Examining the Relationships Between Socio-cognitive Factors and Neural Synchrony During Movie Watching Across Development

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Abstract

While different cognitive abilities mature, the conscious experiences of children likely become richer and more elaborate. A challenge in investigating relationships between cognitive development and real-world experiences is having measures that assess naturalistic processing. Movie watching offers a solution, since following the plot of a film requires cognitive processes that are similar to real-world experiences. When different adults watch the same film, their brain activity begins to align (known as neural synchrony). The strength of this alignment has been shown to reflect the degree to which different individuals are having a similar experience of the movie. While this phenomenon has been established in adults, much less is known about the neural mechanisms supporting naturalistic processing in children and adolescents. The current thesis investigated the neural correlates of movie watching across late childhood and early adolescence. In Chapter 2, I found that autistic children showed more variable brain responses in regions associated with social cognition when watching a movie compared to children without autism. In Chapter 3, I found that adolescents (ages 11-15) with higher cognitive scores showed greater neural synchrony during movie watching in brain regions associated with social processing and executive functions compared to those with below average cognitive scores. This pattern was not evident in children (ages 7-11) who differed in their cognitive scores. In Chapter 4, I found that although the spatial topographies of children’s functional brain networks were nearly indistinguishable during movie watching and rest, these two states differed in the degree of neural synchrony that was present within much of the brain. That is, movies led to significantly more neural synchrony compared to rest, except for in parts of the prefrontal cortex. Taken together, these results suggest that 1) autistic children have more distinct experiences when processing naturalistic stimuli compared to those without autism, 2) adolescents with higher cognitive scores have more similar experiences with each other when watching a movie compared to those with lower scores, and 3) although children’s brain networks during movie watching and rest have a similar functional architecture, processing a film leads to neural synchrony, whereas resting state does not.

Keywords: Neural synchrony, development, fMRI, cognition, inter-subject synchrony
Summary for Lay Audience

When different adults watch the same movie, their brains synchronize; that is, their brain activity correlates to others’ brain activity. Previous work suggests that the presence of neural synchrony is evidence that different people are having a similar experience of the movie they are watching. Much less is known about how children’s brains respond to movies. For instance, do they synchronize with other children? If so, what are the factors that predict whether a child will synchronize with their peers while watching a movie? In this thesis, I aimed to gain a better understanding of whether social and cognitive abilities are associated with neural synchrony during development. First, I found that autistic children show less typical neural responses when watching a movie in brain regions associated with social abilities compared to those without autism. This suggests that autistic children have more distinct experiences when processing naturalistic stimuli compared to those without autism. Second, I found that cognitive ability is predictive of neural synchrony in adolescents. That is, those with higher cognitive scores showed greater synchrony while they watched a movie compared to those with lower scores in several regions of the brain that are associated with plot following. This suggests that adolescents with more mature intellectual abilities have more similar experiences when watching a movie compared to those with poorer cognitive abilities. However, I did not find that individual differences in cognitive scores was predictive of neural synchrony in children. Lastly, I found that the functional architecture of children’s brains while they watched a movie was highly comparable to when they were at rest. However, I found that these two states differed in the degree of neural synchrony present within much of the brain. Movies led to significantly more neural synchrony compared to rest, except for in parts of the prefrontal cortex. Overall, these findings contribute to our understanding of how the developing brain responds to naturalistic experiences and provide evidence that differences in clinical and cognitive features are associated with the degree to which children and adolescents synchronize with each other during movie watching.
Co-Authorship Statement

Chapter 2


This paper has been published in the journal *NeuroImage: Clinical*. Under the guidance of Dr. Ryan Stevenson, Dr. Adrian Owen, and Dr. Bobby Stojanoski, I came up with the conceptualization and methodology of this project, analyzed and interpreted the data, and created the figures and tables. Dr. Bobby Stojanoski assisted me in writing the analysis scripts for this project. I wrote the original draft of manuscript with help from Dr. Adrian Owen and Dr. Bobby Stojanoski, and all three coauthors provided feedback and revisions on the manuscript.

Chapter 3

*Project Title: Investigating the relationships between cognition and neural synchrony during movie watching in children and adolescents*

Under the guidance of Dr. Adrian Owen and Dr. Bobby Stojanoski, I came up with the conceptualization and methodology of this project, analyzed and interpreted the data, created the figures and tables, and wrote the original draft of the manuscript. Dr. Bobby Stojanoski assisted me with writing the analysis scripts for this project. Dr. Adrian Owen and Dr. Bobby Stojanoski provided feedback and revisions on the manuscript. This project was motivated by an idea that Dr. Rae Gibson had.

Chapter 4

*Project Title: Comparing functional brain networks when children are watching a movie versus when they are at rest*

Under the guidance of Dr. Adrian Owen and Dr. Bobby Stojanoski, I came up with the conceptualization and methodology of this project, analyzed and interpreted the data, created the figures and tables, and wrote the original draft of the manuscript. Dr. Bobby Stojanoski assisted me with writing the analysis scripts for this project. Dr. Adrian Owen and Dr. Bobby Stojanoski provided feedback and revisions on the manuscript. This project was motivated by a question that Dr. Stefan Kohler asked me in a CDBS seminar.
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# Table of Contents

Abstract.......................................................................................................................... ii

Summary for Lay Audience............................................................................................ iii

Co-Authorship Statement............................................................................................... iv

Acknowledgments........................................................................................................... v

Table of Contents ............................................................................................................ vii

List of Tables ................................................................................................................ x

List of Figures ............................................................................................................... xi

List of Abbreviations ..................................................................................................... xii

1 Introduction ................................................................................................................. 1

1.1 Cognitive Development............................................................................................ 2

1.2 The link between cognition and brain development............................................. 5

1.2.1 The frontoparietal network ............................................................................. 10

1.2.2 The default-mode network .......................................................................... 11

1.3 Social Development ............................................................................................... 13

1.3.1 The social brain ............................................................................................. 16

1.4 Individual differences in development .................................................................. 17

1.5 Narrative processing .............................................................................................. 21

1.5.1 Socio-cognitive processing associated with movie watching...................... 26

1.5.2 Individual differences in neural synchrony .................................................. 29

1.6 Research goals and hypotheses ............................................................................ 32

1.7 Division of data across chapters .......................................................................... 35

2 Examining the relationship between measures of autistic traits and neural synchrony
during movies in children with and without autism. .................................................. 37

2.1 Introduction ......................................................................................................... 37

