, suggest that children's engagement with educational video stimuli may vary with their inattentive and hyperactive traits. However, as we found both negative and positive associations with ISC for both traits, we cannot yet definitively characterize the nature of these relationships – for example, both positive and negative associations with inattention scores were found in the precuneus, an area often regarded as a core node of the DMN. Due to these mixed results, it is hard to surmise whether screen media, such as the television clips used in this study, are more or less engaging for children depending on their attentive traits. Further research should explore the relationships between inattentive and hyperactive traits, inter-individual synchrony, and engagement with educational videos.

4.4.5. Limitations

This study had several strengths, including an early childhood age range, a dimensional perspective on inattentive and hyperactive traits, and a relatively long scan time (approximately 18 minutes). The study also had several limitations to note. We were unable to calculate the Cronbach's alpha of the SNAP reliability in our sample. However, other studies have found a coefficient alpha for parent raters of around 0.9 and 0.79, for inattention and hyperactivity, respectively (Bussing et al., 2008). We found that children excluded for head motion had higher trait levels of inattention and hyperactivity than the children included in our sample at the trend level, potentially limiting generalizability. Though we controlled for sex in our models, our

sample had more females than males, which is not necessarily representative of the general population, where sex has a significant effect on type, prevalence, and severity of ADHD symptoms (Arnett et al., 2015; Smidts & Oosterlaan, 2007). Finally, we were not able to collect accurate eye-tracking data, so we were unable to directly assess the impact of important confounds such as gaze behavior and visual attention to the stimulus. To partially mitigate this, we calculated models that used FEF synchrony as a covariate to approximate difference in visual attention and gaze behavior between individuals, as has been done in previous work (Moraczewski et al., 2018; Redcay et al., 2010). While the general findings remain unchanged after this control analysis, we cannot definitively conclude that patterns of visual attention to the stimulus was not a driving factor in the associations we found between inattention/hyperactivity and ISC. Further work needs to be done that investigates the extent to which visual attention and gaze behavior contribute to ISC.

4.5. Conclusions

This study found that inattentive and hyperactive traits are differentially associated with inter-individual BOLD signal synchrony during the neural processing of videos by young children. An important future direction will be to ascertain whether these differences are linked with differences in understanding and retention, which could have implications for early childhood education. This work adds to a growing body of literature suggesting meaningful trait-linked variation in brain function in samples with no reported diagnoses.

CHAPTER 5 - Discussion

5.1. Overall Summary

Childhood is a time of rapid physical, emotional, and cognitive development. This development is reflected in the brain function of children across different ages. By linking individual differences in brain function to behaviour and traits, we can better understand children's unique processing and interpretations of the world around them. Historically, group analyses have been employed in the field of developmental neuroimaging to infer changes in brain function with age or to describe differences between clinical groups. However, age and many psychological traits are continuous variables, meaning that 'grouping' approaches can obscure important variation between children and lead to potentially inaccurate inferences regarding development or psychopathology. Therefore, it is crucial to explore the sources of variability in brain function between children, which may result in a better generalizability and applicability of findings.

In this dissertation, I aimed to characterize associations between specific phenotypic traits and brain function in children. In the first empirical chapter, I conducted a scoping review of the fMRI literature to determine how age and development can play a role in changing brain function. In the second empirical chapter, I explored inter-individual differences of brain function between young children in relation to age, and what aspects of brain processing may be contributing to differences between children across the age range of 4-8 years. In the third empirical chapter, I investigated whether attentive traits are a potential source of variability in brain function between children, and whether inattention and hyperactivity have differential relationships with brain function in early childhood.

5.1.1. Chapter 2

In Chapter 2, I reviewed the fMRI literature to synthesize the research on the development of the functional neural architecture of the extended visual system. I also assessed whether the interactive specialization and maturational frameworks of functional brain development were supported in the literature. I found that while a large number of studies found progressive specialization/development of brain function in multiple visual sub-domains, there was not enough evidence for the other sub-hypotheses of these developmental frameworks to fully support either hypothesis. To confirm or deny these frameworks in the context of visual development, experiments must be designed and conducted to explicitly test these elements of their hypotheses. Regardless of the lack of explicit support for the frameworks, there does appear to be progressive specialization of the responses to visual stimuli.

5.1.2. Chapter 3

In Chapter 3, I investigated the associations between age and inter-individual variability of brain response in children aged 4-8 years old. I found that across most of the cortex, ISC increased with the average age of the pair, suggesting a homogenization of the response across this age range. I showed that this increase may be linked to a strengthening of the response to the movie, rather than a decrease in idiosyncratic brain activity and/or noise. I also investigated whether certain aspects of the interactive specialization framework could explain the convergence of the response with age; however, contrary to our hypothesis, we did not find a diffuse-to-localized effect with increasing age. Here, I showed that inter-individual variability in

brain function may decrease with age, and that this is important to take into account when designing developmental neuroimaging studies.

5.1.3. Chapter 4

In the final empirical chapter, Chapter 4, I explored whether there were links between individual differences of attentive traits and brain function in response to movies in children without an ADHD diagnosis. Both inattentive and hyperactive traits were associated with ISC in many parts of the brain, mainly in visual, auditory, associative, and attention-related regions. Further, we showed that inattention and hyperactivity had significantly different relationships with ISC, and that in a number of areas, including in the ventral temporal cortex, the relationship between brain function and hyperactive or inattentive traits had opposite directionality. Together with the previous chapters, this research demonstrates that in "typically developing" populations, or groups of children that would be considered "healthy controls," there are a number of potential sources of inter-individual variability of brain function. My work underscores the importance of both taking an individual differences approach in developmental neuroimaging research, as well as a dimensional approach in neuroimaging studies focused on ADHD in young children.

5.2. Inter-individual Variability of Brain Function in Relation to Age

As with adults, children are distinctive, multifaceted individuals, which is reflected in the way their brains process and respond to the world. In fact, according to previous research (Moraczewski et al., 2018; Scherf et al., 2007; Tian et al., 2021), and as I showed in Chapter 3, younger children may have more inter-individual variation in brain function than older children

and adults. This has important implications for the entire field of developmental cognitive neuroscience.

In Chapter 2 of this dissertation, a common trend that we found in the literature was progressive developmental effects, such as increasing strength, extent, and specificity of the BOLD response with age. A large amount of the historical research in this field has relied on group analyses, and specifically, studies that compare a group of children to a group of adults (Born et al., 1998; Moraczewski et al., 2018; Passarotti et al., 2003; Pine et al., 2001; Scherf et al., 2007; Vuontela et al., 2013). Developmental effects are then inferred from any statistically significant difference between these two groups. However, if children are not only different from adults, but quite different from *each other*, a group analysis could obscure the true nature of the spatial and temporal response in children. If children have responses that are equally as strong in magnitude to adults, but more variability in peak locations, the topographical differences between children could result in the inference that adults have stronger BOLD signal change to the stimulus. On the other hand, if some children have stronger responses to the stimulus than others, only focusing on the average peak would miss important information regarding the variation in amplitude and whether that also associates with age or other traits.

As my findings in Chapters 2 and 3 of this dissertation emphasize, taking this age-related variability into account will be an important step for bettering our understanding of how brain function changes throughout development. This requires designing studies that can reliably detect individual differences between children. Further, the potential clinical and educational applications of fMRI hinge on our ability to generalize our findings to specific individuals (Dubois & Adolphs, 2016; Tervo-Clemmens et al., 2023). Efforts to accurately map the individualized functional topography of children's brains will therefore be a crucial to the

advancement of the field. Recently, precision fMRI techniques have been developed that allow for the reliable characterization of individual functional architecture by collecting hours of data from participants (Gordon et al., 2017; Gratton et al., 2020). While it is difficult to obtain long scans from young children, the use of movie stimuli could be a potential boon to this effort (Vanderwal et al., 2018). Precision mapping of functional responses in children could help determine the baseline level of topographical variability between children of different ages. Engaging narratives could be designed to target specific functions, such as the processing of faces, objects, or higher level concepts such as emotions or theory of mind (Camacho et al., 2023; Richardson & Saxe, 2020). Alternatively, short blocks of more traditional localizer tasks could be interleaved with blocks of movie stimuli, to capitalize on both the control and unambiguity afforded by the more traditional tasks, in addition to the ecological validity and engagement advantages of movie-fMRI (Cantlon, 2020; Hasson et al., 2010).

In the movie-fMRI studies included in the scoping review, we found that a number of studies demonstrated children's responses becoming more "adult-like" with increasing age (Cantlon & Li, 2013; Kamps et al., 2022; Moraczewski et al., 2018, 2020; Yates et al., 2021, 2022). When combining my findings in Chapter 3 with other studies that have found evidence for a "homogenization" or "convergence" of responses with age (Camacho et al., 2023; Tian et al., 2021), it suggests that this increasing similarity between individuals may be an important aspect of development.

5.3. Brain Synchrony and Individual Differences in Children

Both Chapters 3 and 4 of this dissertation used ISC to investigate the links between children's phenotypic traits and individual differences in brain function. I found widespread

associations between age and attentive traits with brain synchrony. In both of my studies, the significant associations between ISC and the traits were seen in perceptual areas that would be expected to be driven by the movie stimulus –visual, auditory, language, social processing, and associative areas in the occipital, parietal, and temporal cortices.

In Chapter 3, results generally aligned with the hypothesis that synchrony would be greater in older pairs of children than younger pairs of children, a pattern that was upheld throughout almost all of the brain, except in the very posterior occipital cortex, which had significant clusters with the opposite association. The areas of the brain that showed significant associations with age difference also followed my hypothesis – that children with greater age difference would have lower synchrony than children who were closer in age. However, in Chapter 4, the results for attentive traits and ISC were surprising. While there were a number of clusters that did conform to our hypothesis (that children with low levels of hyperactivity and inattention would be more synchronized to one another than children with greater levels of these symptoms across the brain – a negative relationship), there were also clusters that showed a positive relationship between ISC and both traits. One of the most notable areas was the ventral temporal cortex, which would likely be driven by the visual content of the movie. As predicted, there was a negative relationship between ISC in the ventral temporal cortex and inattention; however, there was a positive relationship between hyperactivity and ISC in the same area. The finding of not only a relationship opposite to the hypothesis, but also dissociable relationships with inattention and hyperactivity in this area, have interesting implications for how inattention and hyperactivity may be related to processing and interpretation of naturalistic events. This evidence could suggest that inattention and hyperactivity are reflective of different processing alterations, and may support the dimensional separation of the two traits, which is currently still

a matter of debate (Luo et al., 2022; Rostami et al., 2022; Smith et al., 2013; Toplak et al., 2009; Zdorovtsova et al., 2023). This paints a picture of the relationship between brain function and inattention and hyperactivity that may be more nuanced than the relationship with age.

ADHD symptoms decline with age, and there are higher levels of ADHD behaviours in younger children (Biederman et al., 2000; Monuteaux et al., 2010). In fact, hyperactive/impulsive symptoms are frequent in "typically developing" children between the ages of 3-6 years (Smidts & Oosterlaan, 2007). An important aspect of future research should be to explore the links between these two factors (age and attentive traits) and how they may be associated with brain function and attentional biomarkers, such as gaze.

5.4. Strengths and Limitations of Movie-fMRI

Naturalistic fMRI paradigms, such as movie-fMRI, have immense advantages and potential for developmental neuroimaging research (Vanderwal et al., 2018). Importantly, they have the potential to expand the generalizability of fMRI research, as the free-viewing conditions employed by naturalistic stimuli are more ecologically valid and provide a better snapshot of how the brain acts in a real-world context (Nastase et al., 2020; Sonkusare et al., 2019). Brain regions and networks that have been functionally defined by highly controlled tasks may operate differently in a dynamic, multimodal context, so movie-fMRI studies are important for the validation of traditional task-fMRI research. FC during movie watching is both more reliable (Wang et al., 2017) and predictive of behaviour and cognition (Finn & Bandettini, 2021) than resting state methods, and movies have been associated with decreased head motion in young children (Greene et al., 2018; Vanderwal et al., 2015). Because of these advantages, movie-fMRI may play an important role in combatting the current reproducibility crisis in the psychological

and neuroimaging fields (Munafò et al., 2017). It also expands the age range for fMRI research studies, as has been already demonstrated by some studies (Kamps et al., 2022; Richardson et al., 2018).

However, while there are many advantages to using naturalistic paradigms, there are also disadvantages for some research questions. Movies engage visual processing alongside auditory, emotional, language, attention, and spatial processing areas (Bottenhorn et al., 2018), which makes it difficult to disentangle specific functions. Due to the continuous and complex nature of movies, it is more challenging, though not impossible (Camacho et al., 2023) to apply more traditional analysis techniques, like GLM, to describe specific functions and their effect on the BOLD signal. A noteworthy disadvantage to most movie-fMRI studies is the lack of control over the stimulus itself. While new techniques to help describe and annotate specific multimodal features of movies in great detail are being developed (de la Vega et al., 2022; McNamara et al., 2017), researchers still lack ultimate control over the design of almost all movies that are used in the MRI scanner, which can have implications for unintended confounds and the interpretation of results (Cantlon, 2020).

Given the time, creative effort, and financial considerations involved in producing a rich, naturalistic video, this may unfortunately be a limitation that must be accepted and taken into consideration for most movie-fMRI studies. However, there have been some efforts to create specialized movies for specific neuroimaging studies – for example, one study looking at ADHD in adults created a video that was designed to explicitly elicit different processing in the ADHD participants when compared to the controls (Salmi et al., 2020). Further, while feature films and television shows may be relatively easy to access and allow for a dynamic range of social interactions and emotions, artistic choices such as editing and directorial style that do not exist in

real life can on their own drive differences in brain activity (Hasson et al., 2008). Simple videos depicting a naturalistic scene with minimal artistic license and direction may actually be better suited to studying some cognitive functions for this reason, and depending on the resources required, could be within the purview of some research groups to produce. However, depending on the research focus, commercial feature films and televisions shows may better serve the experiment at hand, especially if it is concerned with narrative processing over long time scales.

It is imperative that whether researchers are selecting a pre-existing stimulus or creating their own, the features of the stimulus are carefully considered and appropriate for the research question, and based in strong theoretical considerations, with potential confounding factors in the stimulus stringently modelled and controlled for. In our study, we used a video that was made up of short clips from the children's television show *Elmo's World*. This strategy had a number of advantages, as we were able to include a variety of clips that had face, spoken language, social, and educational content. Nonetheless, there were some limitations to this stimulus, mainly the potential confounding effect of engagement levels that varied with age. While the video was age-appropriate and understandable for both the youngest and oldest children in the sample, we anecdotally noticed that some of the older children found the video "boring." In future studies, it will be important to (1) test enjoyment and engagement levels of a potential stimulus in a sample that is demographically matched to the neuroimaging sample; and (2) collect both objective (i.e. eye tracking) and subjective (post-scanner questionnaires) data regarding engagement with the movie stimulus in order to control for potential effects of this factor.

Variations in attention and engagement are a very important aspect of movie stimuli. An inherent part of movie-fMRI studies is the free viewing or "natural vision" aspect of the paradigm, which may result in engagement differences between participants. Gaze has been

shown to be more variable during movie-watching between younger individuals (Franchak et al., 2016; Kirkorian et al., 2012; Kirkorian & Anderson, 2018). While it is easy to dismiss variability in gaze and attention as a confounding factor that would ideally be entirely controlled for, it also stands to note that these differences in attention may actually be an interesting and important aspect of the variability between individuals. Therefore, whether it is being treated as a confounding factor, potential moderator, or main effect of interest, it will be important to correctly measure attentional biomarkers such as gaze and physiological state (Madsen & Parra, 2022) in future movie-fMRI studies. This can sometimes be challenging; in our scans, we were unable to collect usable eye tracking data. New tools that have been developed to track gaze from the MR signal itself using machine learning, such as PEER (Son et al., 2019) and DeepMReye (Frey et al., 2021) offer potential solutions for this issue, and in the case of DeepMReye, can be applied retroactively to datasets that have already been collected if they have adequate coverage over the eye area. These tools may be able to bridge the effects of ISC and attention if used in future studies.

5.4.1. Strengths and Limitations of ISC

There are a number of strengths and limitations associated with ISC analysis. Firstly, ISC allows for the granular characterization of individual differences in spatiotemporal brain function between individuals (Finn et al., 2020). Similarities in BOLD responses can be directly linked to similarities (or dissimilarities) in behavioural, cognitive, psychological, or physical phenotypes. Next, because of its model-free nature, it can reveal areas with meaningful individual differences in brain function between participants that do not always survive more traditional statistical analysis techniques. For example, significant synchrony between individuals is not limited to

areas or timepoints with high BOLD amplitude responses – low amplitude signal can show significant synchrony between individuals as well (Cantlon & Li, 2013). This can reveal regions or BOLD responses that may be involved in the processing of a stimulus but would otherwise be overlooked in a traditional GLM analysis.