2.2 Methods .............................................................................................................. 39
<table>
<thead>
<tr>
<th>Section</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>2.2.1 Participants</td>
<td>39</td>
</tr>
<tr>
<td>2.2.2 MRI preprocessing</td>
<td>41</td>
</tr>
<tr>
<td>2.2.3 Exploratory whole brain synchronization</td>
<td>42</td>
</tr>
<tr>
<td>2.2.4 Network of interest inter-subject correlation</td>
<td>42</td>
</tr>
<tr>
<td>2.2.5 Percent synchronization across the cortex</td>
<td>43</td>
</tr>
<tr>
<td>2.2.6 Cluster-based inter-subject correlation analysis</td>
<td>44</td>
</tr>
<tr>
<td>2.3 Results</td>
<td>45</td>
</tr>
<tr>
<td>2.3.1 Exploratory whole brain synchronization</td>
<td>46</td>
</tr>
<tr>
<td>2.3.2 Network based synchronization</td>
<td>48</td>
</tr>
<tr>
<td>2.3.3 Percent synchronization across the cortex</td>
<td>50</td>
</tr>
<tr>
<td>2.3.4 Cluster-based inter-subject correlation analysis</td>
<td>51</td>
</tr>
<tr>
<td>2.4 Discussion</td>
<td>53</td>
</tr>
<tr>
<td>3 Examining the relationship between shared experiences during movie watching and cognitive ability in late childhood and early adolescence</td>
<td>58</td>
</tr>
<tr>
<td>3.1 Introduction</td>
<td>58</td>
</tr>
<tr>
<td>3.2 Methods</td>
<td>61</td>
</tr>
<tr>
<td>3.2.1 Participants</td>
<td>61</td>
</tr>
<tr>
<td>3.2.2 MRI Pre-processing</td>
<td>63</td>
</tr>
<tr>
<td>3.2.3 Exploratory whole brain inter-subject correlation analysis</td>
<td>64</td>
</tr>
<tr>
<td>3.2.4 Network-based inter-subject correlation analysis</td>
<td>64</td>
</tr>
<tr>
<td>3.2.5 Cluster-based inter-subject correlation analysis</td>
<td>65</td>
</tr>
<tr>
<td>3.3 Results</td>
<td>65</td>
</tr>
<tr>
<td>3.3.1 Whole brain ISC</td>
<td>65</td>
</tr>
<tr>
<td>3.3.2 Network based ISC</td>
<td>68</td>
</tr>
<tr>
<td>3.3.3 Cluster-based inter-subject correlation analysis</td>
<td>71</td>
</tr>
<tr>
<td>3.4 Discussion</td>
<td>72</td>
</tr>
</tbody>
</table>
4 Investigating differences in functional brain networks during movie watching and resting state in children.................................................................78
4.1 Introduction ......................................................................................78
4.2 Methods ..........................................................................................84
   4.2.1 Participants ..............................................................................84
   4.2.2 MRI Pre-processing ..................................................................84
   4.2.3 Independent component analysis (ICA) ....................................85
   4.2.4 Node-based functional connectivity .........................................85
   4.2.5 Inter-subject correlation .........................................................86
4.3 Results ............................................................................................86
   4.3.1 Independent components analysis .........................................86
   4.3.2 Node-based analysis ..............................................................89
   4.3.3 Inter-subject correlation .........................................................91
4.4 Discussion ......................................................................................93
5 Discussion ..........................................................................................98
   5.1 Summary and Key Findings .......................................................98
   5.2 Contributions to the Field .........................................................102
   5.3 Limitations and Future Directions ...........................................106
   5.4 Conclusions ................................................................................109
References ............................................................................................111
6 References ........................................................................................111
Curriculum Vitae ................................................................................173
List of Tables

Table 2.1. A summary of participant demographics..........................................................41

Table 3.1. Summary of participant demographics. ..............................................................63

Table 3.2. Results from separate ANOVAs calculated to compare ISC in the four IQ groups across the seven networks...........................................................................................................69

Table 3.3. Mean age and WISC scores for the high similarity and low similarity clusters. .72

Table 4.1. Results from paired sample t-tests comparing neural synchrony during the rest and movie conditions in the 18 intrinsic functional networks obtained from the ICA.................92
List of Figures

Figure 2.1. Network of interests used to parcellate the brain........................................44

Figure 2.2. Exploratory whole brain inter-subject correlation analysis ................................47

Figure 2.3. Intra-group network of interest analysis ..........................................................49

Figure 2.4. Percentage of correlated voxels........................................................................50

Figure 2.5. Matrices of pairwise inter-subject correlations.................................................52

Figure 3.1. Histogram displaying the distribution of a) age cohorts and b) IQ scores across the four groups ..................................................................................................................63

Figure 3.2 Whole brain spatial maps with significant intra-group ISC displayed for (a) the child and (b) adolescent cohorts .................................................................................................................................67

Figure 3.3. Boxplots displaying ISC for each IQ group across every network for the child cohort (displayed in panel a) and the adolescent cohort (displayed in panel b). .................................70

Figure 3.4 Pairwise correlation matrices across all subjects from all age and IQ groups for the default mode and frontoparietal networks ..............................................................71

Figure 4.1. Intrinsic network maps for the 18 components obtained from the ICA for the rest and movie scan separately.................................................................................................88

Figure 4.2. Functional connectivity matrices estimated for the movie and rest conditions.................................................................................................................................90

Figure 4.3. Mean ISC calculated for each component for the movie and rest conditions......93
List of Abbreviations

ASD – Autism spectrum disorder
BOLD – Blood-oxygen-level dependent
FC – Functional connectivity
FDR – False discovery rate
fMRI – Functional magnetic resonance imaging
MRI – Magnetic resonance imaging
ICA – Independent components analysis
ISC – Inter-subject correlation
IQ – Intelligence quotient
PFC – Prefrontal cortex
SRS-2 – Social Responsiveness Scale – Revised
ToM – Theory of mind
WISC – Wechsler Intelligence Scale for Children
1 Introduction

The transition from childhood to adulthood is marked by tremendous physical, behavioral, and social changes. This period also involves remarkable improvements in various cognitive abilities; for instance, memory (Crone, Wendelken, et al., 2006; Luciana et al., 2005), problem solving (Injoque-Ricle et al., 2014; Wright et al., 2008), and perspective taking (Hughes & Ensor, 2007) skills vastly improve during this time. While different cognitive systems mature, the conscious experiences of children and adolescents likely become richer and more elaborate (Zelazo, 2004). However, a challenge in investigating the relationship between cognitive development and conscious experiences is identifying measures that assess complex naturalistic processing.

Measuring brain activity in response to narratives offers a potentially powerful way to understand how cognitive development supports the processing of real-world multifaceted stimuli. Understanding a narrative involves the integration of diverse cognitive abilities including attentional, perceptual, memory, language, and emotional systems. For example, to follow the plot of a narrative, listeners are required to integrate sensory stimuli, connect this information to their previous knowledge, and continuously update their memory based on what happens throughout the story.

While the neural activity in response to movies may seem idiosyncratic to the person watching, when different adults are attending to the same film, the activation in their brains begins to align, a phenomenon known as neural synchrony (Chen et al., 2017; Hasson, Landesman, et al., 2008; Hasson et al., 2012; Simony et al., 2016). This is especially true for adults who have a similar understanding of the plot (Hasson, Furman, et al., 2008; Nguyen et al., 2019).

Much less is known about the nature of neural responses during naturalistic processing in development. For instance, do children show similar patterns of neural synchrony when they process a narrative? If so, at what age do children’s brains synchronize with each other when watching the same movie? Moreover, if improvements in cognitive ability lead to more complex naturalistic processing, we would expect that the degree of neural synchrony would differ between children who have different sets of
cognitive abilities. Disentangling how neural synchrony relates to cognitive abilities across development may clarify what processes are required for different individuals to have similar experiences when processing complex stimuli.