While ISC can reveal interesting information and associations, there are some limitations to this technique, primarily around the issue of interpretability. There are a few different perspectives where this arises. One important question is what synchronization between individuals represents on a neurophysiological level. The general interpretation of high ISC in a region of the brain is that the region is likely involved in processing the stimulus, as similar responses are being driven across individuals. However, as previously mentioned, statistically significant ISC can be seen even during low-amplitude fluctuations (Cantlon & Li, 2013). It is currently unclear what role synchronized low-amplitude signal plays in the processing of the stimulus. It will be important for future research to identify these aspects of ISC in order to clarify the meaningful implications of brain synchrony between individuals.

Another barrier to interpretation in ISC studies is the pairwise model construction when investigating the relationship between brain synchrony and a continuous phenotypic metric. A groupwise ISC analysis is relatively easy to interpret – if one group has greater ISC than the other, you can surmise that there is a greater variability of response in the group with the lower ISC. However, as I have discussed before, groupwise studies can obscure meaningful individual differences between subjects. This introduces the problem of how to operationalize a continuous phenotypic metric for pairs. The pairwise formulation of a trait score can drastically change the interpretation of any associations with ISC (Finn et al., 2020), which I demonstrated in Chapter 3, where we used two different pairwise age metrics to investigate different developmental

hypotheses. It also can be difficult to interpret results that vary across the brain – in our results in Chapter 4, we found areas where there were both positive and negative relationships with inattention and hyperactivity, which complicates the conclusions that can be drawn from the analysis. A potential reason for this is that the statistical properties and considerations of pairwise data, especially in the context of the LME with crossed random effects, are complex when compared to traditional inference methods usually employed in fMRI research. Firstly, the number of observations increases dramatically when considering pairs rather than individuals. The total number of pairs that are input to the LME is the combinatorial of n; in our case, with n = 81 participants, the total number of pairs was 3240. This results in small effect sizes reaching significance when using the LME with crossed random effects in combination with traditional cluster based multiple comparisons correction methods. Relatedly, it is not yet known what the correct degrees of freedom should be for a statistic in the LME with crossed random effects (Chen et al., 2020) due to the pairwise nature of the data. It would likely be useful to implement the reporting of effect size estimates as a routine step in ISC analyses in order to aid in the interpretation of the results, until these issues have been more concretely resolved. Another potential solution is the use of Bayesian inference methods instead of traditional hypothesis testing (Chen et al., 2020). An additional possible workaround is to treat ISC as not a pairwise metric, but individual metric, and use a leave-one-out calculation technique (Gruskin et al., 2020; Nastase et al., 2019), where an individual's similarity to a group-average signal is determined and associated with their own phenotypic score or measure. For example, adolescents with higher depressive symptoms are less synchronized to their peers (Gruskin et al., 2020), and older children show greater synchrony to the average adult time course in a number of areas of the brain (Cantlon & Li, 2013; Kamps et al., 2022; Moraczewski et al., 2018, 2020).

In the developmental context, ISC also has some unique interpretability challenges, as it may not easily lend itself to detecting some of the intricacies of developmental change. For example, areas where adults have greater similarity in responses to one another than children could either be: 1) regions that do not show BOLD signal change in children, but do in older individuals (and therefore "emergent"); or 2) regions that show BOLD signal change in both adults and children but have a higher signal-to-noise ratio or more specific and consistent localization in adults. In order to determine the nature of the changes in BOLD signal magnitude between groups, a combination of within- and between-group similarity maps would have to be compared, and even still may not present a clear measure of where and BOLD signal change is different between groups.

5.5. Remaining Questions and Future Directions

As I have shown through the empirical chapters of this dissertation, development and behaviour can reflect substantial differences in brain function. The question that naturally follows these findings is what exactly is causing these differences between children? Are children approaching the world in a different way from one another, while adults have more similar understandings of their shared experiences? Is variable brain function reflective of variable ways of attending to the external environment? Does variability of brain response translate into a variability of interpretation? And how do the trajectories of functional and structural neurodevelopment across childhood contribute to variability in response?

In order to answer these questions, it will be important to collect data on biomarkers of engagement as well as stimulus interpretation in future movie-fMRI ISC studies. These procedures may allow us to better link together what could be causing variability in brain

function between individuals in the first place, as well as meaningfully contextualize the ramifications of these differences between individuals. Another important practice to increase the interpretability of movie-fMRI ISC findings is to improve the validity of the paradigms through careful selection and/or creation and testing of stimuli. Harnessing the complimentary insights from both highly controlled tasks with more naturalistic paradigms can also be important in creating a whole picture of how brain functions work and develop across the entire lifespan (Cantlon & Li, 2013). Further development and exploration of statistical techniques is essential, to ensure that analyses are able to detect developmental effects and brain-behaviour relationships.

All of these strategies must be initially supported by a strong theoretical, falsifiable foundation, so that theories can be proved and disproved according to the strength of the evidence for hypotheses (Crone & Ridderinkhof, 2011). To determine whether convergence of brain function with age is indeed a significant feature of development, it will be important to conduct longitudinal studies that look at the synchrony and variability between child participants at different time points. Current ISC studies are generally cross-sectional. Cross-sectional designs are privy to confounds that could greatly obfuscate the true developmental trajectories (Herting et al., 2018; Louis et al., 1986; McCormick et al., 2017).

Finally, employing best practices for increasing reproducibility in developmental cognitive neuroscience, including (but not limited to) increasing sample sizes, pre-registering research and being transparent with methodology at every stage of research, collecting precision fMRI data from younger children, validation of existing findings in new datasets, and increasing the diversity of samples will be imperative to moving forward in the field (Klapwijk et al., 2021).

5.6. Conclusions

In this dissertation, I demonstrated the importance of individual differences in age and attentive traits and their associations with brain function in young children. My research advocates for an individualized approach to neuroimaging research in children, which could potentially advance the applications of fMRI by making findings more generalizable. Children are unique and idiosyncratic in much the same way as adults, and tailoring research to both accommodate and investigate differences between children will be imperative to a holistic understanding of child psychological, cognitive, and functional brain development.

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APPENDIX A - Supplemental information for Chapter 2

Appendix A1. MEDLINE search terms.

#	Query
1	exp Magnetic Resonance Imaging/
2	exp Brain Mapping/ or exp Functional Neuroimaging/
3	(functional magnetic resonance imaging or functional MRI or fMRI).kf,tw.
4	exp Child/ or exp Psychology, Child/ or exp Child Development/ or exp Child, Preschool/
5	exp Infant/ or exp Adolescent/
6	(child or children or infant or infancy or toddler or preschool or youth or elementary or development or early childhood or middle childhood or school age or school-age or pre-teen or preteen or adolescent* or adolescence or teen* or teenage or teen-age or developmental neuroimaging or developmental fMRI or childhood development or brain development or neural development or neurodevelopment or pediatric neuroimaging or pediatric or paediatric or paediatric neuroimaging).kf,tw.
7	exp Photic Stimulation/ or exp Acoustic Stimulation/
8	exp Motion Pictures/
9	(task or task fMRI or task-fMRI or task-based fMRI or task based fMRI or naturalistic fMRI or movie or film or video or movie fMRI or movie-fMRI or movie-watching fMRI or movie watching fMRI or video watching fMRI or naturalistic neuroimaging or natural vision or passive viewing or naturalistic or passive listening or natural listening or ecologically valid or narrative).kf,tw.
10	exp Brain/
11	exp Cerebral Cortex/
12	(brain or cerebral cortex or cortex or visual cortex or auditory cortex or association cortex or parietal cortex or occipital cortex or temporal cortex or fusiform or fusiform cortex or fusiform face area or ventral temporal cortex or superior temporal or inferior temporal or middle temporal or dorsal visual or dorsal visual stream or ventral visual or ventral visual stream).kf,tw.
13	exp Pattern Recognition, Visual/ or exp Visual Perception/ or exp Visual Cortex/
14	exp Auditory Perception/ or exp Speech Perception/
15	exp Language/ or exp Child Language/ or exp Language Development/
16	(visual perception or visual processing or audiovisual processing or audiovisual perception or auditory perception or speech perception or speech comprehension or language comprehension or language development).kf,tw.
17	1 or 2 or 3
18	4 or 5 or 6
19	7 or 8 or 9
20	10 or 11 or 12
21	13 or 14 or 15 or 16

22	17 and 18 and 19 and 20 and 21

Appendix A2. PsycINFO search terms.

#	Query
1	exp Functional Magnetic Resonance Imaging/
2	exp Neuroimaging/
3	exp Magnetic Resonance Imaging/
4	(functional magnetic resonance imaging or functional MRI or fMRI).mp.
5	exp Childhood Development/ or exp Neural Development/ or exp Development/ or exp Human Development/ or exp Cognitive Development/ or exp Brain Development/ or exp Psychological Development/ or exp Infant Development/ or exp Early Childhood Development/ or exp Adolescent Development/
6	exp Pediatrics/
7	(child or children or infant or infancy or toddler or preschool or youth or elementary or development or early childhood or middle childhood or school age or school-age or pre-teen or preteen or adolescent* or adolescence or teen* or teenage or teen-age or developmental neuroimaging or developmental fMRI or childhood development or brain development or neural development or neurodevelopment or pediatric neuroimaging or pediatric or paediatric or paediatric neuroimaging).mp.
8	exp Films/
9	exp Audiovisual Communications Media/
10	exp Auditory Stimulation/ or exp Perceptual Stimulation/ or exp Visual Stimulation/
11	exp Task/
12	(task or task fMRI or task-fMRI or task-based fMRI or task based fMRI or naturalistic fMRI or movie fMRI or movie-fMRI or movie-watching fMRI or movie watching fMRI or naturalistic neuroimaging or natural vision or passive viewing or naturalistic or passive listening or natural listening).mp.
13	exp Brain/
14	exp Auditory Cortex/ or exp Visual Cortex/ or exp Cerebral Cortex/
15	exp Occipital Lobe/ or exp Parietal Lobe/
16	exp Temporal Lobe/
17	(brain or cerebral cortex or cortex or visual cortex or auditory cortex or association cortex or parietal cortex or occipital cortex or temporal cortex or fusiform or fusiform cortex or fusiform face area or ventral temporal cortex or superior temporal or inferior temporal or middle temporal or dorsal visual or dorsal visual stream or ventral visual or ventral visual stream).mp.
18	exp Face Perception/ or exp Auditory Perception/ or exp Speech Perception/ or exp Visual Perception/
19	exp Language Development/
20	exp Cognitive Processes/
21	(visual perception or visual processing or audiovisual processing or audiovisual perception or auditory perception or speech perception or speech comprehension or language comprehension or language development).mp.

22	1 or 2 or 3 or 4
23	5 or 6 or 7
24	8 or 9 or 10 or 11 or 12
25	13 or 14 or 15 or 16 or 17
26	18 or 19 or 20 or 21
27	22 and 23 and 24 and 25 and 26

Appendix A3. Web of Science search terms.

TS=(("functional magnetic resonance imaging" OR "functional mri" OR fmri) AND (child OR children OR infant OR infancy OR toddler OR preschool OR youth OR elementary OR development* OR "early childhood" OR "middle childhood" OR "school age" OR "school-age" OR "pre-teen" OR preteen OR adolescent* OR adolescence OR teen* OR teenage OR "teen-age" OR "developmental neuroimaging" OR "developmental fmri" OR child AND development OR childhood AND development OR brain AND development OR neural AND development OR neurodevelopment OR "pediatric neuroimaging" OR pediatric OR paediatric OR "paediatric neuroimaging") AND (task OR "task fmri" OR "task-fmri" OR "task-based fmri" OR "task based fmri" OR naturalistic OR "ecologically valid" OR "naturalistic fmri" OR movie OR film OR video OR audiovisual OR "movie fmri" OR "movie-fmri" OR "movie-watching fmri" OR "movie watching fmri" OR "naturalistic neuroimaging" OR "natural vision" OR "passive viewing" OR "passive listening" OR narrative OR "auditory stimulation" OR "visual stimulation") AND ("visual perception" OR "visual processing" OR "audiovisual processing" OR "audiovisual perception" OR "auditory perception" OR "speech perception" OR "speech comprehension" OR "language comprehension" OR visual OR auditory OR language) AND (brain OR "cerebral cortex" or cortex or "visual cortex" or "auditory cortex" or "association cortex" or "parietal cortex" or "occipital cortex" or "temporal cortex" or fusiform or "fusiform cortex" or "fusiform face area" or ffa or "ventral temporal cortex" or vtc or "superior temporal" or "inferior temporal" or "middle temporal" OR "dorsal visual" OR "dorsal visual stream" OR "ventral visual" OR "ventral visual stream"))

Appendix A4. Scopus search terms.

TITLE-ABS-KEY (("functional magnetic resonance imaging" OR "functional
mri" OR fmri) AND (child OR children OR infant OR infancy OR toddler OR prescho
ol OR youth OR elementary OR development* OR "early childhood" OR "middle
childhood" OR "school age*" OR "school-age*" OR "pre-
teen" OR preteen OR adolescent OR adolescence OR teenage OR "teen-
age" OR "developmental neuroimaging" OR "developmental
fmri" OR child AND development OR childhood AND development OR brain AND dev
elopment OR neural AND development OR neurodevelopment OR "pediatric
neuroimaging" OR pediatric OR paediatric OR "paediatric
neuroimaging") AND (task OR "task fmri" OR "task-fmri" OR "task-based
fmri" OR "task based fmri" OR naturalistic OR "ecologically valid" OR "naturalistic
fmri" OR movie OR film OR video OR audiovisual OR "movie fmri" OR "movie-
fmri" OR "movie-watching fmri" OR "movie watching fmri" OR "naturalistic
neuroimaging" OR "natural vision" OR "passive viewing" OR "passive
listening" OR narrative OR "auditory stimulation" OR "visual stimulation") AND ("visual
perception" OR "visual processing" OR "audiovisual processing" OR "audiovisual
perception" OR "auditory perception" OR "speech perception" OR "speech
comprehension" OR "language comprehension" OR visual OR auditory OR language))

Appendix A5. Data extraction form.

GENERAL INFORMATION

Title:

Authors:

Year of publication:

Country of author institutions:

SAMPLE CHARACTERISTICS

Sample size (total):

Child n:

Adult n:

Age groups of subjects (select all that apply):
- Infancy (0 – 1 years)
- Childhood (2 – 12 years)
- Adolescence (13 – 18 years)
- Adulthood (18+ years)

Child age range:

Adult age range:

Child sex distribution:

Adult sex distribution:

Sample country of origin:

Ethnicity:

Socio-economic characteristics:

STUDY DESIGN

Participant state (select all that apply):
- Awake
- Asleep (no sedation)
- Sedated

Analysis design (select all that apply):
- Children only – continuous age association
- Children only – age group comparison
- Children and adults – continuous age association
- Children and adults – age group comparison

Domain studied (select all that apply):
- Faces (non-emotional)
- Faces (emotional)
- Objects
- Characters/word-forms
- Scenes
- Bodies
- Early visual processing
- Motion
- Other (task)
- Naturalistic – movie
- Other (naturalistic)

If other, list here:

Temporal study design (select all that apply):
- Longitudinal
- Cross-sectional

If longitudinal, list time points/intervals:

fMRI stimulus design (select all that apply):
- Task – block design
- Task – event-related design
- Task – mixed block/event-related design
- Task – other
- Naturalistic – passive viewing
- Naturalistic – other
- Both / hybrid (i.e. naturalistic block design)

If task:
Type of task:
Stimulus types:

Number of trials and / or blocks per condition:

If naturalistic:
Length of scan (in minutes):

STATISTICAL ANALYSIS

Scanner strength:

Software used for data analysis (list all):

Preprocessing steps / controls (select all that apply):
- Slice time correction
- Removal of linear trends
- Registration
- Normalization (MNI atlas)
- Normalization (Talairach atlas)
- Normalization (other atlas)
- Regression of head motion parameters
- Global signal regression
- ICA-AROMA
- Band / high pass filtering
- WM / CSF signal regression
- Motion censoring
- Spatial smoothing
- Other (please list):

If yes to motion censoring – list threshold:
If yes to spatial smoothing – list smoothing parameters:

Type of analysis done (select all that apply):
- MVPA
- GLM
- RSA
- ISC
- ISFC
- IS-RSA
- Other (please list):

Key first level contrasts (if applicable):

Confound mitigation strategies (select all that apply):
- Exclusion of subjects based on head motion
- Confound control at higher statistical levels (i.e. including motion as a regressor in a GLM)

- Other (please list):

If yes to excluding based on head motion – list threshold:

Multiple comparisons correction (select all that apply):
- ROI analysis
- Cluster analysis
- Bonferroni correction
- FDR correction
- None
- Other (please list):

If yes to multiple comparisons correction – list parameters / threshold:

DEVELOPMENTAL THEORIES

Developmental theories explicitly tested:
* list whether authors claim interactive specialization and / or maturational theory were explicitly tested

Developmental theories explicitly supported or countered by findings:
* list whether authors interpret/compare their findings in the context of interactive specialization and / or maturational theory and whether they support or counter the theories

SUMMARY

Summary of key findings:

Brain regions with significant findings:

Appendix A6. Summary of findings / supporting evidence for theories.