In this thesis, I investigated the neural correlates of complex narrative processing in children and adolescents. In Chapter 1, I summarise what is and is not known about the link between high-level cognition and brain development. I also describe how neural synchrony during movie watching is an ideal tool to help better understand how children and adolescents process real-world stimuli. I outline previous research which demonstrates that understanding a complex narrative requires a diverse set of cognitive abilities, and that neural synchrony is dependent on individuals having a similar experience while processing external stimuli. Much of the work that has investigated neural synchrony has been conducted in adult populations, therefore less is known about how children’s brains respond to naturalistic stimuli, such as stories and movies. Finally, I describe how this thesis will address this gap in the literature by investigating the neural correlates of movie watching in children and adolescents.

1.1 Cognitive Development

Far from being immutable, cognition continuously changes across the lifespan. Cognitive abilities improve across infancy into early adulthood, and thereafter, they begin to decline during middle and older age (Hartshorne & Germine, 2015; Lövdén et al., 2020; Luca et al., 2003; Walhovd et al., 2016). At the earliest stages, cognitive development can be likened to the scaffolding structure of a building; that is, the development of cognitive abilities at one stage set the foundation for maturation later on (Ayoub & Fischer, 2006). As a neonate grows into a toddler, they become highly acute at distinguishing faces (Nelson, 2001), words (Cheour et al., 1998), and object categories (Arterberry & Bornstein, 2012). They also develop the ability to walk (Malina, 2004), and once they learn how to navigate in their environment, their depth perception and spatial abilities significantly improve (Adolph et al., 1993; Burnay & Cordovil, 2016; Richards & Rader, 1981). Once toddlers learn how to speak, single word utterances are strung together to create sentences (Bruner, 1979; Kuhl, 1994; Nelson, 1973; Saffran et al., 2001). This sets the stage for expressing more sophisticated linguistic abilities, such
as asking and answering questions (Callanan & Oakes, 1992; Chouinard, 2007; Nelson, 1981; Ruggeri et al., 2021), using pronouns (Charney, 1980; Nelson, 1981; Wexler & Chien, 1985), and taking turns in conversation with someone else (Casillas et al., 2016; Keitel & Daum, 2015). As toddlers grow into children, their cognitive abilities become more refined, capable of more complex processes. For instance, children become better at reasoning through problems (Dumontheil et al., 2010; Wright et al., 2008) and focusing their attention on challenging tasks (Betts et al., 2006; Duan et al., 2010; Klenberg et al., 2001; Miller & Vernon, 1997). They also begin to think symbolically and use abstract representations (Dumontheil, 2014; Hatcher et al., 1990; Marini & Case, 1994). These abilities help children master academic skills such as reading, writing, and mathematics (Blankenship et al., 2019; Britton & Others, 1975; Cragg & Gilmore, 2014; Floyd et al., 2008; Houdé Olivier et al., 2010; McCaskey et al., 2018; Nation & Cocksey, 2009; Söderqvist & Bergman Nutley, 2015; Yeniad et al., 2013).

The period between late childhood to early adulthood is thought to be especially important for the development of executive functions, which are the abilities required to control and coordinate complex thoughts and behaviors. These include abilities such as cognitive flexibility, working memory, and inhibition (Alvarez & Emory, 2006; Diamond, 2013; Miyake et al., 2000). Cognitive flexibility is the ability to switch between two or more tasks or internal states (Crone et al., 2004; Diamond, 2013). Working memory is the ability to maintain and manipulate information in mind for a short period of time after the information is no longer perceptually available (Diamond, 2013; Miyake et al., 2000; Miyake & Friedman, 2012). Inhibition is the ability to control thoughts, behaviors, and attention to prevent an automatic response (Bedard et al., 2002; Diamond, 2013; Logan et al., 1997). These executive processes are effortful, and require the integration of external sensory information and internal motivations (Miller & Cohen, 2001; Sakai, 2008).

While evidence for rudimentary executive functioning has been found during infancy, these abilities undergo considerable improvement in childhood and into late adolescence (Conklin et al., 2007, Crone, Wendelken, et al., 2006; Kwon et al., 2002). Performance improvements on simple executive function tasks often plateau in
childhood, while performance on more challenging tasks continue to improve throughout adolescence. For instance, while young children can switch between two simple tasks (Diamond et al., 2005; Gupta et al., 2009), performance on more complex cognitive flexibility tasks continues to improve in adolescence and into early adulthood (Crone, Donohue, et al., 2006; Crone et al., 2004; Dajani & Uddin, 2015; Theodoraki et al., 2020). Similarly, while young children can perform simple memory span tasks (Luciana & Nelson, 1998), these abilities continue to improve throughout childhood (Luciana & Nelson, 2002). More complex forms of working memory, such as in tasks where recall is required to organize thoughts or behaviors, continue to develop into late adolescence (Luciana et al., 2005). Young children often find inhibiting a response exceptionally difficult (Diamond et al., 2002; Diamond & Taylor, 1996; Dowsett & Livesey, 2000; Shoda et al., 1990), but by adolescence, they have significantly improved at controlling their thoughts and behaviors (Luna et al., 2001; Prencipe et al., 2011; Stevens et al., 2007; Tamm et al., 2002).

These three abilities (cognitive flexibility, working memory, and inhibition) are highly correlated with each other, which has led some to propose that there is a common ability that supports performance on all executive tasks (Friedman et al., 2008; Friedman & Miyake, 2017; Karr et al., 2018; Miyake et al., 2000; Miyake & Friedman, 2012; Wiebe et al., 2011). Friedman & Miyake (2017) propose that this common ability represents differences in an individual’s ability to maintain and implement goals across various tasks. Similarly, Doebel (2020) proposes that, instead of comprising of multiple abilities, executive function is a singular ability that allows one to activate relevant knowledge and beliefs to complete a specific goal.

Executive functions are engaged during more complex cognitive processes, such as fluid reasoning (Diamond, 2013). Fluid reasoning is the ability to think logically and solve problems in novel situations (Otero, 2017). Measures of fluid reasoning, such as Raven’s Progressive Matrices, are highly correlated with performance on executive function tasks, including measures of cognitive flexibility (Colzato et al., 2006; Salthouse et al., 1998), working memory (Engel de Abreu et al., 2010; Unsworth et al., 2014), and inhibition (Aydmune et al., 2020). Fluid reasoning is thought to develop in the first few
years of life, but shows rapid advances during childhood, reaching peak levels by early adulthood (Ferrer et al., 2009; McArdle et al., 2002; Otero, 2017; Wright et al., 2008). This ability is thought to support the development of many other important skills and is predictive of mathematic (Green et al., 2017), writing (Cormier et al., 2016) and reading (Guerin et al., 2020) abilities, academic achievement (Greiff & Neubert, 2014; Zaboski et al., 2018), and knowledge acquisition (Pagani et al., 2017; Prat et al., 2020; Reeve, 2004).

In summary, cognitive development is a complex process that continues across infancy and into adulthood, and involves improvements in a diverse set of capacities, such as memory, attention, and problem solving. Though these different abilities have unique developmental trajectories, they are often supported by development in other cognitive domains (Ayoub & Fischer, 2006). The period between late childhood and adolescence involves vast improvements in executive functions and fluid reasoning (Best et al., 2011; McArdle et al., 2002; Taylor et al., 2013; Theodoraki et al., 2020), and this development is associated with an increased ability to learn new skills (Best et al., 2011; Prat et al., 2020; Reeve, 2004; Rhodes et al., 2014; St Clair-Thompson & Gathercole, 2006). Developmental improvements in cognitive ability are thought to be supported by underlying changes to the brain that allow for more efficient processing (Baum et al., 2017; Luna et al., 2001; Stevens et al., 2009).

1.2 The link between cognition and brain development

Much has been learned about the neural correlates of development using neuroimaging tools, such as structural magnetic resonance imaging (MRI) and functional magnetic resonance imaging (fMRI). Structural MRI generates images of the brain, which can then be used to investigate clinical diagnoses and compare brain morphology across subjects (Giedd & Rapoport, 2010; Wattjes, 2011). These images can distinguish grey matter (i.e. brain cell bodies) from white matter (i.e. myelinated axons), both of which undergo substantial change during development (Giedd, 2004; Hagmann et al., 2010; Mills et al., 2016; Stevens et al., 2009). Magnetic resonance imaging can also be used to record changes in neural activity, known as fMRI. In a typical fMRI study, participants perform a task while the Blood Oxygenation Level Dependent (BOLD) signal, a proxy for changes in brain activity, is measured in the MRI
scanner. Regions that show significant change in BOLD activity during a task are thought to be associated with that cognitive process (Kannurpatti & Biswal, 2012; Logothetis, 2008). Another common technique used to understand basic properties of human brains has been to measure brain activation while participants are in a resting state; often, participants are asked to lay in the MRI scanner, with their eyes opened or closed, and do nothing (Bijsterbosch & Beckmann, 2017). Resting state fMRI measures spontaneous fluctuations in brain activity which can tells us about functional connectivity within the brain (Lee et al., 2013).

Both structural and functional MRI have been used to examine how the brain changes across development. Although most neurogenesis (i.e., the creation of new neurons) occurs prenatally, the brain continues to mature after birth (Stiles & Jernigan, 2010). For instance, glial cells continue to proliferate and migrate throughout childhood (Cayre et al., 2009; Levison & Goldman, 1993; Stiles & Jernigan, 2010). Early brain development involves the overproduction of neurons and synapses (Innocenti & Price, 2005), and as children and adolescents develop, these excessive connections are gradually pruned (Paolicelli et al., 2011; Sakai, 2020; Stiles & Jernigan, 2010). Experience influences this process, such that synapses that fire more frequently are less likely to be eliminated (Braun, 1996; Faust et al., 2021; Gambino & Holtmaat, 2012; Piochon et al., 2016; Stent, 1973). Development is associated with linear increases in white matter and non-linear changes in grey matter into early adulthood (Casey et al., 2005; Giedd et al., 1999; Huttenlocher & Dabholkar, 1997; Jernigan & Gamst, 2005; Paus, 2005). These changes are thought to be a result of a proliferation in myelination (Giedd, 2004; Giedd et al., 1999) and synaptic pruning (Huttenlocher & Dabholkar, 1997). The timing of this process differs across the brain; for example, grey matter volume peaks at approximately age 12 for frontal and parietal regions but continues to increase in the temporal and occipital lobe until late adolescence (Giedd et al., 1999). Adolescence, in particular, is associated with an explosion of white matter and a decline in grey matter across various regions associated with high-level cognition (Baker et al., 2015; Giedd et al., 1999; Tamnes et al., 2017). These structural brain changes have been linked to developmental improvements to cognitive ability (Baum et al., 2017; Casey et al., 2000; Koenis et al., 2018).
In conjunction with structural changes to the brain, development is also associated with changes to how the brain functions and responds to external stimuli. Developmental fMRI studies have discovered that children tend to show more extensive brain activation patterns compared to adults while they are engaged in an explicit task, such as attentional (Konrad et al., 2005), inhibition (Marsh et al., 2006; Rubia et al., 2007; Tamm et al., 2002b), verbal fluency (Gaillard et al., 2000), and working memory tasks (Ciesielski et al., 2006). For instance, in a longitudinal sample of children, Durston et al. (2006) found that age was associated with decreased activity in the dorsolateral prefrontal cortex, posterior cingulate, and superior temporal gyrus during a go/no-go task. However, some regions show increased activity during task performance as children age, especially in the frontal brain regions (Ciesielski et al., 2006; Luna et al., 2010; Marsh et al., 2006; Rubia et al., 2007; Taylor et al., 2012; Wright et al., 2008). For example, Marsh et al. (2006) found that age was associated with greater activation in the inferolateral prefrontal cortex during a Stroop task, and this increase in activity was associated with better performance. These findings suggest that as children age, brain activity in regions correlated with task performance becomes more specialized and regions that are not associated with task performance decrease in activity (Casey et al., 2005; Durston et al., 2006).

The prefrontal cortex, in particular, is one of the last brain regions to reach adult maturity (Casey et al., 2000; Fuster, 2002). Activation in the prefrontal cortex (PFC) is associated with a diverse set of mental processes, including working memory (Conklin et al., 2007; Curtis & D’Esposito, 2003; Funahashi, 2006; Kane & Engle, 2002; Klingberg et al., 2002), inhibition (Aron et al., 2003; Knight et al., 1999; Konishi et al., 2005; Ridderinkhof et al., 2004), task switching (Dove et al., 2000; Johnston et al., 2007; Shallice et al., 2008; Sohn et al., 2000), theory of mind (Hartwright et al., 2013; Krause et al., 2012; Shamay-Tsoory & Aharon-Peretz, 2007), emotional processing (Etkin et al., 2011; Shamay-Tsoory et al., 2010), fluid reasoning (Duncan, 2005; Ferrer et al., 2009; Hampshire et al., 2011; Wright et al., 2008), and even creativity (Beaty et al., 2021; Dietrich, 2004; Kleibeuker et al., 2013; Shi et al., 2018). Neuroimaging and lesion studies have shown that subdivisions of the PFC specialize in different cognitive functions. For instance, the ventromedial PFC is thought to be involved in emotional and social processing (Barrash et al., 2000; Hiser & Koenigs, 2018; Schneider & Koenigs, 2017;
Tranel et al., 2002), and the dorsolateral PFC appears to be especially important for working memory tasks (Blumenfeld et al., 2011; Kondo et al., 2004; Levy & Goldman-Rakic, 2000; Murray & Ranganath, 2007). The maturation of these PFC subdivisions is associated with improvement in these same cognitive domains (Crone, Wendelken, et al., 2006; Dumontheil, 2014; Durston et al., 2006; Luna et al., 2010; Ridderinkhof et al., 2004; Velanova et al., 2008). For instance, developmental changes to the dorsolateral PFC is uniquely associated with improvements in visuospatial working memory (Kwon et al., 2002; Scherf et al., 2006). In addition, the prefrontal cortex becomes increasingly involved in executive functions across adolescence (Baker et al., 2015; Bunge et al., 2002; Lewis and Todd, 2007; Rubia et al., 2000). This process is termed ‘frontalization’ and is thought to lead to gains in behavioural control observed later in development (Lewis and Todd, 2007).