Progressive development refers to an increase in some metric (magnitude, extent, or selectivity of BOLD signal change, etc.) with age; regressive development refers to a decrease in responses to other stimuli/functions in the adult functional region and/or loss of BOLD signal change in other areas of the brain for that stimuli (e.g. if both FFA and STS show change in children but only FFA in adults); emergence refers to the region coming "online" with no evidence of BOLD signal change prior to that age (e.g. no change before age of 7 years, or no evidence of change in the child group). IS = interactive specialization; MF = maturational framework; PD = progressive development.

Study	Progressive development in adult regions?	Regressive development in child regions?	Emergence of adult regions?	IS	MF	PD only	Insufficient evidence
Interactive specialization	✓	✓		✓			
Maturational theory	✓		✓		✓		
Early visual processing							
Born et al. 1998	✓	✓		✓			
Martin et al. 1999	✓	✓		✓			

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Muramoto et al. 2002							✓
Kang et al. 2003							✓
Richter & Richter, 2003							✓
Wenger et al. 2004							✓
Bucher et al. 2006							✓
Dekker et al. 2015	✓		✓		✓		
Gomez et al. 2019	✓					✓	
Ellis et al. 2021	✓					✓	
Kim et al. 2021							✓

Face processing (non-affective)

Passarotti et al. 2003	✓	✓		✓			
Gathers et al. 2004	✓	✓		✓			
Aylward et al. 2005	✓	~				✓	

Joseph et al. 2006	✓	~			✓	
Golarai et al. 2007	✓				✓	
Dalton et al. 2007						✓
Scherf et al. 2007	✓	✓		✓		
Joseph et al. 2011	✓	✓		✓		
O'Hearn et al. 2011	✓		✓	✓		
Cantlon et al. 2011	✓	✓	✓			✓
Haist et al. 2013	~	✓				✓
Vuontela et al. 2013	✓	✓		✓		
Jiang et al. 2014	✓	~			✓	
Scherf et al. 2014	✓				✓	
Joseph et al. 2015	✓		✓	✓		
Natu et al. 2016	✓				✓	
Deen et al. 2017	✓	✓		✓		
Golarai et al. 2017	✓				✓	

Nordt et al. 2018	✓		~		✓	
Dehaene-Lambertz et al. 2018						✓
Keulers et al. 2019						✓
Nordt et al. 2021	✓	✓				✓
Tian et al. 2021	✓				✓	
Kamps et al. 2022	✓	✓		✓		
Face processing (affective)						
Pine et al. 2001		✓				✓
Yurgelen-Todd & Killgore 2006	✓				✓	
Killgore & Yurgelen-Todd 2007	✓	✓		✓		
Monk et al. 2008						✓
Guyer et al. 2008		✓				✓

Killgore & Yurgelen-Todd 2010		✓			✓
Maheu et al. 2010					✓
Rahko et al. 2010					✓
Hoehl et al. 2010	~	✓			✓
Weng et al. 2011					✓
Blair et al. 2011	✓			✓	
Todd et al. 2011	✓	~			✓
Gee et al. 2012	✓	✓	✓		✓
Garrett et al. 2012	✓			✓	
van den Bulk et al. 2013					✓
Cohen Kadosh et al. 2013a	✓			✓	
Cohen Kadosh et al. 2013b	✓			✓	
Perlman et al. 2013					✓
Pagliaccio et al. 2013		✓			✓

Study				
Scherf et al. 2015				✓
Cservenka et al. 2015	~			✓
Telzer et al. 2015	~			✓
Wu et al. 2016	✓			✓
Kryza-Lacombe et al. 2019	✓			✓
Hildesheim et al. 2020				✓
Lee et al. 2020	~			✓
Sahraei et al. 2022	✓			✓

Object processing

Study				
Gathers et al. 2004	~	~	~	✓
Golarai et al. 2007				✓
Scherf et al. 2007				✓
Turkeltaub et al. 2008				✓
Dekker et al. 2011				✓

Study	Col 1	Col 2	Col 3	Col 4
O'Hearn et al. 2011	✓		✓	
Scherf et al. 2015				✓
Nishimura et al. 2015	✓		✓	
Deen et al. 2017	✓		✓	
Golarai et al. 2017		✓		✓
Dehaene-Lambertz et al. 2018	✓		✓	
Meissner et al. 2019		✓		✓
Keulers et al. 2019				✓
Nordt et al. 2021	✓		✓	
Tian et al. 2021				✓
Kamps et al. 2022	✓		✓	

Scene processing

Study	Col 1	Col 2	Col 3	Col 4
Aylward et al. 2005	✓		✓	

Study					
Golarai et al. 2007	✓			✓	
Scherf et al. 2007					✓
Chai et al. 2010	✓			✓	
O'Hearn et al. 2011	✓	✓	✓		
Vuontela et al. 2013	~	~			✓
Jiang et al. 2014	~	~			✓
Scherf et al. 2014	~				✓
Scherf et al. 2015					✓
Deen et al. 2017	✓	✓	✓		
Golarai et al. 2017					✓
Dehaene-Lambertz et al. 2018	✓			✓	
Meissner et al. 2019	✓	✓	✓		
Nordt et al. 2021	✓			✓	
Tian et al. 2021	✓			✓	

Kamps et al. 2022	✓			✓	
Sahraei et al. 2022					✓

Body/limb processing

Ross et al. 2014	✓			✓	
Deen et al. 2017		✓			✓
Dehaene-Lambertz et al. 2018					✓
Ross et al. 2019	✓			✓	
Nordt et al. 2021		✓			✓

Character/symbol processing

Turkeltaub et al. 2008	✓			✓	
Cantlon et al. 2011	✓	✓	✓		
Dekker et al. 2014					✓

Dehaene-Lambertz et al. 2018	✓		✓		✓		
Kersey et al. 2019	✓					✓	
Nordt et al. 2021	✓	✓		✓			
Motion processing							
Bucher et al. 2006							✓
Carter & Pelphrey 2006	✓					✓	
Klaver et al. 2008	✓	✓		✓			
Lichtensteiger et al. 2008	✓	✓		✓			
Anderson et al. 2013							✓
Biagi et al. 2016	✓	✓		✓			
Sapey-Triomphe et al. 2017	✓	✓		✓			
Kirby et al. 2018							✓
Taylor et al. 2018	✓					✓	

Movie processing

Cantlon & Li 2013	✓			✓	
Moraczewski et al. 2018	✓	~		✓	
Camacho et al. 2019					✓
Kersey et al. 2019	✓	✓	✓		
Moraczewski et al. 2020	✓			✓	
Lerner et al. 2021	✓			✓	
Kamps et al. 2022	✓	✓	✓		
Cohen et al. 2022		✓			
Benear et al. 2022	✓			✓	
Park et al. 2022					✓
Yates et al. 2022	✓			✓	

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Appendix A7. Summary of studies investigating development of early visual processing.

Study	Sample	Sub-domain	Methodology	Main developmental findings
Born et al. 1998	$n = 13$ Child ages 3d-48mo Child $n = 10$ Adult $n = 3$	Flickering light	Cross-sectional Block design task	Children were either sedated or asleep, while adults were awake with eyes closed. BOLD signal change detected in the occipital region for 10/11 children. BOLD response did not extend to the surface of the brain for younger children but did for older children (32- and 36-months of age). In younger children the response was more anterior with lateral

extensions. Adults had responses along the whole calcarine sulcus. No detectable age dependence for size of response.

| Martin et al. 1999 | $n = 58$ No adults Child ages 1d-12y | Flickering light | Cross-sectional Block design task | Children were either awake or sedated. Responses to visual stimulus were both positive and negative, with negative signal located more anterior in the calcarine sulcus. No stimulus-related signal detected in 20 children. When put into 3 age groups (1d-4mo, 4mo-3.5y, 4y+), distribution of children with |

detectable positive and negative responses showed a main effect of age.

The positive BOLD response increases with age, while the negative BOLD response increases until 1-2y of age and decreases after.

Muramoto et al. 2002	$n = 26$ Child ages 0-32 weeks Child $n = 20$ Adult $n = 6$	Flickering light	Cross-sectional Block design task	Infants were sedated and adults were awake. Younger infants showed a task-related signal increases in the anterolateral region of the calcarine fissure, while older infants showed a task-related signal decrease.

				Adults had a task-related signal decrease.
Kang et al. 2003	$n = 32$ Child ages 7-8y Child $n = 16$ Adult $n = 16$	Flickering checkerboard	Cross-sectional Event-related task	No significant differences in the average response between adults and children in bilateral visual cortex, bilateral SMA, left sensorimotor medial and lateral, right sensorimotor lateral. Significant time course x age interaction in the right sensorimotor medial. No significant difference in maximum/peak level of BOLD response between children and adults.

				No significant differences in locations of BOLD response between children and adults in any ROIs. No significant differences in the variability of response location between groups.
Richter and Richter 2003	$n = 30$ Ages 6-61y Do not specify specific child or adult n	Flickering checkerboard	Cross-sectional Block design task	No correlation between age and the extent of BOLD response. No correlation between age and the magnitude of the peak BOLD signal change. Found a significant age dependence of the HRF.

Wenger et al. 2004	$n = 20$	Flickering	Cross-sectional	No significant
	Child ages 7-9y	checkerboard	Mixed block and	differences between
	Child $n = 10$		event-related task	groups in time courses
	Adult $n = 10$			or peak magnitudes in
				the early visual cortex.
Bucher et al. 2006	$n = 32$	Luminance shapes	Cross-sectional block	Pattern of response for
	Child ages 15-17y		design	luminance forms similar
	Child $n = 16$			between adolescents
	Adult $n = 16$			and adults (responded in
				V1 bilaterally, and V2
				in lingual and MOG).
				No significant
				differences in the adult
				vs. adolescent contrast.
Dekker et al. 2015	$n = 29$	Depth disparity from	Cross-sectional	In younger children, no
	No adults	binocular disparity or	Block design task	evidence for integration
	Child ages 8-12y	motion		in V3b; after 10.5y, V3b
				showed BOLD response
				patterns for integration.

The brain pattern for integration corresponded with behavioural performance on the task.

Gomez et al. 2019	$n = 41$	Retinotopic mapping	Cross-sectional	Topographic
	Child ages 5-12y		Block design task	organization of
	Child $n = 18$			eccentricity and polar
	Adult $n = 43$			angle maps within the
				lateral visual stream are
				stable after the age of 5
				years.
				pRFs in the LO (object
				form) and TO (motion
				processing) clusters
				undergo different
				developmental
				trajectories. The visual
				field coverage increases

centrally for the LO and peripherally for the TO.

Ellis et al. 2021a	n = 17	Retinotopic mapping	Cross-sectional	Evidence for
	No adults		Block design task	arealization of the
	Child ages 4.8-23.1mos			retinotopic visual cortex in 16/17 infants. 3 participants under 6mos showed a gradient organization pattern. Sensitivity to spatial frequency showed a foveal to peripheral gradient, even in infants under 6 months, and it did not reliably correlate with age in V1, V2, V4, or V3a/b, though was stronger in older children in V3. Spatial frequency differences were present

in infants, though the mapping was less precise than in adults. Infants were more similar to the adult retinotopic atlas than they were to other infants, and similarity to the adult map increased with age. Significant relationship between size and age in V1 and V2. Development may reflect fine tuning of visual cortex.

Kim et al. 2021	$n = 33$ Child ages 8.1-12.8y Child $n = 22$ Adult $n = 11$	Retinotopic mapping	Cross-sectional Block design task	Colourful squares were shown either sequentially at varying angles of eccentricity, or simultaneously.

Sequential >
simultaneous maps
looked qualitatively
similar in adults and
children.
No main effect of age
group or interactions
with age group for
sequential >
simultaneous.
Significant interaction
in area and age group
driven by children
showing suppression of
simultaneous relative to
sequential stimuli in
MT to a lesser extent
than adults.

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Appendix A8. Summary of studies investigating development of (non-affective) face processing.

Study	Sample	Sub-domain	Methodology	Main developmental findings
Passarotti et al. 2003	$n = 31$ Child ages 10-12y Child $n = 15$ Adult $n = 16$	Neutral faces	Cross-sectional Block design task	In the right hemisphere there was a significant age group x ROI interaction for volume of response, where adults exhibited more extensive medial fusiform response compared to lateral response, while children showed approximately even volumes of response in the lateral and medial fusiform. The extent of medial fusiform response did not significantly differ between children and adults, while children had significantly greater extent of lateral

fusiform response than adults.

In the left hemisphere, adults did not show a difference in extent of medial and lateral fusiform response, while in children, the extent of lateral response was greater than medial.

Children had greater extent of response to faces in the MTG than adults (no hemispheric differences).

No main effect or interaction of age group with percent signal change in any ROI to faces.

Gathers et al. 2004	$n = 29$	Human faces	Cross-sectional	Only adults and 9-11y old children showed preferential face responses near the "classically defined" FFA,
	Child ages 5-11y		Block design task	
	Child $n = 20$			
	Adult $n = 9$			

				whereas children 5-8y only showed face-preferential responses in the occipital gyri (more posterior ventral stream). Magnitude of BOLD signal change and variability of response within face-preferential ROIs did not differ with age.
Aylward et al. 2005	$n = 21$ No adults Child ages 8-14	Neutral male faces	Cross-sectional Block design task	The faces > houses contrast was greater for older (12-14y) children than younger (8-10y) children in the right fusiform gyrus, MTG, ITG, MOG, ITG. Younger children had no regions where faces > houses contrast was greater than older children.

Magnitude of response and total number of significantly responding voxels in the fusiform gyrus for faces > houses did not differ between groups.

Proportion of voxels with a significant response in the fusiform for faces > houses was significantly greater in the older children than the younger children.

Joseph et al. 2006	$n = 32$ Child ages 7-11y Child $n = 16$ Adult $n = 16$	Human faces	Cross-sectional Block design task	Adults had extensive differences in BOLD response for inverted > upright faces in the ventral stream and associative areas (IOG, MOG, right anterior fusiform gyrus). For adults, upright > inverted only had a

significant cluster in the calcarine sulcus.

Children showed less extensive differences in response for inverted > upright (differences seen in fusiform gyrus, MOG, IOG, and SOG, all left hemisphere). Children showed upright > inverted responses in the right fusiform gyrus and the lingual gyrus.

Adults and older (9-11y) children had greater BOLD signal change for inverted > upright faces, while younger (7-9y) children had greater change for upright > inverted.

Only adults showed a significant difference in

inverted > upright face processing in the MOG and the right fusiform.

| Golarai et al. 2007 | $n = 50$ Child ages 7-16y Child $n = 33$ Adult $n = 17$ | Male neutral faces | Cross-sectional Block design task | The FFA was more reliably detected in adults than children. It also increased in size with age, but the amplitude of BOLD signal change in the FFA was not different between adults and children. Face selectivity and responsiveness increases in the area immediately surrounding children's right FFA over development. In this area, there are no significant differences in responses to objects between adults and children, so face |

selectivity increases due to increasing response to faces. No significant differences between age groups in the extent or magnitude of respons to faces in the STS. Face recognition memory is correlated with right FFA size.

Dalton et al. 2007	$n = 12$ One group, 10-21y	Familiar faces, unfamiliar faces	Cross-sectional Task design (unclear if block or event-related)	No significant associations with age for brain response to faces.
Scherf et al. 2007	$n = 18$ Child ages 5-14y Child $n = 9$ Adult $n = 9$	Short movie clips of faces	Cross-sectional Hybrid (naturalistic block design)	Adults showed BOLD signal change in the FFA, OFA, and STS when viewing faces. Adolescents had similar responses in the FFA, OFA, and STS to adults, though it

was more right lateralized (it was bilateral in adutls). Children did not have responses in any of the classically-defined face regions (had a small cluster of face related BOLD response in the posterior lateral fusiform gyrus). Children had BOLD signal change in the adult FFA when viewing faces, but the change was not specific to faces.

Children showed less face specificity than adults, though adolescents' face specificity was not significantly different from either children nor adults. Children also showed less face specificity than adults

and adolescents in the OFA and the pSTS, while there were no differences between adults and adolescents in either of those ROIs.

In FFA, OFA, and pSTS, children had significantly smaller volumes of BOLD response than both adults and adolescents.

Joseph et al. 2011	$n = 90$	Human faces	Cross sectional	Younger children recruit left hemisphere face regions more than older children and adults, while older children and adults have similar response patterns. Face-preferential BOLD signal change is shown in every group (though not in the same areas).
	Child ages 5-12y		Block design task	
	Child $n = 47$			
	Adult $n = 43$			

The left FFA, right MTG, and right IFG all showed a shift from non-specific responses in children to face-preferential responses in adults.

All brain regions that were face-preferential in adults (bilateral FFA, right OFA, bilateral MTG, right IFG) showed increasing face specialization index with age in children.

In regions that were face-preferential in the youngest children (right ITG, left MTG, left postcentral gyrus, left angular gyrus, left precentral gyrus, right IFG), face specialization decreased with age.

O'Hearn et al. 2011	$n = 18$ (controls)	Neutral human faces	Cross-sectional	Older group (CA) had
	"Mental age" matches		Block design task	greater BOLD signal change
	6-9y			than the younger group for
	"Chronological age"			faces > scrambled in the
	matches 12-27y			bilateral FFA and OFA.
	MA $n = 9$			Younger group (MA) had
	CA $n = 9$			little BOLD signal change in
				the right FFA and no signal
				change in the left FFA.
				No differences between CA
				and MA in the OFA
				(posterior face area).
Cantlon et al. 2011	$n = 29$	Faces	Cross-sectional	Children and adults both
	Child ages 4-5.8y		Event-related task	showed a typical adult
	Child $n = 15$			pattern of activity in
	Adult $n = 14$			response to faces in the right
				mid-fusiform gyrus.
				Only adults showed BOLD
				signal change to faces in the
				left mid-fusiform gyrus.

Both adults and children showed a spatial dissociation of responses for faces and words in the occipitotemporal cortex (i.e. right mid-fusiform for faces, left lateral fusiform/ITG for symbols).

Increase in children's facial recognition happens congruently with a decrease in response to non-preferred categories in face-preferring cortex.

Haist et al. 2013	$n = 71$ Child ages 6-16y Child $n = 50$ Adult $n = 21$	Male and female faces	Cross-sectional Block design task	No significant differences across the 3 groups (adults, adolescents, children) in terms of right FFA detection. Significant difference in detection of left FFA driven

by lower detection rates in the adolescents.

Significant increase with age in the size of the right FFA, but not in the left FFA.

No significant association between age and amplitude of BOLD signal change. Voxels in the right middle fusiform gyrus were more likely to be included in the FFA with age.

In a whole-brain analysis, there were no regions with an association between BOLD signal change and age. Within the face-processing system (ITG, MTG, amygdalae, PCC, right hippocampus, insula, IFG, left ACC) responses decreased with age.

Vuontela et al. 2013	$n = 27$	Neutral faces	Cross-sectional	FFA was detected more often in the right hemisphere than the left, and in adults more than in children.
	Child ages 7-11y		Block design task	
	Child $n = 16$			
	Adult $n = 11$			

The remember-face-ignore-scene (Fs) task had greater activity in the right FFA than the remember-scene-ignore-face (Sf) task in adults, but not in children.

No correlation with age (continuous) and level of BOLD signal change in either task in adults or in children in the FFA.

In the whole-brain analysis, there was a significant main effect of age group on several regions in the brain, but not age group x task interactions. Adults had

greater signal change than children in ventral visual/perceptual areas (occipital pole, lingual gyrus, supramarginal gyrus, insula, pre- and post-central gyri) while children showed responses in prefrontal/parietal/associative areas more than adults (MFG, SFG, cingulate gyrus, angular gyrus, parahippocampal gyrus, ITG, STG, MTG).

Processing of face information and regulation of activity was weaker for children in the right FFA than adults.

Jiang et al. 2014	*n* = 29 Child ages 7-11y	Faces	Cross-sectional Block design task	Also did the Fs and Sf task as in Vuontela et al. 2013.

Child $n = 16$

Adult $n = 13$

Main effect of age group – children had greater BOLD responses in prefrontal areas (SFG, MFG), while adults had greater BOLD responses in insula, cingulate gyri, and parietal cortex (PCC/SMG, precuneus, insula, mid-CC, precentral gyrus, parietal opercular cortex) for both tasks.

Age group x task interaction in the medial PFC, ACC, and subcallosal cortex – Sf and Fs elicited negative signal in these areas in both groups, and the [(Sf > rest) – (Fs > rest)] difference was greater in adults than children.

In the RSC, Sf > Fs, and this contrast was greater in children than adults. There

				were no significant correlations between age and the signal in either task in the RSC.
Scherf et al. 2014	$n = 35$ Child ages 6-20y Child $n = 23$ Adult $n = 12$	Movie clips of faces	Cross-sectional Hybrid (naturalistic block design)	Both the left and right face ROIs in the fusiform gyrus increased in size with age. Magnitude of BOLD signal change within the fusiform face ROIs did not significantly change with age. Neither did the variability of the locus of response. Bilateral OFA ROIs also increased in size with age, though magnitude and location variability of response did not.

Joseph et al. 2015	$n = 42$ No adults Child ages 5-18y	Faces	Cross-sectional Block design task	Face specialization index was correlated positively with age in the left FFA and the right amygdala (with a positive trend for right FFA), in the control group. Majority of control group did not have a preference for faces before the age of 9 years and a positive face specialization index was present from the age of 9 through adolescence.
Natu et al. 2016	$n = 35$ Child ages 5-12y Child $n = 23$ Adult $n = 12$	Child and adult faces (functional localizer); face-morph experiment	Cross-sectional Block design task	Volume, response-amplitudes, and selectivity of face-selective regions was larger in adults than children, though children did demonstrate face-selectivity, just to a lesser extent.

In both children and adults, face-selective responses in the ventral temporal cortex increased with increasing facial dissimilarity, and this effect was greater in adults than children.

There was a general increase in the amplitude of response to faces in both face- and object-selective regions with age, but increases in neural sensitivity to faces only occurred in the face-selective regions (which was coupled with better discriminability for faces).

Deen et al. 2017	$n = 12$	Faces (movie clips)	Cross-sectional	Face > scene regions are seen
	Child ages 3-8mo		Hybrid (naturalistic	in infants in the fusiform
	Child $n = 9$		block design)	gyrus, lateral occipital
	Adult $n = 3$			

cortex, STS, and medial PFC.

However, no regions showed a higher response for faces compared to object in infants, whereas in face-selective areas in adults, there was a significantly higher response to faces than to other categories.

Multivariate pattern of reponses for faces and scenes were dissimilar from each other in both infants and adults, but the face representation in infants was also dissimilar to that in adults, and the pattern of dissimilarity between categories was different in adults and children too.

Golarai et al. 2017	$n = 24$	Male child faces,	Cross-sectional	Multivariate pattern (MVP)
	Child ages 7-11y	male adult faces	Block design task	for faces in children had
	Child $n = 12$			higher responses in the
	Adult $n = 12$			fusiform gyrus and lower
				responses in medial VTC.
				In both adults and children,
				MVPs were highly similar
				within a category but
				different across categories.
				The large scale structure of
				the representational
				similarity matrix is stable
				across development (i.e.,
				faces were more similar to
				objects than scenes in both
				children and adults).
				Classification was high for
				category but varied across
				categories for age group
				(higher for faces than
				objects).

Classification accuracy for adult vs. child faces in adults was higher for adult faces, while in children, the decoding accuracy was similar for adult and child faces.

Irrespective of age of the face, there is an increase in the volume of face-selective regions with age.

Amplitude and selectivity of response to faces also increased with age in the bilateral posterior and mid-fusiform gyrus.

Nordt et al. 2018	*n* = 28 Child ages 7-10y Child *n* = 14 Adult *n* = 14	Neutral faces (adaptation paradigm and localizer)	Cross-sectional Block design task	In the right FFA, activity across all adaptation conditions was greater in adults than children.

Both children and adults showed adaptation effects to the repetition of an individual's face (different faces > same faces).
Adults, but not children, showed and adaptation effect when different images of the same person were shown.
FFA of adults had greater image invariance than children.
In the left FFA, children and adults again showed sensitivities to face identity, with a smaller degree of image invariance in children. This was only in FFA-1, not FFA-2.

Dehaene-Lambertz et al. 2018	*n* = 10 No adults Child ages 5-7y	Faces	Longitudinal Block design task	Faces elicited BOLD responses in the fusiform gyri, amygdala, and STS. No longitudinal increase in response to faces across the sessions. No significant change in the volume of face response over the sessions. Emergence of the VWFA and reliable activastion for words did not occur at the expense of face-selective BOLD response in the VTC.
Keulers et al. 2019	*n* = 42 No adults Child ages 12-17y	Faces	Cross-sectional Block design task	No significant age differences found for the visual task.
Nordt et al. 2021	*n2* = 29 No adults Child ages 5-17y	Adult faces, child faces	Longitudinal Block design task	Face-selective BOLD response in the lateral VTC increased with age.

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Bilateral face response grew in the posterior fusiform gyrus (pFus), but there was no change with age in the mid-fusiform (mFus).

In emerging pFus, selectivity to faces increased while selectivity to limbs decreased (not significant for any other category), due to an increasing amplitude of the response to faces in the pFus. Words and string instruments also had an increasing amplitude of response within the pFus, so the face-selectivity was more dependent on the strength of the preferred category increasing rather than the response to others decreasing.

In the OTS, where it was originally limb-selective, there was a limbs > faces response for children aged 5-9y, but faces > limbs in children 13-17y.

In OTS, in some individuals limb selectivity is replaced by face selectivity, and in others, it is replaced by word-selectivity.

| Tian et al. 2021 | $n = 266$
Child ages 9-14y
Child $n = 111$
Adult $n = 144$ | Faces (movie clips) | Cross-sectional
Hybrid (naturalistic
block design) | Child-to-adult representational similarity was significantly lower than adult-to-adult representational similarity in the right FFA and bilateral OFA (children did not show "adult-like" patterns of activity). |

Child-to-child similarity was significantly lower than adult-to-adult similarity in right FFA and bilateral OFA (more variability between children than between adults).

Children's representations in the right FFA and right OFA (but not left OFA) were more similar to adults with increasing facial recognition performance.

Kamps et al. 2022	$n = 168$	Faces (movie clips)	Cross-sectional	In the face-responding FFA,
	Child ages 3-12y	for functional	Naturalistic paradigm	OFA, and pSTS, the
	Child $n = 122$	localizer	Block design task	correlation between
	Adult $n = 46$			children's time course and
				the adult time course
				increased with age.
				In the FFA and OFA, 3-year-
				olds were as or more

correlated to the average 3-year-old time course as they were to the average adult time course.

In pSTS, however, while the older children (7y+) were the most correlated to the adult pSTS, the younger children's pSTS showed similar correlations to the adult pSTS, FFA, and LOC.

In the pSTS, 3-year-olds and 4-year-olds were both more correlated to the 3-year-old timecourse than the 4-year-old time course, and 5-year-olds were marginally closer to adults. 7-12-year-olds all were more correlated to the adult pSTS.

In the 3-year-olds, the shifted/lagged time course of

the pSTS had greater correlation to the adult pSTS time course than the non-shifted, and this effect dimished with age, with 8-12-year-olds showing greater correlation between the non-shifted time course and the adult time course.

Appendix A9. Summary of studies investigating development of emotional face processing.

Study	Sample	Sub-domain	Methodology	Main developmental findings
Pine et al. 2001	$n = 16$ Child ages 12-16y Child $n = 8$ Adult $n = 8$	Masked faces; fearful faces, happy faces	Cross-sectional Block design task	Masked happy > fixation was greater in adolescents compared to adults in the right posterior object processing stream (bordering on occipital and temporal lobes). No differences for masked fearful > fixation, and no areas where adults > adolescents. Adolescents had a greater contrast than adults for masked happy > masked fearful in the ventromedial association

				cortex of parieto-occipital junction. Adolescents had a greater contrast than adults for masked fearful > masked happy in the STG/MTG/amygdala border.
Yurgelen-Todd & Killgore 2006	*n* = 16 No adults Child ages 8-15y	Fearful faces, happy faces	Cross-sectional Block design task	In bilateral PFC, there was a significant positive correlation between response amplitude to fearful faces and age. No significant associations with age and amygdala activity for fearful faces. No significant correlations between response to happy faces and response in PFC or

amygdala (had expected
a negative correlation
with age for amygdala).

| Killgore & Yurgelen-Todd 2007 | $n = 22$
Child ages 9-17y
Child $n = 10$
Adult $n = 12$ | Masked sad faces, masked happy faces | Cross-sectional
Event-related design | No significant differences for responses to masked happy faces between adults and children. Children had greater responses to sad faces in the amygdala than adults. In the whole-brain analysis, adults had greater responses to masked happy faces than children in the left cerebellum and left anterior MTG. Children had greater responses to masked happy faces than adults in |

the SMA, middle
cinculate gyrus, bilateral
temporal gyri, right
supramarginal gyrus,
precentral gyrus, MFG,
and calcarine cortex.
Adults had greater
responses to sad faces
than children in then
cerebellum and left SPL.
Children had greater
responses than adults to
sad faces in the SFG,
IFG, cerebellum, right
MOC, fusiform gyrus,
and STG.

Monk et al. 2008	*n* = 39	Morphed emotional	Cross-sectional	No significant
	No adults	faces (happy, fearful)	Block design task	relationships between age
	Child ages 10-18y			and BOLD signal change
				in either the amygdala or
				the nucleus accumbens.

Guyer et al. 2008	$n = 61$	Happy, angry, fearful,	Cross-sectional	Adolescents had greater
	Child ages 9-17y	and neutral faces	Event-related design	BOLD responses for
	Child $n = 31$			fearful > neutral in the
	Adult $n = 30$			amygdala, while adults
				showed no differentiation
				of response in the
				amygdala for fearful >
				neutral.
				No other significant
				differences for other
				facial expressions
				between adolescents and
				adults in the amygdala.
				Age was not
				continuously associated
				with amygdala response
				to fearful faces in either
				age group.
				Fearful > neutral was also
				greater for adolescents

				compared to adults in the fusiform gyrus.
Killgore & Yurgelen-Todd 2010	$n = 23$ No adults Child ages 8-18y	Masked faces (angry, fearful, happy, neutral)	Cross-sectional Block design task	No significant associations between age and angry > neutral in the bilateral amygdala. Significant negative correlation between age and fearful > neutral in the left amygdala but not the right. No signification correlations with age and happy > neutral in the amygdala.
Maheu et al. 2010	$n = 19$ No adults Child ages 9-18y	Angry, fearful, happy, neutral faces	Cross-sectional Mixed block and event-related task	No significant changes between amygdala responses and peak BOLD signal change for any emotions / contrasts.

Rahko et al. 2010	*n* = 27 No adults Child ages 11-17y	Happy faces, fearful faces	Cross-sectional Hybrid (naturalistic block design)	No age effects for either expression or contrast.
Hoehl et al. 2010	*n* = 36 Child ages 5-6y Child *n* = 18 Adult *n* = 18	Happy child / adult faces, angry child / adult faces, ape faces (baseline)	Cross-sectional Event-related design	Amygdala responses for both happy faces > baseline and angry faces > baseline were greater for children than adults. Adults showed stronger responses in the right amygdala than children for child angry faces > adult angry faces, while children showed the opposite (adult angry > child angry). In the left amygdala, children showed greater activity for the child happy > adult happy than

				adults, and adults showed the opposite tendency (did not reach significance).
Weng et al. 2011	$n = 20$ No adults Child ages 10-18y	Sad, happy, fearful, and neutral faces	Cross-sectional Event-related design	Among controls, amygdala responses did not correlate with age for any expression.
Blair et al. 2011	$n = 39$ Child age range not listed (avg = 14.09y, SD = 2.03y) Child $n = 16$ Adult $n = 23$	Fearful faces, angry faces, neutral faces	Cross-sectional Event-related design	No diagnosis x age, emotion x age, or diagnosis x emotion x age interactions. Main effect of age – adults had greater BOLD signal change than adolescents in bilateral IFG, left MFG, MTG, cerebellum, right cingulate gyrus, postcentral gyrus, and MOG.

Todd et al. 2011	$n = 45$	Own/different mother	Cross-sectional	Response to faces >
	Child ages 3-8y	happy faces,	Block design task	scrambled images
	Child $n = 31$	own/different mother		increased linearly both in
	Adult $n = 14$	angry faces		the whole group and in
				the child group in the
				amygdala.
				In amygdala, happy >
				angry for children, but
				angry > happy for adults.
				Linear increase in the
				response to angry faces
				with age in the amygdala.
				In the whole brain
				analysis, main effect of
				age was driven by adults
				> children in right
				putamen, precentral
				gyrus, IPL, SFG, MFG,
				PCC, ACC, MTG, STS,
				fusiform.

				Age x expression interaction in the whole brain by children having happy > angry response in the putamen and amygdala, while adults had angry > happy response in the amygdala.
Gee et al. 2012	$n = 14$ Child ages 15-17y Child/adult n not listed	Angry, happy, scared, surprised faces	Cross-sectional Block design task	Controls had increasing BOLD signal change to emotional labelling > gender labelling with age in the VLPFC, and decreasing BOLD signal change to emotion labelling > gender labelling in the amygdala with age.
Garrett et al. 2012	$n = 21$ No adults	Happy, sad, neutral faces	Cross-sectional Block design task	Significant positive correlation with age and

				response of the DLPFC in the late phase for sad > baseline.
van den Bulk et al. 2013	*n* = 27 or 26 No adults Child ages 12-19y	Fearful, happy, neutral faces	Longitudinal Block design task	No main effect of time for response to emotional faces, fearful faces, happy faces, or neutral faces compared to baseline in either the PFC or amygdala.
Cohen Kadosh et al. 2013a ("Differential face-network…"	*n* = 42 Child ages 6-14y Child *n* = 28 Adult *n* = 14	Happy, angry, and neutral faces (also did a gaze task and identity task)	Cross-sectional Block design task	Significant main effect of age in the occipital lobes, ventral temporal stream, right precuneus, right IFG, across all 3 tasks. All 3 tasks elicited BOLD signal change in the core face processing network, but participants recruited different

additional regions at different ages.