The PFC is also one of the most connected cortical regions in the brain, with reciprocal connections within the prefrontal cortex itself as well as to cortical and subcortical regions across the entire brain (Fuster, 2002). An important function of the PFC is to integrate incoming information and coordinate activity across the rest of the brain, and these diverse connections make this process possible (Groenewegen & Uylings, 2000; Mansouri et al., 2009; Miller & Cohen, 2001). This is an example of how individual brain regions do not work independently in their support of cognition. Instead, complex mental processes are supported by the integration of different brain areas, creating several brain networks, such as the visual, frontoparietal, and default mode networks (Dosenbach et al., 2006; Marek & Dosenbach, 2018; Satterthwaite et al., 2013). These networks are made up of distinct brain regions that are connected through white matter tracts (i.e., structural connectivity; Sporns & Betzel, 2016) and show synchronized activity (i.e., functional connectivity; Grayson & Fair, 2017). Structural connectivity is often investigated through post-mortem and diffusion weighted imaging studies (Alexander et al., 2007; Eickhoff et al., 2005; O’Donnell & Westin, 2011; Tendler et al., 2022). Functional connectivity is a measure of how correlated the activation of discrete brain regions are (Bijsterbosch & Beckmann, 2017). These connected brain networks work together to support diverse cognitive functions (Dwyer et al., 2014; Fair et al., 2009).
Functional and structural brain networks are observed in infancy, and by age two resemble adult networks (Gao et al., 2015; Grayson & Fair, 2017; Marek & Dosenbach, 2018; van den Heuvel et al., 2015), but they continue to change throughout childhood and adolescence (Baker et al., 2015; Baum et al., 2017; Ciesielski et al., 2006; Fair et al., 2007; Li et al., 2019; Sherman et al., 2014; Wendelken et al., 2017). Structural brain networks become more segregated and integrated during development; specifically, they become less connected to regions in other networks and more connected to regions within their own network (Bassett et al., 2011; Baum et al., 2017; Grayson & Fair, 2017). These structural changes are proposed to be, at least in part, the result of synaptic plasticity (Damicelli et al., 2019). In line with these structural findings, studies have found that functional networks develop from a ‘local to distributed’ organization (Fair et al., 2009); that is, across development, functional connectivity within networks increases, while connectivity between networks decreases (Dosenbach et al., 2007, 2010; Grayson & Fair, 2017; Satterthwaite et al., 2013). Increases in connectivity within networks is associated with reductions in overall brain activity (Dwyer et al., 2014; Ghuman et al., 2008).

Structure-function coupling is a measure of how correlated structural and functional connectivity is between regions, and it is thought to reflect how specialized a network is (Baum et al., 2020; Cocchi et al., 2014; Griffa et al., 2022). In adults, brain regions that have a high degree of correlated activity also tend to be structurally connected, and the relationship between structural and functional connectivity strengthens from childhood into early adulthood (Baum et al., 2020; Hagmann et al., 2010; Honey et al., 2009; Uddin, 2013).

These developmental increases in network segregation and integration are thought to lead to more efficient information processing (Baum et al., 2017). Accordingly, network development is associated with improvements in various cognitive processes. For instance, improved cognitive functioning coincides with decreases in between-network connectivity and increases in within-network connectivity across childhood (Baum et al., 2017; Dwyer et al., 2014; Fair et al., 2007; Stevens et al., 2009). Moreover, individuals with greater structural and functional network segregation perform better on tasks measuring working memory, cognitive flexibility, processing speeds, fluid intelligence, and theory of mind (Cohen & D’Esposito, 2016; Kong et al., 2020; Mohr et
al., 2016; Schurz et al., 2020; Wang, Su, et al., 2021; Wang, Liu, et al., 2021). Two networks in particular are associated with improvements in executive functions and fluid reasoning: the frontoparietal and default mode networks (however, see Uddin, Yeo, & Spreng (2019) for a discussion about the challenges associated with assigning labels to neural networks). These two networks also happen to undergo significant change during late childhood and adolescence.

1.2.1 The frontoparietal network

The frontoparietal network is implicated in the flexible control of thoughts and behaviors (Dosenbach et al., 2008; Marek & Dosenbach, 2018). It is composed of regions in the lateral prefrontal cortex and posterior parietal cortex (Cui et al., 2020; Dosenbach et al., 2006; Marek & Dosenbach, 2018; Yeo et al., 2011). The frontoparietal network is proposed to be a ‘flexible hub’ that is well connected to many cortical regions (Cole et al., 2015). These diverse connections are thought to allow for the coordination of other brain networks while also being able to actively maintain task-relevant information (Cole et al., 2015; Dosenbach et al., 2006; Marek & Dosenbach, 2018). Activation in the frontoparietal network is associated with performance on working memory (Burzynska et al., 2011; Satterthwaite et al., 2013), cognitive flexibility (Peters et al., 2016; Uddin, 2021), inhibition (Dwyer et al., 2014), and reasoning tasks (Wendelken et al., 2017).

The frontoparietal network is one of the last networks to fully mature (Chai et al., 2017; Cui et al., 2020), undergoing significant changes in structural connectivity (Wierenga et al., 2018) and functional segregation (Baum et al., 2017) in childhood, with adolescence appearing to be in an ‘intermediate’ stage of development between children and adults (Fair et al., 2007). These changes continue into early adulthood, albeit to a smaller degree relative to earlier in development (Baker et al., 2015). Developmental changes to the frontoparietal network coincide with performance improvements in several high-level cognitive domains, including attention, executive functions, and reasoning ability (Baum et al., 2017; Beaty et al., 2016; Dwyer et al., 2014; Spreng et al., 2010; Stevens et al., 2009; Velanova et al., 2008; Wendelken et al., 2017). The structure-function coupling of regions within the frontoparietal network also increases with age, which in turn is associated with improved performance on executive function tasks,
especially in adolescents (Baum et al., 2020). Baum et al. (2020) proposes that this protracted period of development allows for more flexibility in the networks associated with executive function to change in response to environmental stimulation during adolescence.

1.2.2 The default-mode network

The default-mode network includes regions of the medial PFC, angular gyrus, medial temporal lobes, and posterior cingulate cortex (Davey et al., 2016; Raichle, 2015; Smallwood et al., 2021). This network, sometimes called the task negative network (Spreng, 2012), was discovered when researchers noticed these brain regions showed reduced activity when someone is engaged in an external task (Raichle et al., 2001; Shulman et al., 1997). Subsequent studies found that those ‘task-negative’ regions were structurally connected with each other and showed correlated activity, suggesting they work together as a brain network (Davey et al., 2016; Raichle, 2015; Smallwood et al., 2021). While its exact role in mental processes remains unclear, there is now mounting evidence that although the default-mode network is less influenced by external stimuli than other regions of the cortex, it is still associated with higher-level cognition (Smallwood et al., 2021). For instance, the default mode network is implicated when participants think about themselves (Davey et al., 2016; van Buuren et al., 2010; Wen et al., 2020) or others (Fareri et al., 2020; Li et al., 2014; Schilbach et al., 2008), and when they imagine future or past events (Kim, 2010; Sestieri et al., 2011; Wen et al., 2020; Xu et al., 2016). Research has also shown that activity in the default-mode network is associated with moral judgement (Chiong et al., 2013; Reniers et al., 2012), spatial navigation (Spreng et al., 2009), decision making (Marín-Morales et al., 2022; McCormick & Telzer, 2018; Reniers et al., 2012; Smith et al., 2021), emotional processing (Grimm et al., 2009; Pletzer et al., 2015; Sreenivas et al., 2012), social cognition (Hughes et al., 2019; Li et al., 2014; Spreng et al., 2009), and even some types of learning (Dohmatob et al., 2020; Howard-Jones et al., 2016; Marstaller et al., 2017, 2017). Smallwood et al. (2021) proposes that what ties all these tasks together is that they involve processes that combine abstract features of thoughts linked to events from our
past and our future. Far from being “task negative”, the default-mode network appears to be involved in numerous tasks important for our well-being and survival.