While overall signal responses were comparable across age groups, there were differential effects of recovery from adaptation.

Main effect of age group was seen in the right IOG.

The bilateral IOG and the right STS showed a significant task x adaptation condition x age group interaction.

No adaptation effects were seen in adolescents.

Children had lower levels of hemisphereic specialization.

Cohen Kadosh et al. 2013b ("Effects of age…")	$n = 48$ Child ages 7-17y Child $n = 34$ Adult $n = 14$	Happy, angry, and neutral faces (also did a gaze task and identity task)	Cross-sectional Block design task	Increases in BOLD signal with age during the expression identification task in the left fusiform gyrus, right ITG, and the cerebellum.
Perlman et al. 2013	$n = 20$ No adults Child age range not specified (avg = 13.52y, SD = 2.13y)	Morphed expressions (neutral, happy, sad, angry, fearful)	Cross-sectional Block design task	Age did not have an independent effect on the response to angry faces in the fusiform gyrus.
Pagliaccio et al. 2013	$n = 52$ No adults Child ages 7-12y	Neutral, sad, angry, happy, and fearful faces	Cross-sectional Event-related design	No significant correlations were found between age and amygdala response for any emotion type. Negative correlation between age and response to neutral faces in the left SMG.

				Negative correlation between age and response to sad faces in the left precentral gyrus. Negative correlation between age and response to fearful faces in the cerebellum, parahippocampal gyrus, insula, cuneus, MOG, and cingulate gyrus.
Scherf et al. 2015	$n = 12$ No adults Child ages 11-17y	Neutral faces, fearful faces	Cross-sectional Block design task	No regions with a correlation between age and face-related response.
Cservenka et al. 2015	$n = 44$ No adults Child ages 10-15y	Emotional conflict task (happy faces, fearful faces, congruent/incongruent)	Cross-sectional Block design task	Negative relationship with age and incongruent > congruent contrast in the bilateral MFG.

Telzer et al. 2015	$n = 52$ No adults Child ages 4-18y	Angry, happy, neutral faces	Cross-sectional Block design task	Negative relationship between age and the opposite-sex > same-sex contrast in the bilateral dorsal amygdala. No regions in whole brain analysis with an association between age and same-sex > shapes or opposite-sex > shapes.
Wu et al. 2016	$n = 61$ Child ages 7-18y Child $n = 37$ Adult $n = 24$	Angry, fearful, happy faces	Cross-sectional Block design task	Decreasing BOLD signal change with age for happy faces in the vmPFC, but not for angry or fearful faces.
Kryza-Lacombe et al. 2019	$n = 51$ Child ages 9-18y Child $n = 29$ Adult $n = 22$	Morphed expressions (happy, angry, fearful, neutral)	Cross-sectional Event-related design	In the medial PFC and lingual gyrus, healthy control adolescents showed a greater adaptation effect for

repeated presentations of the faces compared to control adults. Adolescents also had greater responses to negative (fearful/angry) faces than adults in the lingual gyrus and TPJ. No differences in response between adults and adolescents for neutral faces in the TPJ. Adults had less BOLD signal change to all faces compared to adolescents in the mPFC and left MFG.

Hildesheim et al. 2020	n = 19 Child ages 7-9y Child n = 9 Adult n = 10	Neutral, sad, and fearful faces	Cross-sectional Block design task	No statistically significant differences in BOLD response between children and adults.

Lee et al. 2020	$n = 181$	Morphed expressions	Cross-sectional	Adolescents more
	Child ages 12-15	(angry, happy, neutral	Block design task	similarly represented
	Child $n = 101$	faces)		lower intensity emotional
	Adult $n = 80$			faces (15% happy vs 15%
				sad) than adults did in the
				FFA and OFA.
				Neural perceptual
				uncertainty negatively
				correlated with age
				across the whole sample.
Sahraei et al. 2022	$n = 18$	Neutral, sad, and	Cross-sectional	Children had greater
	Child ages 7-9y	fearful faces	Block design task	BOLD response for faces
	Child $n = 8$			> houses than adults in
	Adult $n = 10$			the left amygdala, IFG,
				and right insula.
				No significant age group
				x condition interaction
				(faces > houses age
				changes were not driven
				by only one condition).

No significant effects of emotion.

Stronger left-lateralized activity in the IFG to faces > houses for children compared to adults.

Children had increased responses in the extended face network compared to adults.

Appendix A10. Summary of studies investigating development of object processing.

Study	Sample	Sub-domain	Methodology	Main developmental findings
Gathers et al. 2004	$n = 29$ Child ages 5-11y Child $n = 20$ Adult $n = 9$	Natural objects, manufactured objects	Cross-sectional Block design task	Children ages 5-8y had no selective BOLD response for either object category. 9-11y old children had selective responses for natural objects in the right IPL and bilateral MFG. They also had selective responses for manufactured objects in the left temporal pole and the right IFG. Adults showed selective responses for natural objects in the left SPL and temporal pole, and for manufactured objects

				in the right calcarine sulcus and MOG.
Golarai et al. 2007	$n = 50$ Child ages 7-16y Child $n = 33$ Adult $n = 17$	Abstract sculptures	Cross-sectional Block design task	In object-sensitive cortex in the LOC, there were no differences in response extent or in amplitude between children, adolescents, and adults.
Scherf et al. 2007	$n = 18$ Child ages 5-14y Child $n = 9$ Adult $n = 9$	Common objects (movie clips)	Cross-sectional Hybrid (naturalistic block design)	Adults, adolescents, and children all showed responses in the medial fusiform gyrus and the ventral lateral occipital cortex to objects. No age group differences in magnitude of BOLD signal change in LOC. No age group differences in

lateralization (R > L for all) and extent of BOLD signal change in LOC.

Turkeltaub et al. 2008	$n = 37$ Child ages 6-11y Child $n = 22$ Adult $n = 15$	Object line drawings	Cross-sectional Block design task	Main effect of age were mostly driven by differences of BOLD signal change between children and adults in the letter-naming task rather than the object-naming task.
Dekker et al. 2011	$n = 44$ Child ages 6-10y Child $n = 33$ Adult $n = 11$	Tools	Cross-sectional Block design task	No regions where tool selectivity varied with age. Both dorsal and ventral stream areas for tool-preference show an adult-like spatial distribution early in life.

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O'Hearn et al. 2011	$n = 18$ (controls) "Mental age" matches 6-9y "Chronological age" matches 12-27y MA $n = 9$ CA $n = 9$	Shoes	Cross-sectional Block design task	Older group had greater BOLD signal change in response to objects than the younger group in the right fusiform, IOG, lingual gyrus, and left fusiform and IOG.
Scherf et al. 2015	$n = 12$ No adults Child ages 11-17y	Common objects, novel objects	Cross-sectional Block design task	No regions with a significant correlation between and object-related BOLD responses.
Nishimura et al. 2015	$n = 41$ Child ages 5-17y Child $n = 26$ Adult $n = 15$	Common objects (localizer task), objects with varying size, objects with varying views (size & view adaptation paradigms)	Cross-sectional Block design task	Adults, adolescents, and children all showed BOLD responses in LOC in response to objects, and the extent of BOLD signal change in LOC was similar between the 3 groups. In the LOC, adults and adolescents had

significantly greater magnitude of BOLD signal change than children.

Magnitude of response was lower in children but there were no differences in the selective sensitivity to objects in LOC between groups.

Adaptation effects for size were similar between all 3 groups (only difference: adolescents had a greater adaptation effect in the left LOC compared to the right, and this was not seen in adults or children).

				Adults showed adaptation effects for the same objects shown from different views, while there was no conclusive evidence for view adaptation in children or adolescents.
Deen et al. 2017	$n = 12$ Child ages 3-8mo Child $n = 9$ Adult $n = 3$	Toys (movie clips)	Cross-sectional Hybrid (naturalistic block design)	In adults, face- and scene-selective regions showed robust greater responses to their preferred categories compared to objects (ventral and lateral face & scene regions, STS face region). In infants, no region showed a significantly higher response to faces

				or scenes compared to objects. Infants showed regions of the temporal and parietal cortex that robustly preferred objects compared to faces and scenes (with adult-like spatial organization).
Golarai et al. 2017	$n = 24$ Child ages 7-11y Child $n = 12$ Adult $n = 12$	Abstract sculptures, common cars	Cross-sectional Block design task	Scenes, objects, and faces evoked distinct multivariate representations in the ventral temporal cortex in children. The multivariate pattern in response to objects had higher BOLD signal change in the medial fusiform gyrus and

lower responses in the lateral fusiform and media VTC.

For both adults and children, the correlation between the object- and the face-MVP was higher than the correlation between face- and scene-MVPs. Classification accuracy for age group was lower for objects than faces. There were no associations with age for classification accuracy of cars vs. scultptures (while own-age vs. other-age faces did show an association with age). Volume of BOLD response for novel

				objects decreased with age. Volume of response in the mid fusiform gyrus was 30-50% lower in adults than children.
Dehaene-Lambertz et al. 2018	$n = 10$ No adults Child ages 5-7y	Objects, tools	Longitudinal Block design task	No longitudinal increase for strength of BOLD signal change. No longitudinal increase in the number of voxels with a significant BOLD response. MVPA pattern reliability for tools was present across sessions 1 and 2, and stayed stable.
Meissner et al. 2019	$n = 39$ Child ages 7-12y Child $n = 26$ Adult $n = 13$	Hand-size to larger-than-body objects	Cross-sectional Block design task	In the OPA, responses to objects decreased with age. Objects also showed responses the bilateral

				PPA more in children than adults (while scene activity did not significantly change between the two groups).
Keulers et al. 2019	$n = 42$ No adults Child ages 12-17y	Pictures of objects	Cross-sectional Block design task	No age differences were found in the visual task.
Nordt et al. 2021	$n = 29$ No adults Child ages 5-17y	String instruments, cars	Longitudinal Block design task	In the left pOTS-words, responses to string instruments increased significantly with age. Responses to string instruments also increased with age in the pFus-faces (and there was a trend towards increase with age for cars).

Tian et al. 2021	$n = 266$ Child ages 9-14y Child $n = 111$ Adult $n = 144$	Objects (movie clips)	Cross-sectional Hybrid (naturalistic block design)	No age differences in within-group representational similarity for objects in the FFA, OFA, PPA, or V1.
Kamps et al. 2022	$n = 168$ Child ages 3-12y Child $n = 122$ Adult $n = 46$	Objects (movie clips) for functional localizer task, also showed a movie	Cross-sectional Hybrid (naturalistic block design) Naturalistic movie task	In the object-responding LOC, the correlation between children's time course and the adult time course increased with age. In the LOC, 3-year-olds were as correlated to the average 3-year-old time course as they were to the average adult time course.

Appendix A11. Summary of studies investigating development of scene processing.

Study	Sample	Sub-domain	Methodology	Main developmental findings
Aylward et al. 2005	$n = 21$ No adults Child ages 8-14	Houses	Cross-sectional Block design task	While the houses > faces contrast was not significant anywhere over the entire group, older children had greater BOLD responses for houses > faces than younger children in a region medial and superior to the region with a response to faces in the fusiform gyrus.
Golarai et al. 2007	$n = 50$ Child ages 7-16y Child $n = 33$ Adult $n = 17$	Indoor scenes, outdoor scenes	Cross-sectional Block design task	The left PPA increased in size with age (adults > children), but not the right PPA. The left PPA increased into the area immediately surrounding the children's PPA.

				No significant differences in the response amplitudes in either right or left PPA to scenes between adults and children. Recognition memory for places was correlated positively with the size of the left PPA.
Scherf et al. 2007	$n = 18$ Child ages 5-14y Child $n = 9$ Adult $n = 9$	Buildings, open fields	Cross-sectional Hybrid (naturalistic block design)	Adults, adolescents, and children showed BOLD signal change in the bilateral PPA in response to scenes. No significant main effects of age for magnitude or extent of response in bilateral PPA. Hemisphere x age interaction in extent of response in the PPA was driven by adults and children having equal

extent of the PPA showing BOLD response by scenes bilaterally, whereas adolescents had a greater extent of response in the right PPA.

Chai et al. 2010	$n = 46$ Child ages 8-17y Child/adult distribution not reported	High and low complexity scenes	Cross-sectional Event-related task	Across all participants (children and adults), there were greater responses in the occipital and posterior medial temporal lobe for high complexity scenes compared to low complexity scenes. There was a significant increase in the high > low complexity contrast with age in the right posterior parahippocampal gyrus and the premotor cortex / supplementary motor area.

O'Hearn et al. 2011	n = 18 (controls) "Mental age" matches 6-9y "Chronological age" matches 12-27y MA n = 9 CA n = 9	Houses	Cross-sectional Block design task	Older group had greater BOLD response to houses > scrambled than the younger group in the medial fusiform gyrus, IOG, and parahippocampal gyrus, while the younger group had greater BOLD response than the older group in other right fusiform regions. The regions in the right fusiform that the younger group had responses for houses in were areas that were showed responses for faces in the older group.
Vuontela et al. 2013	n = 27 Child ages 7-11y Child n = 16 Adult n = 11	Outdoor scenes	Cross-sectional Block design task	The PPA was detected in all adults and 14/16 children, and there was no significant main effect or interactions of

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age group, nor a significant correlation between age and PPA response.

Across both the face task and the place task, there was a main effect of age group, but no task x age group interactions.

For both tasks, adults had greater response than children in ventral visual/perceptual areas (occipital pole, lingual gyrus, supramarginal gyrus, insula, pre- and post-central gyri) while children responded in prefrontal/parietal/associative areas more than adults (MFG, SFG, cingulate gyrus, angular gyrus, parahippocampal gyrus, ITG, STG, MTG).

Jiang et al. 2014	*n* = 29 Child ages 7-11y Child *n* = 16 Adult *n* = 13	Outdoor scenes	Cross-sectional Block design task	Similar to Vuontela et al. 2013, across both face and scene tasks, PFC regions were more had greater BOLD signal change in children compared to adults, while adults had greater response in insular, cingulate, and parietal cortex. No correlation between amplitude of response in the retrosplenial cortex and age. No age group main effect or age group x task interaction in the PPA.
Scherf et al. 2014	*n* = 35 Child ages 6-20y Child *n* = 23 Adult *n* = 12	Buildings, open fields	Cross-sectional Hybrid (naturalistic block design)	The extent of response in the right (not left) PPA increased with age. Magnitude of selectivity for places and variability of

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				locus of response did not significantly vary with age.
Scherf et al. 2015	$n = 12$ No adults Child ages 11-17	Houses	Cross-sectional Block design task	No brain regions with a significant correlation between age and house-related response.
Deen et al. 2017	$n = 12$ Child ages 3-8mo Child $n = 9$ Adult $n = 3$	Scenes	Cross-sectional Hybrid (naturalistic block design)	Infants showed scene > face BOLD signal change in the parahippocampal gyrus and the lateral occipital cortex. In infants, no region showed a higher response to scenes over objects, but in adults, the scene-preferring regions showed a higher response to scenes than all other categories. In both adults and children, the multivariate spatial response pattern to faces and

scenes were dissimilar from one another.

Golarai et al. 2017	$n = 24$	Indoor scenes,	Cross-sectional	In children, scenes, faces,
	Child ages 7-11y	outdoor scenes	Block design task	and objectd elicited distinct
	Child $n = 12$			multivariate patterns in the
	Adult $n = 12$			ventral temporal cortex.

For the scenes multivariate pattern, the medial ventral temporal cortex showed high BOLD signal change, while the fusiform gyrus had low change.

In both children and adults, multivariate patterns were similar within a category but different across categories.

Pairwise correlations in multivariate patterns between children (for all categories) did not significantly differ

				from the pairwise correlations between adults.
Dehaene-Lambertz et al. 2018	$n = 10$ No adults Child ages 5-7y	Houses	Longitudinal Block design task	There was a longitudinal linear increase in the BOLD response across sessions for houses in [32 -78 32] (IPS?). Peak of response for houses was not displaced by the emergence of the VWFA. House -responsive voxels from sessions 6 & 7 were already specific to bodies in sessions 1-5. In voxels that were preferential to houses, the preferences were temporally stable.
Meissner et al. 2019	$n = 39$ Child ages 7-12y Child $n = 26$	Natural scenes, man-made scenes, public scenes, private scenes	Cross-sectional Block design task	Higher detection rate of OPA and PPA in adults compared to both younger children (7-

Adult $n = 13$

8y) and older children (11-12y). No differences in RSC detection rate.

PPA and OPA increased in volume in both hemispheres with age driven by adults > both child groups (child groups did not differ). No significant increase in RSC with age.

The locus of response changed with age only in the left PPA; was located more medial and more inferior with age; maximal absolute difference between groups was only 3mm, so significant, but small magnitude.

Variability of locus of response for the left PPA along the x axis decreased

with age, while location variability for the right PPA in the y and z axes increased in age between the child groups but decreased again between older children and adults.

Scene selectivity was greater in adults compared to both child groups in the bilateral OPA and the left PPA, trending in right PPA, and not significant in the RSC. Age-related increases in scene-selectivity in the PPA and OPA were driven by higher responses to scenes and lower responses to objects with age in both the core and the peripheral areas of these ROIs.

Nordt et al. 2021	n = 29	Houses, corridors	Longitudinal	The volume of response in
	No adults		Block design task	the left lateral VTC to houses
	Child ages 5-17y			increased with age.
				The selectivity in the top
				20% most selective voxels
				for houses increased
				significantly with age in the
				left lateral VTC.
				There was no significant
				effect of age on the volume
				of ROI-defined CoS-places
				in either hemisphere (ventral
				place-selective region).
Tian et al. 2021	n = 266	Scenes (movie clips)	Cross-sectional	Children had less similarity
	Child ages 9-14y		Hybrid (naturalistic	to adult multivariate response
	Child n = 111		block design)	patterns (to scenes) than
	Adult n = 144			adults did to one another in
				the right RSC (adults were
				more similar to one another
				than children were to adults –

children's responses are still developing).

Children's similarity to the "child template" response to scenes was not significantly different than children's similarity to the "adult template."

Similarity of scene representation patterns within children was significantly lower than within adults.

Child responses to scenes "homogenize" over development.

Kamps et al. 2022	$n = 168$	Scenes (movie clips)	Cross-sectional	In scene-responding ROIs
	Child ages 3-12y	for functional	Hybrid (naturalistic	(PPA, OPA, RSC), the
	Child $n = 122$	localizer task, also	block design)	correlation between
	Adult $n = 46$	showed a movie	Naturalistic movie	children's time course and
			task	

the adult time course increased with age. In the OPA, PPA, and RSC, 3-year-olds were as correlated to the average 3-year-old time course as they were to the average adult time course.

Sahraei et al. 2022	$n = 18$ Child ages 7-9y Child $n = 8$ Adult $n = 10$	Houses	Cross-sectional Block design task	No significant group x condition (faces > baseline, houses > baseline) interaction in core- and extended-face processing network ROIs.

Appendix A12. Summary of studies investigating development of visual body/limb processing.

Study	Sample	Sub-domain	Methodology	Main developmental findings
Ross et al. 2014	$n = 50$ Child ages 6-11y Child $n = 24$ Adult $n = 26$	Bodies	Cross-sectional Block design task	Adults had a greater contrast for bodies > objects in bilateral occipitotemporal areas, pSTS, fusiform, amygdalae, thalamus, and IFG. No areas where children had a greater contrast for bodies > objects than adults. Location of response was similar in both children and adults. Extent of activity in ROIs was higher in adults than children in the right FBA and left EBA.

Deen et al. 2017	$n = 12$	Bodies	Cross-sectional	In face-preferring
	Child ages 3-8mo		Hybrid (naturalistic	regions of the ventral
	Child $n = 9$		block design)	temporal and lateral
	Adult $n = 3$			occipital cortex, infants
				showed similar
				responses to bodies and
				faces, while adults
				showed significantly
				greater responses to
				faces than all other
				categories.

Dehaene-Lambertz et al. 2018	$n = 10$ No adults Child ages 5-7y	Bodies	Longitudinal Block design task	No longitudinal increase in response or volume in body-responding cortex across one year. Emergence of VWFA did not alter functional organization of body-selective cortex.
Ross et al. 2019	$n = 69$ Child ages 6-17y Child $n = 43$ Adult $n = 26$	Bodies	Cross-sectional Block design task	In whole-brain analysis, adults had greater BOLD signal change in the lingual gyrus than both children and adolescents. Adults had greater BOLD signal change to bodies than both children and adolescents in the FBA, EBA, and amygdala ROIs.

Body-selective activity was more right-lateralized in adults than both children and adolescents.

Nordt et al. 2021	$n = 29$	Limbs and bodies	Longitudinal	In lateral ventral
	No adults		Block design task	temporal cortex: word-
	Child ages 5-17y			and face-selective

responses increased while limb-selective responses decreased. Volume of word-selective response doubled while limb-selective response halved (when comparing 5-9yos to 13-17yos).
No significant change in body-selective

responses, only limb-selective.
In the OTS and pFus, selectivity to words and faces respectively replace initial selectivity to limbs.

Appendix A13. Summary of studies investigating development of character/symbol processing.

Study	Sample	Sub-domain	Methodology	Main developmental findings
Turkeltaub et al. 2008	$n = 37$ Child ages 6-11y Child $n = 22$ Adult $n = 15$	Letters	Cross-sectional Block design task	Both children and adults showed BOLD responses in a number of areas in the ventral occipitotemporal cortex. Main effect of age that was mainly driven by differences in the letter task in mid/posterior fusiform gyrus bilaterally (adults > children). Letter task was bilateral for both children and adults. No clear evidence for increasing specialization of any

				area for letter recognition.
Cantlon et al. 2011	$n = 29$ Child ages 4-5.8y Child $n = 15$ Adult $n = 14$	Symbols (letters, numbers)	Cross-sectional Event-related task	Children had greater contrast of symbols > non-symbols than adults in the left lateral mid-fusiform gyrus and the ITG. This area was equally active for letters and numbers in children, while adults showed greater responses in this area to letters. Symbol area becomes more specialized to letters over development.
Dekker et al. 2014	$n = 26$ Child ages 7-10y	Words (tool words, animal words)	Cross-sectional Block design task	Tool- and animal-picture selective regions

	Child n = 13 Adult n = 13			in the fusiform gyrus (both tools and animals), MTG (tools), and EBA (animals) responded to tool- and animal-words, respectively, in adults, while children did not show responses in the picture-selective regions when viewing the corresponding words.
Dehaene-Lambertz et al. 2018	n = 10 No adults Child ages 5-7y	Words, numbers	Longitudinal Block design task	Numbers did not show any areas with a greater response compared to other visual categories. Words showed responses in the left VWFA (anterior fusiform), pSTS,

parietal regions, inferior frontal regions.

Longitudinal increase over sessions for BOLD signal change to words compared to all other categories in left VWFA, occipital areas, pSTS, precentral gyrus, inferior parietal areas, and in right inferior parietal region.

Increase for words began after 3rd imaging session, which occurred 2-4 months after school onset.

Transient BOLD signal change increase for words in the left IFG, ACC, anterior occipitotemporal sulcus,

and insula within the first few months of reading acquisition (declined after that). Sudden increase in the number of voxels that were selective for words after session 2 (corresponding to the start of school). Voxels that showed specificity for words in the last sessions (6 & 7) showed preferences for words starting in session 3. Reliability of the multivariate response pattern for words and numbers increased between sessions 3 & 4.

				VWFA emerged quickly and superimposed itself overtop of the "mosaic" of category-responsive voxels in the ventral temporal cortex.
Kersey et al. 2019	$n = 71$ Child ages 4.11-8.77y Child $n = 42$ Adult $n = 29$	Numbers, words	Cross-sectional Block design task	Children and adults both had significant BOLD signal change in the bilateral IPS for numbers, and the bilateral MTG and the VWFA (in left hemisphere) for words. Adults showed significant change in the bilateral IFG for numbers, while children showed trending responses for both

				numbers and words in the left IFG. For all areas where both children and adults showed BOLD signal change, adults had greater magnitude of change than children.
Nordt et al. 2021	$n = 29$ No adults Child ages 5-17y	Characters (pseudowords, numbers)	Longitudinal Block design task	In lateral ventral temporal cortex: word- and face-selective responses increased while limb-selective responses decreased. Volume of word-selective responses doubled while limb-selective responses halved (when comparing 5-9yos to 13-17yos).

No significant change in
body-selective
responses, only limb-
selective.
In the OTS and pFus,
selectivity to words and
faces respectively
replace initial selectivity
to limbs.

Appendix A14. Summary of studies investigating development of visual motion processing.

Study	Sample	Sub-domain	Methodology	Main developmental findings
Bucher et al. 2006	$n = 32$ Child ages 15-17y Child $n = 16$ Adult $n = 16$	Motion coherence	Cross-sectional Block design task	Motion responses were seen in the V1, V2, V3, middle occipital gyrus, and MT+ in both adolescents and adults. No significant differences in response amplitude or lateralization between adolescents and adults; motion coherence is likely matured by late adolescence.
Carter & Pelphrey 2006	$n = 9$ No adults Child ages 7-10y	Biological motion	Cross-sectional Event-related task	Biological motion elicited responses in posterior occipitotemporal regions, ventral temporal regions, the

				STS, the IFG, MFG, precentral and postcentral gyrus, IPS, SPL, IPL. Biological > non-biological motion contrast was positively correlated with age in the STS.
Klaver et al. 2008	*n* = 20 Child ages 5-6y Child *n* = 10 Adult *n* = 10	Motion coherence	Cross-sectional Block design task	Random motion > static contrast was greater in adults than children in the V3a (V3a activity also increased with age). For structure-from-motion > random motion, the contrast was greater in adults in the IPL and SPL, while it was greater in children

				in the lingual gyrus. The contrast decreased with age in the hMT+ and V3a, but increased with age in the parietal shape area.
Lichtensteiger et al. 2008	$n = 31$ Child ages 5-7y Child $n = 13$ Adult $n = 18$	Biological motion	Cross-sectional Event-related task	Adults had a greater contrast for biological motion > scrambled motion than children in the pSTS. Children had a greater contrast for biological motion > scrambled motion than adults in the fusiform gyrus and the caudate nucleus.
Anderson et al. 2013	$n = 86$ Child ages 4-16y Child $n = 38$	Biological motion	Cross-sectional Block design task	Biological motion elicited responses in the

	Adult n = 48			pSTS and the fusiform in both age groups. Sex differences were seen in children in the hypothalamus and vmPFC. Sex differences were seen in adults in the amygdala, LGN, hypothalamus, MTG, temporal pole, and cerebellum.
Biagi et al. 2016	n = 24 Child ages 7-15y Child n = 12 Adult n = 12	Action observation (biological motion)	Cross-sectional Hybrid (naturalistic block design)	Children had bilateral responses in the ITG, STS, IPS, IPL, SPL, precentral gyrus, IFG, MFG, and fusiform gyrus. Adults had left lateralized BOLD responses.

| Sapey-Triomphe et al. 2017 | $n = 44$ Child ages 8-17y Child $n = 24$ Adult $n = 16$ | Social interaction movements | Cross-sectional Event-related task | There were 5 core regions that overlapped over all 3 groups for discriminating social interaction from neutral movement (pMTG/pSTS, pITG, aMTG, IFG, MOG) Adolescents had greater BOLD responses in core human motion processing areas (pSTS, pMTG, MOG) than adults. Adults recruited the FPN/mirror/social brain regions more than adolescents. Younger groups tended to use more occipitotemporal regions to process social |

				interaction while older used more fronto-parietal.
Kirby et al. 2018	$n = 40$ No adults Child ages 7-13y	Biological motion	Cross-sectional Block design task	No significant age-related differences in the magnitude of pSTS actication in response to biological motion in this age range.
Taylor et al. 2018	$n = 28$ Child ages 7-8y Child $n = 13$ Adult $n = 15$	Motion coherence	Longitudinal Block design task	Adults had bilateral V5/MT activity while children only had activity in R V5/MT. Children had a greater extent of BOLD response than adults but no differences in location or amplitude. No changes in location, extent, or amplitude of

coherent motion

processing

longitudinally in the

children over 1 year.

Appendix A15. Summary of studies investigating development of naturalistic visual (movie) processing.

Study	Sample	Sub-domain	Methodology	Main developmental findings
Cantlon & Li 2013	$n = 47$ Child ages 4-10y Child $n = 27$ Adult $n = 20$	Educational mathematics/reading video	Cross-sectional Naturalistic paradigm Block design task	During passive viewing, children had similar responses to adults in the occipital cortex, lateral temporal cortex, language areas in the frontal and temporal cortex, IPS. ISC to adults increased with age across a large section of the brain including sensory, motor, and association cortex (including the IPS) and Broca' area. Adults were more synchronized to each other than children were

to adults in the left hemisphere (IPS, Broca's area, IFG, MFG, STS, fusiform gyrus, ITG).

Children were more synchronized to each other than they were to adults in the STS.

Children were more synchronized to each other than adults were to each other in also in the STS.

"Neural maturity" in Broca's area and the VTC was associated with verbal scores, while "neural maturity" in the IPS was associated with math scores.

Moraczewski et al. 2018	$n = 67$ Child ages 4y, 6y Child $n = 46$ Adult $n = 21$	Feature film clip	Cross-sectional Naturalistic paradigm	Adults had stronger ISC than children in the bilateral TPJ, MTC, STC, SPC, and extrastriate cortex. ISC to adults increases with age in the TPJ. Significant ISCs were more diffuse and weaker within the child group, while the in the adult group, they were stronger and more focal.
Camacho et al. 2019	$n = 51$ Child ages 6-10y Child $n = 30$ Adult $n = 21$	Feature film clips with varying affective content	Cross-sectional Naturalistic paradigm	Support vector classification was able to classify children vs. adults successfully in the positive, negative, and neutral movie clip conditions (they had different enough

				responses from one another they could be classified). However, SVC was not able to classify children vs. adults across all conditions. No support vector regression were able to accurately predict child age within the child group from the response to the movie clips.
Kersey et al. 2019	$n = 71$ Child ages 4-8y Child $n = 42$ Adult $n = 29$	Educational mathematics/reading video	Cross-sectional Naturalistic paradigm Block task design	Found developing (adult-to-adult > child-to-adult), adult-like (adult-to-adult = child-to-adult), as well as child-unique (child-to-child > adult-to-adult)

| | | | | areas of the brain during passive viewing. Developing areas were the bilateral IPS, IFG, MTG, posterior STG, ITC, and occipital cortex. Adult-like areas were the bilateral STG, as well as more medial regions. Child-unique areas were the left angular gyrus, bilateral postcentral gyrus, the IFG, insula, SFG, MFG, and the anterior temporal lobe. |
| Moraczewski et al. 2020 | $n = 55$ Child ages 6-13y Child $n = 31$ Adult $n = 24$ | Intact episodes, scrambled episodes | Cross-sectional Naturalistic paradigm | Child group had a similar pattern of neural dynamics (i.e. low-frequency vs. high- |

frequency power) between regions. Adult group had a greater proportion of low-frequency power in the TPJ than children. Within the child group, there was no significant affect of age on the proportion of low-frequency power. Adults had greater ISC for intact clips compared to scrambled clips in the bilateral TPJ, IPS, SMG, precuneus, middle ITG, and dmPFC (whole brain) and in the ROIs the TPJ, dmPFC, and precuneus. Children had a qualitatively similar pattern for intact >

scrambled compared to the adult group in the whole brain analysis, but in the ROI analysis, only the precuneus survived. Intact > scrambled was greater in adults than children (significantly) in the TPJ, SMG, dlPFC, dmPFC, IFG, precuneus, ITC, and extrastriate.

Lerner et al. 2021	$n = 28$ Child ages 9-19y Child $n = 18$ Adult $n = 10$	Feature film clip	Cross-sectional Naturalistic paradigm	When comparing groups, there was no significant main effect of age on the total brain surface that showed significant intra-SC (similarity to self). For within-group ISC, there was a significant increase in the percent of

cortex that had significant within-group ISC across the age groups (young adolescents, older adolescents, adults), driven by the adults > young adolescents contrast. Age was also continuously associated with within-group ISC. For between-group ISC, in the group analysis, there was no significant effect of age.

Kamps et al. 2022	n = 168 Child ages 3-12y Child n = 122 Adult n = 46	Feature film clip	Cross-sectional Naturalistic paradigm Block design task	For all movie-defined ROIs (bilateral FFA, pSTS, LOC, OPA, PPA, RSC), time courses in children were significantly associated

with the corresponding regions in adults by 3 years of age.

Strength of correlation to adult time courses increased with age in all ROIs.

In all regions but the pSTS, the child time course showed the same pattern of correlation to all the adult ROIs (i.e., FFA correlations were ordered from strongest to weakest as FFA, LOC > pSTS, EVC > OPA, PPA, RSC in young children, older children and adults).

In pSTS, however, while the older children (7y+) were the most correlated

to the adult pSTS, the younger children's pSTS showed similar correlations to the adult pSTS, FFA, and LOC. For most ROIs, 3-year-olds were equally correlated (OPA, PPA, RSC, LOC) or more strongly correlated (FFA) to the adult time course than the average 3-year old time course, except in the pSTS. In the pSTS, 3-year-olds and 4-year-olds were both more correlated to the 3-year-old timecourse than the 4-year-old time course, and 5-year-olds were marginally closer to

adults. 7-12-year-olds all were more correlated to the adult pSTS. Magnitude of response to the adult-defined movie "events" (identified through reverse correlation) increased with age in all ROIs.

In the 3-year-olds, the shifted/lagged time course of the pSTS had greater correlation to the adult pSTS time course than the non-shifted, and this effect dimished with age, with 8-12-year-olds showing greater correlation between the non-shifted time course

				and the adult time course.
Cohen et al. 2022	$n = 414$ No adults Child ages 5-18y	Feature film clip	Cross-sectional Naturalistic paradigm	ISC increases with age in low level sensory regions (auditory cortex) and decreases with age in some higher level association regions (RSC, TPJ). Majority of parcels (81/100) showed age-specific responses, including in the DMN (TPJ, posterior medial cortex [precuneus]), and higher cognition regions (dlPFC, ITC, OFC). In the majority (71/100) parcels, the optimal time scale was highly correlated between the

youngest and the oldest children (sensory → association, increasing time scales).