Recent research has also implicated the default mode network in task switching, a key component of the executive functions. For instance, activity in the default mode network briefly increases when participants change the task they are performing, especially for more demanding tasks (Crittenden et al., 2015; Smith et al., 2018). Moreover, functional connectivity between the default mode and frontoparietal networks becomes more anticorrelated during more demanding tasks (Avelar-Pereira et al., 2017; Persson et al., 2007), and the degree to which these two networks are negatively correlated during rest is predictive of cognitive ability (Hampson et al., 2010; Keller et al., 2015; Kim & Kang, 2018; Reineberg et al., 2018). As external task demands go up, the frontoparietal network increases in activity and the default mode network decreases in activity, and this balance is thought to help an individual focus on the task at hand (Fair et al., 2010; Mills et al., 2018; Smith et al., 2018). These findings have led to the proposal that the default mode network plays a crucial role in the control of both internally and externally focused cognition (Smith et al., 2018).

The default mode network shows a similar developmental trajectory as the frontoparietal network. Compared to adults, children show weaker functional connections across this network (Supekar et al., 2010). Longitudinal studies show that mean functional connectivity within the default mode network increases in adolescence (Fan et al., 2021; Li et al., 2019; Sherman et al., 2014), with much of the change occurring in the precuneus, medial PFC, and posterior cingulate cortex (Dosenbach et al., 2010; Fan et al., 2021). Early in childhood, functional connectivity between the frontoparietal and default-mode network is positive, but these two networks become increasingly anticorrelated across development (DeSerisy et al., 2021). Compared to the frontoparietal network, much less is known about how developmental changes to the default mode network are related to cognition. However, there is evidence that the maturation of this network is associated with improvements in episodic memory (Chai et al., 2014; Østby et al., 2012), intelligence scores (DeSerisy et al., 2021) and social cognition (He et al., 2018; Lynch et al., 2013).
1.3 Social Development

Childhood and adolescence are also important periods for social development. Children and adolescents become increasingly concerned with what their peers think and are more sensitive to peer exclusion (Oh et al., 2008; Stroud et al., 2009; Vidal et al., 2007; Warrington & Younger, 2011). They also start spending more time with friends (Csikszentmihalyi et al., 2014; Kandel, 1986; Scholte & van Aken, 2006) and taking more risks when they are in the presence of others (Goldstein et al., 2005; Kiesner et al., 2010; Siennick & Osgood, 2012; Willoughby et al., 2014). Developing social competence is an important milestone during this period (Allemand et al., 2015; Dawes, 2017; Wentzel & Erdley, 1993). For instance, adolescents who struggle to develop social skills or experience peer rejection are more likely to experience depression, anxiety, and low self-esteem (Bijstra et al., 1994; Flanagan et al., 2008; Lev-Wiesel et al., 2006; Nilsen et al., 2013; Pedersen et al., 2007; Prinstein & Aikins, 2004). Social cognition is the collection of abilities that allows one to make sense of social interactions (Frith & Frith, 2007; Renfrew et al., 2008). These abilities help humans learn from others and work towards a shared goal (Saxe, 2006; Stephenson et al., 2021). They include several distinct processes, including social perception, theory of mind, and emotional understanding.

Social perception involves making sense of and organizing complex social information (Augoustinos et al., 2014). For example, social perception involves being able to recognize faces, voices, facial expressions, and body motion (Meinhardt-Injac et al., 2018). These abilities begin early in development but continue to be refined into childhood and adolescence (Camras & Allison, 1985; Herba & Phillips, 2004). For example, we are primed, even as infants, to attend to faces above other types of object categories (Goren et al., 1975; Walton & Bower, 1993), and early in development, infants learn to recognize the faces of their caregivers (Pascalis et al., 1995). Gaze following, which supports joint attention and information sharing across individuals, may be present in neonates (Farroni et al., 2004), but continues to improve within the first year of life (Del Bianco et al., 2019; Farroni et al., 2004; Stephenson et al., 2021). Children also become better at recognizing facial expressions, which allows for a better understanding
of what others are feeling (Camras & Allison, 1985; Herba et al., 2008). Although being able to make sense of social cues is a key element of successful social interactions, we also must be able to use this information to reason about others’ mental and emotional states.

Theory of mind (ToM) is the ability to understand the mental state of others, and to use this knowledge to predict what people will do (Amodio & Frith, 2006; Baron-Cohen et al., 1985; Frith & Frith, 2007). A key milestone in the development of theory of mind is being able to recognize that another person’s knowledge or perspective may be different from ours. This ability is often tested through false belief tests, such as the Sally Anne Task. In this task, a child watches a doll, Sally, put her marble in a basket and then leave the room. While Sally is gone, a second doll, Anne, moves the marble out of the basket into a box. When Sally comes back to the room, the child is asked where Sally will look for the marble; the correct answer is that Sally will look in the basket (Baron-Cohen et al., 1985). If the child is unable to take Sally’s perspective, they will say she will look in the box, since they know the marble is in the box. Children tend to pass this test around age 3 or 4, which is taken as evidence that they have theory of mind as they understand Sally has a different perspective than they have (Baron-Cohen et al., 1985; Ruggeri et al., 2021; Wellman et al., 2001; Wellman & Bartsch, 1988). Other studies have found evidence that even younger children can perform simpler versions of false belief tests (Buttelmann et al., 2009; Slaughter, 2015; Wellman & Woolley, 1990).

However, theory of mind continues to develop after children can pass simple false belief tasks. Although adolescents can easily pass the Sally Anne Task, they still make more errors on more complex ToM tasks than adults (Dumontheil et al., 2010; Valle et al., 2015). Theory of mind in the real world often involves more complex inferences; for instance, what does Anne think about Sally’s mental state? This is known as recursive theory of mind. By age 7, children can attribute second-order beliefs, for instance “Anne thinks that Sally thinks” (Astington et al., 2002). By age 10, children begin to attribute third-order beliefs, for instance “My mom thinks that Anne thinks that Sally thinks” (Liddle & Nettle, 2007). The abilities required for more complex ToM tasks take longer to mature and are dependent on the development of other cognitive systems. Thinking
about someone else’s perspective of a third person’s mental state is cognitively
demanding; for instance, it involves working memory to keep the relevant information in
mind and inhibition to stop yourself from activating what your own perspective is
(Kilford et al., 2016; Richardson et al., 2018). Longitudinal studies have shown that
executive function skills early in development predict later theory of mind skills, but not
vice versa (Carlson et al., 2004; Hughes, 1998; Marcovitch et al., 2015). Improvements
across all executive functions, but in particular inhibition, are associated with increases in
theory of mind in adolescence (Vetter, Leipold, et al., 2013). These results highlight the
interconnectedness between cognitive and social development.

Social beings must not only understand others’ mental states, but also others’
emotions. Emotional understanding (also known as affective theory of mind) is the ability
to comprehend the emotional states of ourselves and others (Gallese et al., 2004).
Although theory of mind and emotional understanding are highly correlated (Bigelow et
al., 2021), they are independent abilities (Kalbe et al., 2010; Shamay-Tsoory & Aharon-
Peretz, 2007). Shamay-Tsoory et al. (2010) proposes that one must be able to make
inferences about others’ mental states before one can understand the emotions of others,
and as such, these abilities develop later. As children age, they become better at
recognizing when two people are showing the same emotion (Bigelow et al., 2021),
predicting the emotional states of others (Harwood & Farrar, 2006; Ruffman & Keenan,
1996), and distinguishing emotional states from only observing another person’s eyes
(Gabriel et al., 2021). By age 10, children can understand that someone can have a belief
about someone else’s emotions, known as a second-order emotional belief (Baron-Cohen
et al., 1999). Emotional understanding continues to develop across adolescence, with
younger adolescents needing more time to think about the appropriateness of others’
emotional responses (Baron-Cohen et al., 1999; Keulers et al., 2010) and making more
errors when attributing emotional states to others (Gabriel et al., 2021) compared to
adults. Just as attributing complex mental states to others is cognitively demanding, so
too is understanding others’ emotions. Improvements in emotional understanding is
associated with the development of working memory, inhibition, and cognitive flexibility
(Vetter, Altgassen, et al., 2013).
In sum, the social worlds of children and adolescents become increasingly complex and influential, and how young people navigate these social changes is an important predictor of well-being and quality of life (Bijstra et al., 1994; Demir et al., 2012; Segrin & Taylor, 2007). Developmental improvements to theory of mind and emotional understanding during this time help individuals successfully navigate social situations (Frith & Frith, 2007; Gabriel et al., 2021; Liddle & Nettle, 2007; Renfrew et al., 2008; Saxe, 2006; Slaughter, 2015). These improvements are also associated with the maturation of a specific brain network, known as the social brain, which is thought to support social cognition.

1.3.1 The social brain

The social brain, also known as the theory of mind network, is a constellation of brain regions that work together to perform a diverse set of social tasks. This network includes regions in the anterior cingulate, medial prefrontal cortex, bilateral temporo-parietal junction, precuneus, insula, and right superior temporal sulcus (Blakemore, 2012b; Dufour et al., 2013; Sebastian et al., 2010). fMRI studies have implicated this network in social cognition because it shows greater brain activation when participants perform false belief tasks (Dufour et al., 2013; Richardson et al., 2018), passively watch other people interact (Isik et al., 2017; Koldewyn et al., 2011), and perceive facial expressions (Skerry & Saxe, 2014).

Similar to the default mode and frontoparietal networks, the social brain becomes functionally specialized as children mature into adolescents. For instance, young children show activation in the temporo-parietal junction (a core region of the social brain) during tasks that do not involve social cognition, but this area becomes selective to mentalizing tasks early in adolescence (Saxe et al., 2009). The development of this network is also predictive of performance on social cognition tasks (Gweon et al., 2012). For instance, developmental increases in theory of mind ability are associated with greater functional connectivity within regions of the ToM network, particularly within the temporo-parietal junction, precuneus, and medial PFC (Xiao et al., 2019). Functional connectivity patterns can predict a child brain from an adult brain based on 5-minutes of resting state fMRI data with 93% accuracy, with the precuneus being the second most predictive region in
the brain (Dosenbach et al., 2010). Even after controlling for age, children aged 3-5 who can pass a false belief task showed greater within network functional connectivity in the social brain compared to those who failed (Richardson et al., 2018). The importance of the theory of mind network in social cognition has also been established in clinical populations. Autistic individuals, and those with schizophrenia or psychopathic personality disorder, tend to show less specialized brain activation in response to social stimuli compared to typically developed individuals (Cheng et al., 2015; Cherkassky et al., 2006; Kana et al., 2009, 2014, 2015; Kronbichler et al., 2017; Motzkin et al., 2011; Philippi et al., 2015; Thijssen & Kiehl, 2017). These results suggest that the specialization of this network supports the development of social cognition.

1.4 Individual differences in development

The research I have discussed so far has focused on group averages, but individuals develop at different rates in different domains (Ayoub & Fischer, 2006; Foulkes & Blakemore, 2018). For example, there is considerable variation in how children of the same age perform on tasks measuring different cognitive abilities, such as delayed gratification (Duckworth et al., 2013), response inhibition (Bub et al., 2006), and working memory (Bayliss et al., 2003). Relatedly, there are large individual differences in the trajectories of brain developmental (Tamnes et al., 2017; Vijayakumar et al., 2016; Wallace et al., 2015), and these individual differences are associated with various behavioural and cognitive outcomes (Casey, Giedd, & Thomas, 2000; Dosenbach et al., 2010; Giedd et al., 1999). For instance, delayed development in the prefrontal cortex is associated with better cognitive functioning (Shaw et al., 2006). In turn, individual differences in executive function, fluid reasoning, and social cognition are significant predictors of overall health (Mascarenhas, 2016; Moffitt et al., 2013; Stonnington et al., 2013), academic success (Best et al., 2011; Cragg & Gilmore, 2014; Lam & Kirby, 2002; Moffett & Morrison, 2019), and quality of life (Davis et al., 2010; Karim & Shah, 2014; Sharfi & Rosenblum, 2016; Stern et al., 2017). Due to the robust relationship between cognitive ability and well-being across the lifespan, understanding the causes and consequences of these individual differences has become a priority in developmental neuroscience (Foulkes & Blakemore, 2018).
One of the most common ways to measure individual differences in general cognitive function has been intelligence (IQ) tests (Richardson, 2002). IQ tests require individuals to complete several tasks that measure a diverse set of cognitive abilities. Scores from each task are combined to generate a singular standardized score which reflects performance relative to others who are a similar age. This standardized score, termed an IQ score, is meant to represent an individual’s general cognitive ability. The most popular IQ test in use for children is the Weschler Intelligence Scale for Children (WISC), which is used for children between the ages of 6 and 16 (Kaufman et al., 2006). The WISC has five subscales that make up the IQ score: verbal comprehension, visual-spatial, fluid reasoning, working memory, and processing speed ability. Each of these subscales are assessed using 2-4 tests. IQ scores on the WISC in the general population are normally distributed, with a mean of 100 and a standard deviation of 15. Most children (approximately 64%) fall between the scores of 85 and 115, and approximately 5% of children have scores lower than 70 or higher than 130 (Kaufman et al., 2016). This brings up a question that has vexed psychologists for over a century: why do children’s IQ scores vary so much?