In areas that differed with age (auditory and visual cortex, parietal operculum, dlPFC), the change with age corresponded with a better fit to the event model in older children. Event-boundaries were earlier in time for younger children in the auditory and visual cortex, dlPFC, precuneus.

Benear et al. 2022	$n = 45$ Child ages 4-10y Child $n = 25$	Feature film clips with varying affective content	Cross-sectional Naturalistic paradigm	For both adults and children, and for all ROIs (hippocampus,

Adult *n* = 20

perirhinal cortex, parahippocampal cortex, and V1), within-movie representations varied more than across-movie representations, with no significant differences in this between adults and children, and no significant difference with age continuously and the within-across difference in children. Adults showed this within-across difference in the hippocampus regardless of if they had prior exposure to the movie the clip was from, while children only showed this difference if they had prior exposure.

In perirhinal cortex, adults showed this significant within-across difference, but children did not.

Both adults and children showed the significant within-across difference in the parahippocampal cortex, and they did not significantly differ from each other.

In V1, neither group showed a within-across difference, and the groups were not significantly different from each other.

| Park et al. 2022 | $n = 70$ No adults Child ages 4-11y | Short film with varying emotional | Cross-sectional Naturalistic paradigm | No significant relationships with age were found for the |

		valences and social interactions		positive affect, negative affect, or social interaction sections of the film.
Yates et al. 2022	$n = 48$ Child ages 3-12mos Child $n = 24$ Adult $n = 24$	Short film clip	Cross-sectional Naturalistic paradigm	Whole brain ISC was highest in the visual cortex adults, and significant ISC was detected in all ROIs (EVC, LOC, angular gyrus, PCC, precuneus, mPFC, hippocamppus, early auditory cortex). ISC was weaker overall in infants compared to adults, but like adults was highest in the visual cortex, and significant ISC was detected in all ROIs except for early auditory cortex (the clip had no sound).

Adults had a hierarchical gradient of event structure across the cortex, while children did not (model performed optimally for longer events across the whole brain).

In leave-one-out event models, event structure was coarser than adults for infants, but infants were still able to be modelled by the leave-one-out models, so there was some shared event structure between infants.

Event structure models that were trained on adults fit better to adults

than infants (infants still developing).

In the LOC only, older infants had a better fit with the adult event structure.

Infant models fit adult models better than chance, though in infants, except in the early visual cortex, infant data was better explained by adult models than infant models.

APPENDIX B - Supplemental information for Chapter 3

Appendix B1. Significant clusters for average age.

MNI coordinates are reported in RAI orientation.

Cluster size	β (r)	t-stat	x	y	z	Peak / sub-peak location
16593	0.050	14.053	-58	30	-2	R Middle temporal gyrus (posterior)
	0.052	13.481	-64	20	-2	R Superior temporal gyrus (posterior)
	0.053	12.249	-30	62	-2	R Temporal occipital fusiform cortex
	0.032	11.989	-52	78	-8	R Lateral occipital cortex (inferior)
	0.030	11.140	16	70	64	L Lateral occipital cortex (superior)
	0.031	10.035	4	74	32	L Precuneus
	0.031	9.972	-40	62	60	R Lateral occipital cortex (superior)
13612	0.058	16.418	66	18	4	L Superior temporal gyrus (posterior)
	0.060	14.858	28	64	-12	L Occipital fusiform gyrus
	0.051	14.838	68	36	-2	L Middle temporal gyrus (posterior)
	0.041	12.076	52	40	24	L Parietal operculum cortex
	0.044	11.063	4	86	-20	L Lingual gyrus
	0.028	9.993	-12	104	6	R Occipital pole
	0.023	8.422	50	-18	-18	L Temporal pole
	0.021	8.255	18	36	-8	R Parahippocampal gyrus (posterior)

2953	0.035	11.298	28	10	52	L Precentral gyrus
	0.023	8.193	38	-8	48	L Middle frontal gyrus
	0.015	6.095	26	-26	54	L Superior frontal gyrus
1262	0.026	8.993	-24	-2	56	R Superior frontal gyrus
	0.022	7.207	-40	-6	36	R Middle frontal gyrus
	0.021	6.702	-52	-8	38	R Precentral gyrus
	0.016	5.762	-42	-10	22	R Inferior frontal gyrus
1055	0.029	9.931	40	70	34	L Lateral occipital cortex (superior)
584	0.020	6.831	-48	-4	-30	R Middle temporal gyrus (anterior)
	0.012	5.032	-40	0	-44	R Inferior temporal gyrus (anterior)
478	0.021	7.057	-44	-38	24	R Frontal pole
332	-0.024	-7.516	20	100	-6	L Occipital pole
305	0.017	5.896	28	44	44	L Superior parietal lobule
262	0.027	7.688	-24	68	12	R Intracalcarine cortex
177	-0.016	-6.126	-34	96	2	R Occipital pole
172	0.019	7.433	-24	34	-6	R Hippocampus
172	0.012	5.076	32	34	58	L Postcentral gyrus
167	0.015	6.604	8	-52	48	L Frontal pole

301

Appendix B2. Significant clusters for age difference.

MNI coordinates are reported in RAI orientation.

Cluster size	β (r)	t-stat	x	y	z	Peak / sub-peak location
1212	-0.012	-6.054	36	18	50	L Precentral gyrus
1002	-0.019	-8.596	48	46	28	L Supramarginal gyrus
383	-0.016	-6.480	-30	56	-28	R Cerebellum
370	-0.015	-6.462	22	76	-28	L Cerebellum
315	-0.011	-5.429	-62	40	26	R Supramarginal gyrus
203	-0.010	-5.742	-8	58	70	L / R Precuneus
158	-0.016	-6.159	-48	64	-6	R Lateral occipital cortex

APPENDIX C - Supplemental information for Chapter 4

Appendix C1. Included vs. excluded participant demographics.

Comparison of demographics between children included and excluded from analysis (included $n = 81$; excluded $n = 54$). Children were excluded if they had less than 16 minutes (384 volumes) of non-motion corrupted data. A motion-corrupted volume was defined as a volume with a framewise displacement greater than 0.2 mm (Xia et al., 2013).

	Age (years)	Censored volumes	Average relative FD (mm)	FSIQ	SNAP-I	SNAP-H	Sex
Included (SD)	5.88 (0.94)	21.32 (16.69)	0.076 (0.030)	111.1 (12.77)	0.73 (0.49)	0.76 (0.59)	F = 51 M = 30
Excluded (SD)	5.58 (0.91)	123.28 (68.60)	0.337 (0.357)	106.87 (12.77)	0.85 (0.49)	0.95 (0.63)	F = 28 M = 26
Test-statistic	$t_{53} = 1.861$	$t_{53} = -12.840$	$t_{53} = -6.559$	$t_{53} = 1.859$	$t_{53} = -1.451$	$t_{53} = -1.761$	$\chi^2_1 = 1.648$
p-value	0.065	< 0.001	< 0.001	0.065	0.149	0.081	0.199

Appendix C2. Inattention cluster details.

MNI coordinates of cluster peaks and subpeaks are reported in right-anterior-inferior (RAI) orientation.

Cluster size	Peak β	*t*-stat	x	y	z	Brain Regions
13284	-0.112	-12.990	44	70	-6	Left lateral occipital cortex
	-0.101	-12.862	-14	80	-24	Right Crus I
	-0.076	-12.079	22	62	8	Left intracalcarine cortex
	-0.084	-11.353	14	86	-28	Left Crus I
	-0.078	-11.230	-36	82	6	Right lateral occipital cortex
	-0.093	-11.072	-28	62	-26	Right VI
	-0.068	-9.899	-22	54	10	Right precuneus
	-0.062	-9.600	16	88	32	Left lateral occipital cortex
	-0.057	-7.988	36	56	-18	Left temporal occipital fusiform cortex
	-0.045	-7.383	10	76	-10	Left lingual gyrus
	-0.048	-7.280	-26	88	-18	Right occipital fusiform cortex
	-0.050	-6.387	-24	94	-2	Right occipital pole
	-0.022	-4.326	32	94	22	Left occipital pole
	-0.021	-3.830	-12	72	0	Right lingual gyrus
1227	-0.065	-9.054	-56	34	24	Right parietal operculum cortex
	-0.034	-5.604	-64	46	30	Right angular gyrus
674	0.067	8.405	-58	12	-2	Right superior temporal gyrus
587	-0.041	-8.535	58	64	34	Left lateral occipital cortex
586	0.043	6.471	24	56	40	Left superior parietal lobule
	0.035	6.091	10	54	42	Left precuneus
	0.031	4.320	48	48	16	Left supramarginal gyrus
563	-0.108	-16.874	68	26	2	Left superior temporal gyrus
	-0.036	-6.978	68	44	-2	Left middle temporal gyrus (temporooccipital)
	-0.037	-5.868	54	30	20	Left parietal operculum cortex

	-0.031	-5.041	50	32	38	Left supramarginal gyrus
	-0.031	-4.980	40	36	12	Left planum temporale
495	-0.034	-6.029	-48	-12	38	Right middle frontal gyrus
	-0.025	-4.217	-44	-8	24	Right inferior frontal gyrus
443	0.053	6.854	58	44	2	Left middle temporal gyrus (temporooccipital)
	0.033	5.374	44	60	18	Left angular gyrus
417	-0.042	-6.994	46	-4	22	Left precentral gyrus
376	0.040	6.130	16	92	16	Left occipital pole
341	0.043	6.479	-58	50	-6	Right middle temporal gyrus (temporooccipital)
321	0.030	5.650	38	-22	-32	Left temporal pole
	0.029	5.139	48	-22	-6	Left frontal orbital cortex
294	0.032	5.666	-32	-44	34	Right frontal pole
256	-0.036	-5.337	52	-2	-10	Left superior temporal gyrus (anterior)
	-0.035	-5.447	52	-2	-8	Left planum polare
255	0.042	6.737	54	4	34	Left precentral gyrus

Appendix C3. ISC and inattention, FEF synchrony control.

Colour gradient indicates the β values, in units of Pearson's r. Cool colors denote negative associations (where ISC decreases as average trait score per pair increases) and warm colors denote positive associations (where ISC increases as average trait score per pair increases). Images are thresholded at a voxelwise threshold of p < 0.001 and a cluster-forming threshold of α = 0.05. All supplementary figures were created with BrainNet Viewer (Xia et al. 2013).
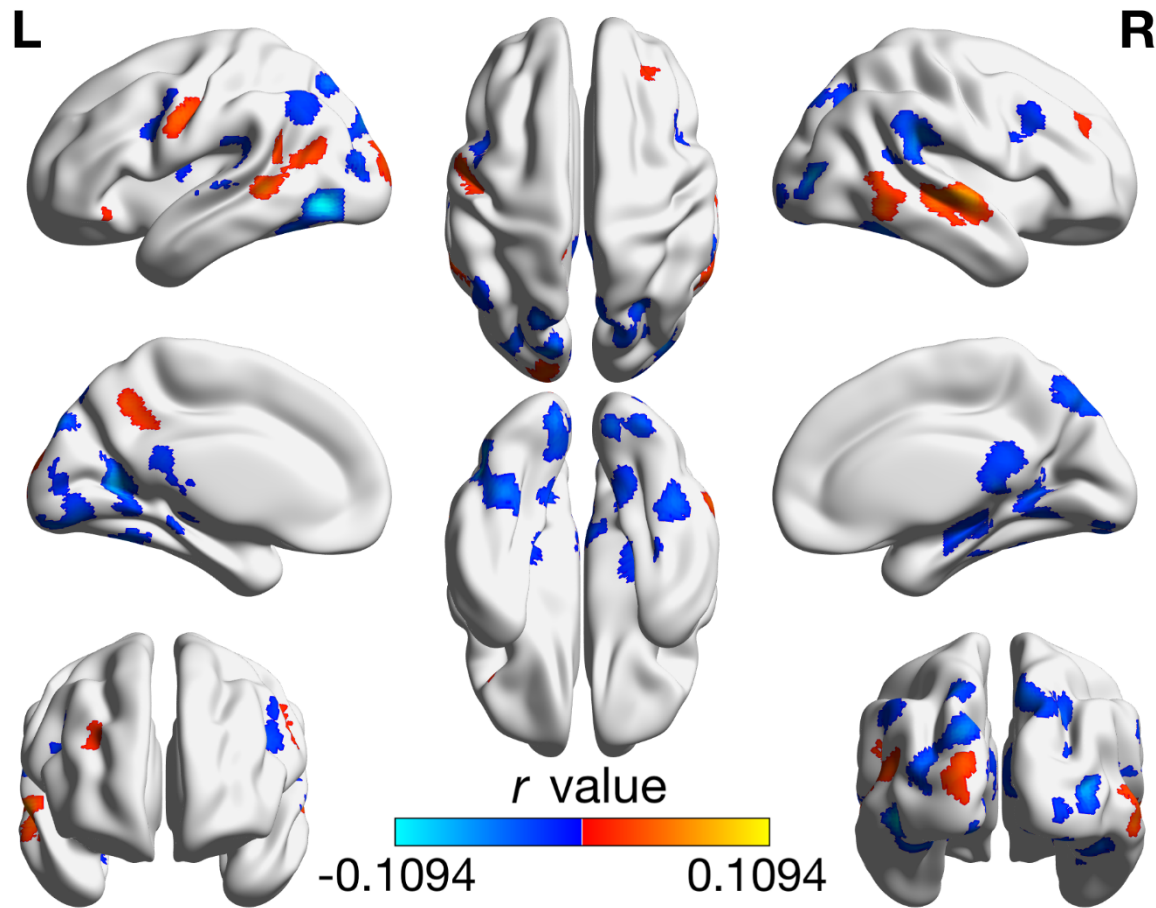
Appendix C4. Hyperactivity cluster table.

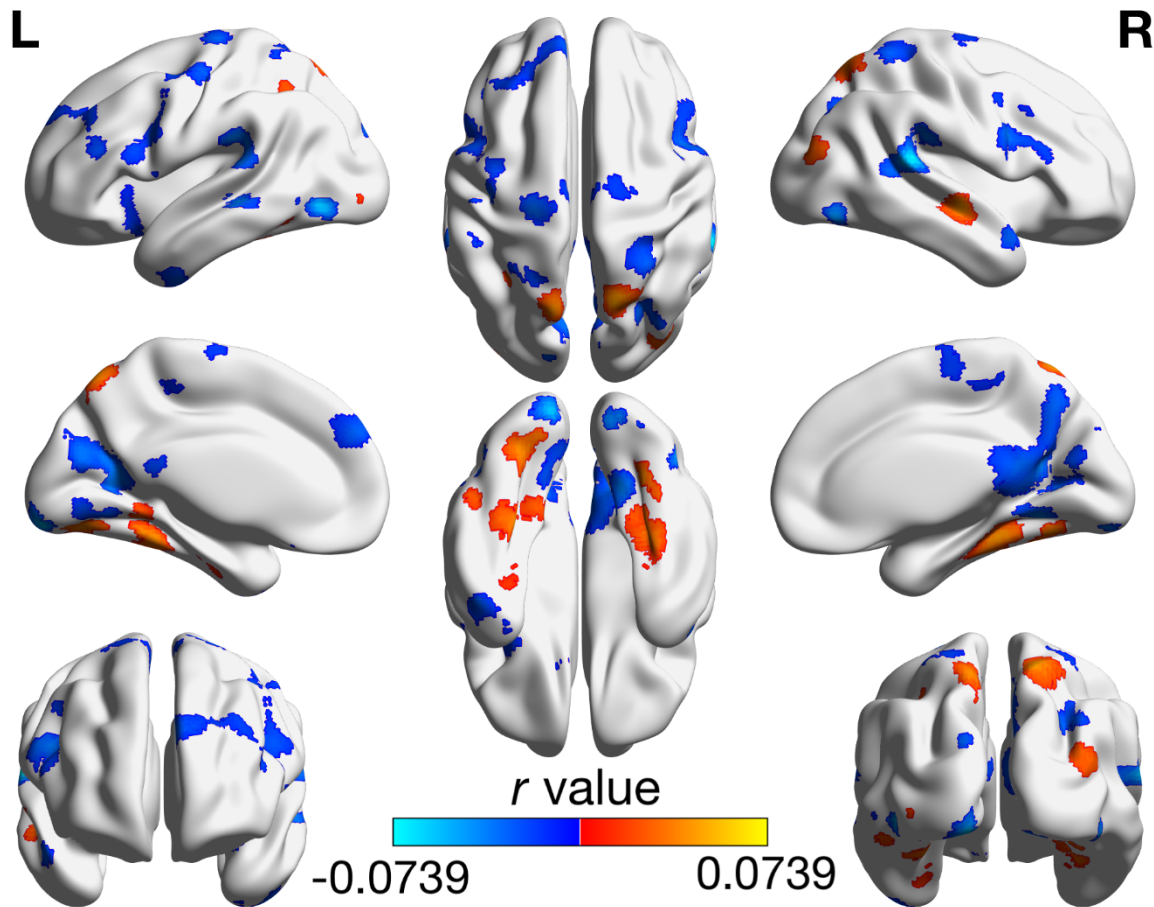MNI coordinates of cluster peaks and subpeaks are reported in right-anterior-inferior (RAI) orientation.

Cluster size	Peak β	*t*-stat	x	y	z	Brain Regions
3812	-0.051	-8.434	-24	64	2	Right intracalcarine cortex
	-0.049	-8.228	-20	54	14	Right precuneus
	-0.034	-6.507	16	94	32	Left occipital pole
	-0.035	-6.502	-8	46	-10	Right I-IV
	-0.034	-5.855	8	76	22	Left cuneus
	-0.024	-4.560	-10	44	2	Right posterior cingulate gyrus
	-0.023	-4.234	16	64	-6	Left lingual gyrus
1630	-0.072	-11.226	-14	88	-22	Right Crus I
	-0.051	-8.606	-52	76	-10	Right lateral occipital cortex
1576	0.047	6.535	26	46	-14	Left temporal occipital fusiform cortex
	0.045	7.016	30	42	-16	Left temporal fusiform cortex
	0.030	6.196	18	48	-6	Left lingual gyrus
	0.036	5.484	22	44	-24	Left V
	0.028	4.881	48	52	-14	Left inferior temporal gyrus
	0.022	3.840	38	88	-2	Left lateral occipital cortex
900	0.050	7.094	-28	40	-16	Right temporal occipital fusiform cortex
	0.036	7.772	-22	46	-2	Right lingual gyrus
	0.038	5.882	-20	50	-24	Right V
801	-0.036	-6.504	-48	-8	26	Right precentral gyrus
	-0.030	-5.729	-54	-10	40	Right middle frontal gyrus
775	-0.056	-7.680	12	94	-12	Left occipital pole
	-0.042	-6.609	28	80	-28	Left Crus I
749	-0.064	-10.783	68	26	2	Left superior temporal gyrus
	-0.041	-7.160	56	30	22	Left parietal operculum cortex

	-0.042	-6.011	58	30	-4	Left middle temporal gyrus
	-0.028	-4.967	48	36	38	Left supramarginal gyrus
713	-0.070	-10.638	-60	34	16	Right planum temporal
	-0.030	-5.100	-44	46	8	Right middle temporal gyrus
702	0.046	7.328	12	68	56	Left lateral occipital cortex
521	-0.029	-5.493	-32	46	66	Right superior parietal lobule
	-0.016	-3.966	-28	36	54	Right postcentral gyrus
519	-0.029	-6.227	8	-52	32	Left superior frontal gyrus
	-0.021	-4.496	32	-36	40	Left middle frontal gyrus
	-0.019	-4.443	24	-40	38	Left frontal pole
493	0.053	8.614	-16	64	60	Right lateral occipital cortex
450	-0.026	-4.952	48	-6	26	Left inferior frontal gyrus
	-0.015	-3.771	62	-8	24	Left precentral gyrus
354	-0.034	-6.144	20	22	66	Left precentral gyrus
315	0.047	7.040	-56	14	-8	Right middle temporal gyrus
	0.025	5.970	-48	6	-18	Right superior temporal gyrus
307	0.042	6.598	-36	74	20	Right lateral occipital cortex
287	-0.023	-5.689	28	-16	-14	Left frontal orbital cortex
283	0.048	6.628	54	6	-8	Left superior temporal gyrus
	0.037	5.716	56	22	8	Left planum temporale
238	-0.029	-4.424	-10	14	68	Right precentral gyrus
237	-0.054	-6.757	42	70	-6	Left lateral occipital cortex
229	-0.032	-5.292	-28	70	38	Right lateral occipital cortex

Appendix C5. ISC and hyperactivity, FEF synchrony control.

Colour gradient indicates the *β* values, in units of Pearson's *r* Cool colors denote negative associations (where ISC decreases as average trait score per pair increases) and warm colors denote positive associations (where ISC increases as average trait score per pair increases). Images are thresholded at a voxelwise threshold of *p* < 0.001 and a cluster-forming threshold of *α* = 0.05.

**Appendix C6. Inattention—hyperactivity contrast cluster table.**

MNI coordinates of cluster peaks and subpeaks are reported in right-anterior-inferior (RAI) orientation. The contrast was calculated as inattention – hyperactivity, so that negative clusters are where the *β* for inattention was more negative/less positive than the *β* for hyperactivity, and vice versa for positive clusters.

Cluster size	Peak β	*t*-stat	x	y	z	Brain Regions
13197	-0.181	-10.271	10	82	-20	Left occipital fusiform cortex
	-0.173	-12.231	24	46	-12	Left temporal occipital fusiform cortex
	-0.127	-12.203	48	82	-12	Left lateral occipital cortex (inferior)
	-0.149	-11.002	-38	82	8	Right lateral occipital cortex (inferior)
	-0.130	-10.854	-34	32	-26	Right temporal fusiform cortex
	-0.176	-10.649	-16	78	-20	Right VI
	-0.126	-10.613	18	52	-4	Left lingual gyrus
	-0.151	-10.072	26	46	-24	Left VI
	-0.124	-9.261	16	72	50	Left lateral occipital cortex (superior)
	-0.121	-9.048	-16	66	54	Right lateral occipital cortex (superior)
	-0.062	-6.261	18	32	-10	Left parahippocampal gyrus
	-0.047	-4.780	-52	46	-28	Right inferior temporal gyrus (temporooccipital)
2354	0.098	7.958	-10	66	24	Right precuneus
	0.092	7.400	-14	74	26	Right cuneus
	0.075	7.162	10	50	38	Left precuneus
	0.082	6.510	6	76	22	Left cuneus
1108	-0.135	-8.802	54	4	-6	Left superior temporal gyrus (anterior)
	-0.092	-6.887	48	28	6	Left planum temporale
	-0.042	-4.147	42	-8	-32	Left temporal pole
816	0.070	6.173	44	-34	26	Left middle frontal gyrus
740	0.109	6.855	58	28	-4	Left middle temporal gyrus (posterior)
	0.067	5.147	48	48	12	Left supramarginal gyrus
724	0.079	7.568	46	-18	-14	Left temporal pole

668	0.091	6.469	-56	52	-4	Right middle temporal gyrus (temporooccipital)
	0.091	6.532	-62	38	12	Right supramarginal gyrus
523	-0.088	-6.470	-50	36	26	Right parietal operculum cortex
	-0.074	-6.327	-68	28	32	Right supramarginal gyrus
456	0.072	6.173	-50	2	44	Right precentral gyrus
435	0.095	7.556	62	32	26	Left supramarginal gyrus
429	0.088	7.810	56	2	30	Left precentral gyrus
424	-0.085	-6.854	26	8	54	Left precentral gyrus
	-0.056	-5.140	20	-4	58	Left superior frontal gyrus
347	0.101	6.389	-60	16	0	Right superior temporal gyrus (posterior)
	0.084	7.934	-64	0	-14	Right middle temporal gyrus (anterior)
329	0.063	5.890	-32	-44	32	Right frontal pole
316	0.131	10.501	-52	74	-14	Right lateral occipital cortex (inferior)
315	0.112	6.799	-30	76	-32	Right Crus I
251	0.099	6.831	32	74	-32	Left Crus I
243	-0.055	-4.931	48	66	42	Left lateral occipital cortex (superior)
233	0.090	7.225	-42	44	42	Right supramarginal gyrus
226	0.085	6.388	-34	74	40	Right lateral occipital cortex (superior)

Appendix C7. Contrast between inattention and hyperactivity, FEF synchrony control.

Figure shows the difference in β values, in units of Pearson's r, corresponding to the inattention – hyperactivity contrast. Negative (cool) clusters indicate that inattention had a more negative/less positive association than hyperactivity, and positive (warm) clusters indicate that hyperactivity had a more negative/less positive association than inattention. Results are thresholded at a voxelwise threshold of $p < 0.001$ and a cluster-forming threshold of $\alpha = 0.05$.
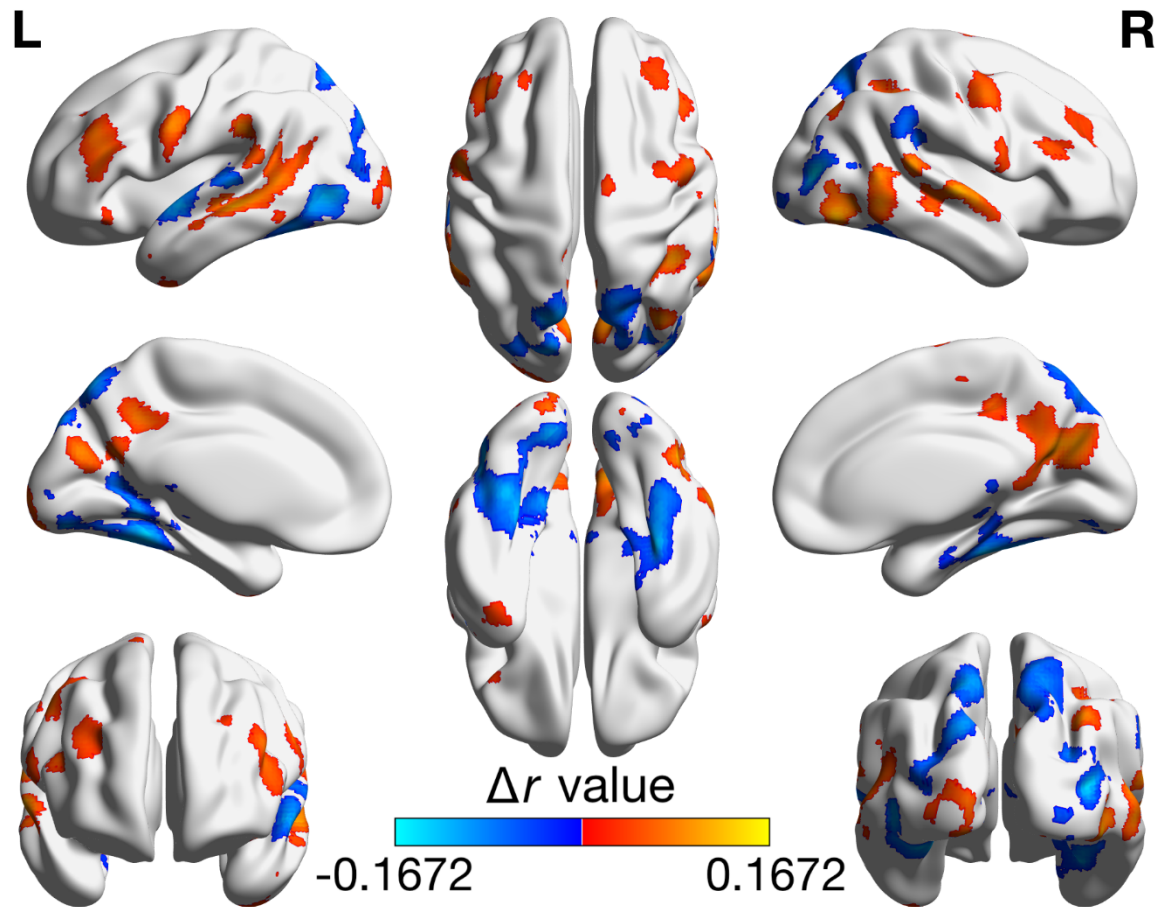
From: Ryann Tansey
Sent: 01 August 2023 10:54
To: Kirk Graff; Christiane Rohr; Dennis Dimond; Amanda Ip; Shelly Yin; Deborah M. Dewey; Shefali Rai; Daria Merrikh; Kate Godfrey; Tamara Vanderwal; Signe Lauren Bray
Subject: Permission to include papers in my dissertation

Hello everyone,

If this email is reaching you, you are one of my co-authors! I need permission from you to include my papers that you are a co-author on in my thesis.

If you would be able to reply to this email letting me know if you are okay with this, I can include it in my dissertation. My thesis is due on Tuesday, August 8th, so please reply by Monday, August 7th so I have time to include your email in the document.

These are the manuscripts:

R. Tansey, K. Graff, C.S. Rohr, D. Dimond, A. Ip, D. Dewey, S. Bray. Inattentive and hyperactive traits differentially associate with interindividual functional synchrony during video viewing in young children without ADHD. (2022) Cerebral Cortex Communications, 3(1). https://doi.org/10.1093/texcom/tgac011

R. Tansey, K. Graff, C.S. Rohr, D. Dimond, A. Ip, S. Yin, D. Dewey, S. Bray. Functional MRI responses to naturalistic stimuli are increasingly typical across early childhood. (2023) Developmental Cognitive Neuroscience, 62. https://doi.org/10.1016/j.dcn.2023.101268

R. Tansey, K. Graff, S. Rai, D. Merrikh, K.J. Godfrey, T. Vanderwal, S. Bray. Development of visual functional neuroanatomy: A scoping review of task- and naturalistic-fMRI studies through the lens of the interactive specialization and maturational frameworks. (unpublished, will be submitting after the defense)

Thank you so much for all your work and collaborative efforts on these projects, it would not be possible without all of you!

Ryann

Subject: Re: Permission to include papers in my dissertation

Date: Tuesday, August 1, 2023 at 10:54:25 AM Mountain Daylight Time

From: Signe Lauren Bray

 To: Ryann Tansey

You have my permission.

Subject: Re: Permission to include papers in my dissertation

Date: Tuesday, August 1, 2023 at 10:59:55 AM Mountain Daylight Time

From: Shefali Rai

To: Ryann Tansey

You have my permission, Ryann. Great work!

Subject: Re: Permission to include papers in my dissertation

Date: Tuesday, August 1, 2023 at 11:13:47 AM Mountain Daylight Time

From: Kirk Graff

To: Ryann Tansey

I approve.

Subject: Re: Permission to include papers in my dissertation

Date: Tuesday, August 1, 2023 at 11:31:48 AM Mountain Daylight Time

From: Tamara Vanderwal

To: Ryann Tansey

[ΔEXTERNAL]

Hi Ryann,
This is fine by me, permission granted. Best,
Tammy

Subject: Re: Permission to include papers in my dissertation
Date: Tuesday, August 1, 2023 at 11:32:19 AM Mountain Daylight Time

From: Christiane Rohr
To: Ryann Tansey
CC: Signe Lauren Bray

[ΔEXTERNAL]

Of course Ryann! You have my permission to include the papers that I am a co-author on in your thesis.
Very excited for you that all your hard work is near wrapping up and leading you to this milestone achievement! It was a pleasure working with you, so happy to have been able to contribute to your projects.
All the best for your submission and the defense! Don't worry, you'll be great!
Christiane

Subject: Re: Permission to include papers in my disserta4on

Date: Tuesday, August 1, 2023 at 11:38:01 AM Mountain Daylight Time

From: Amanda Ip

To: Ryann Tansey

You have my permission! Best of luck! :)

Subject: Re: Permission to include papers in my dissertation

Date: Tuesday, August 1, 2023 at 11:39:12 AM Mountain Daylight Time

From: Shelly Yin

To: Ryann Tansey

Hi Ryann,

You have my permission to include the paper of which I am a co-author.

Congrats on getting to the final steps of your PhD and good luck with the dissertation!!!

Shelly

Subject: Re: Permission to include papers in my dissertation

Date: Tuesday, August 1, 2023 at 11:50:45 AM Mountain Daylight Time

From: Deborah M. Dewey

To: Ryann Tansey

Dear Ryann,

I give you permission to include the following papers on which I am included as a co-author in your disserta;on.

R. Tansey, K. Graff, C.S. Rohr, D. Dimond, A. Ip, D. Dewey, S. Bray. Inattentive and hyperactive traits differen;ally associate with interindividual func;onal synchrony during video viewing in young children without ADHD. (2022) Cerebral Cortex Communica;ons, 3(1). https://doi.org/10.1093/texcom/tgac011

R. Tansey, K. Graff, C.S. Rohr, D. Dimond, A. Ip, S. Yin, D. Dewey, S. Bray. Func;onal MRI responses to naturalistic stimuli are increasingly typical across early childhood. (2023) Developmental Cognitive Neuroscience, 62. https://doi.org/10.1016/j.dcn.2023.101268

Deborah Dewey

Subject: Re: Permission to include papers in my dissertation

Date: Tuesday, August 1, 2023 at 12:11:53 PM Mountain Daylight Time

From: Daria Merrikh

To: Ryann Tansey

Dear Ryann,

You have my permission to use the listed manuscript in your dissertation.

Kind Regards,

Daria

Subject: RE: Permission to include papers in my dissertation

Date: Tuesday, August 1, 2023 at 3:41:04 PM Mountain Daylight Time

From: Dennis Dimond

To: Ryann Tansey

Hi Ryann,
You absolutely have my permission to include the below mentioned papers in your thesis. Congrats!

Dennis Dimond

Subject: Re: Permission to include papers in my dissertation

Date: Wednesday, August 2, 2023 at 11:31:11 AM Mountain Daylight Time

From: Kate Godfrey

To: Ryann Tansey

Hi Ryann,

You have my permission to include the listed papers which I co-authored in your dissertation.

Big congratulations for being so close to the finish line!

Kate