Individual differences in cognitive abilities are thought to be due to complex interactions between genetic predispositions and environmental stimulation (Hanscombe et al., 2012; Hoekstra et al., 2007; Luciano et al., 2001; Posthuma et al., 2001; Turkheimer et al., 2003; van Leeuwen et al., 2008). One proposed reason for the considerable variation in IQ scores is that earlier development influences later maturity, such that the advancement of distinct cognitive abilities facilitate the improvement of others (Kievit, 2020). For example, developmental improvements in vocabulary have been shown to lead to better reasoning abilities, which then facilitates further gains in vocabulary (Kievit, 2017). The interaction between the development of distinct cognitive domains means that disruptions early in life will impact later maturation across seemingly disparate cognitive abilities. In support of this, research has consistently shown that early deprivation can lead to lifelong effects on intellectual abilities (Beckett et al., 2006; Geoffroy et al., 2016; Rutter et al., 2007; Sonuga-Barke et al., 2017; Spratt et al., 2012), and that environmental enrichment (i.e. complex sensory-motor stimulation) can improve cognition (Astle et al., 2015; Bergman-Nutley & Klingberg, 2014; Bredy et al., 2003a,
Certain developmental disorders are also associated with differences in cognitive ability; individuals with attention deficit hyperactivity disorder tend to perform worse on measures of response inhibition (Winstanley et al., 2006; Wodka et al., 2007), those with fetal alcohol syndrome have worse IQ scores than average (Kodituwakku, 2009; Lewis et al., 2012; Mattson et al., 1997), and children with dyslexia have more difficulty learning how to read (Shaywitz & Shaywitz, 2005; Vellutino et al., 2004). Autism is associated with lower social cognition scores; autistic children tend to pass false belief tasks later in childhood (Frith, 2001; Girli & Tekin, 2010; Happé, 1995), they have difficulties attending to socially relevant information (Senju, 2013), and they report challenges in interpersonal interactions (Bauminger et al., 2008; Bauminger & Kasari, 2000; Benford & Standen, 2009; Hobson et al., 2013; Jones et al., 2013; Mendelson et al., 2016). Though, even among children with developmental disorders, there is substantial variability in abilities. For instance, many autistic individuals perform equally well on traditional theory of mind tasks compared to neurotypical individuals (Gernsbacher & Yergeau, 2019). Moreover, when explicitly instructed to think about the mental states of others, autistic children who have trouble with theory of mind can perform well on social cognitive tasks (Didehbani et al., 2016; Senju, 2013).

No matter the underlying cause, individual differences in cognitive ability are strongly associated with differences in brain function. The parieto-frontal integration theory (also known as the P-FIT model) proposes that the frontoparietal network is the seat of intelligence; thus, differences in the structure and function of this network lead to differences in cognitive ability (Jung & Haier, 2007). For instance, differences in frontoparietal network connectivity are associated with performance on matrix reasoning (Fraenz et al., 2021; Wendelken et al., 2017), working memory (Pineda-Pardo et al., 2016), attention (Fiebelkorn et al., 2018; Gong & Liu, 2020), divergent thinking (Beaty et al., 2021), and IQ tests (Baum et al., 2017; Cox et al., 2019; DeSerisy et al., 2021; Yoon et al., 2017).
However, several studies have recently found evidence that high-level mental abilities are not solely linked to the frontoparietal network; functional connectivity in other networks, including the default mode and dorsal attention networks, are also predictive of performance on various tasks (DeSerisy et al., 2021; Hilger et al., 2017, 2017; Savi et al., 2021). These findings have led to the proposal that connectivity across the entire brain, as opposed to the frontoparietal network alone, is critical for understanding human intelligence. Jaušovec (2019) proposes that more intelligent brains are better at minimizing the cost of information processing while maximizing output. This is thought to be achieved through network specialization, which allows for efficient communication between different brain regions (Barbey, 2018).

Still, there is a considerable amount we do not understand about individual differences in cognition and brain development. For instance, Zelazo (2004) proposes that cognitive development results in more complex conscious experiences. Do these developmental differences in cognitive abilities lead to differences in how the brains of children process real-world experiences?

Much of what we know about the links between cognition and the brain comes from studies that isolate humans from their real-world environment (Hasson et al., 2012). Common tasks used in this field, such as the N-back task, measure specific cognitive domains, allowing for a high degree of experimental control over what a participant is doing. These studies have taught us a great deal about the neural correlates of human cognition. Another common technique used to understand the basic properties of human brains has been to measure brain activity while participants are in a resting state (Lee et al., 2013). Resting state may mimic real-world experiences more than other fMRI paradigms, but it is also an unconstrained paradigm, which means experimenters have little control over what participants think about (Finn, 2021). Despite this, many similar functional patterns have been observed across participants in a resting state (Calhoun et al., 2008; Calhoun & Adali, 2012; Esposito et al., 2005; Lee et al., 2013; Smith et al., 2013; Smitha et al., 2017; Yeo et al., 2011).
Nevertheless, we still do not have a good understanding of how the brain supports real-world processing in development. An experience in the real-world is complex; it involves various cognitive, emotional, and social processes that are often unique to the individual. Part of the issue is having the right tools to measure cognition in naturalistic contexts.

One solution to this problem is to use narratives to measure real-world processing. Understanding a narrative involves the integration of many cognitive systems, including attentional, memory, verbal, social, and emotional processing. When an individual adult listens to a story or watches a movie, their brain activity becomes highly correlated to other people processing the same story or film. This measure of correlated brain activity is termed neural synchrony, and has been shown using fMRI (Hasson, Landesman, et al., 2008), EEG (Laforge et al., 2020), fNIRS (Rowland et al., 2018), and MEG (Lankinen et al., 2014). Neural synchrony across people is also observed in real-life scenarios, such as during social interactions (Kinreich et al., 2017; Reindl et al., 2018), while listening to a lecture (Dikker et al., 2017; Meshulam et al., 2021), and even when two individuals solve a puzzle together (Nguyen et al., 2020). These findings support the external validity of this measure. Another major advantage of measuring brain activation while participants process a narrative is that it allows for greater experimental control compared to resting state fMRI, because participants are processing the same stimuli at the same time.

1.5 Narrative processing

Stories come in many forms: legends, myths, fables, parables, novels, memoirs, plays, autobiographical tales, etc. They have been around for thousands of years and are ubiquitous in human societies (Scalise Sugiyama, 2001). We share and consume stories throughout our lives. Starting in infancy, stories are often how we learn about our history, our culture, our family, and our friends. For many, stories are also a major source of entertainment, in the form of books, TV programs, music, movies, books, news, music, etc. For example, Barnes (2012) calculates that collectively, humans have spent more than 235,000 years reading and viewing the Harry Potter series. We also use stories to express ourselves, build relationships, and cope with negative events. Rimé, Mesquita, Philippot, & Boca (1991) found that almost all of our emotional experiences are
communicated to other people within a few days after they occur. We even tend to interpret ambiguous events as being a coherent narrative. For instance, Hieder and Simmel (1944) found that when participants were presented with a video depicting moving geometric shapes, almost everyone perceived the shapes as animated beings with emotions, and many interpreted the events as a connected story. Stories play an essential role in the human experience.

Stories are especially important in development when humans are first learning about their world. The types of stories that children hear early in their development impact how they themselves tell stories. Children whose parents tell more elaborative stories when they are young tend to include more details in their own autobiographical stories (Mol & Neuman, 2014; van Kleeck et al., 1997), and training parents to tell more elaborative stories led to their children including more details when they expressed themselves (Peterson, Jesso, and McCabe, 1999). This difference in parental story-telling is predictive of language and literacy development (Current et al., 2008; Marjanovič Umek et al., 2005; Marjanovič-Umek et al., 2012; Ong’ayi et al., 2020; Roopnarine & Dede Yildirim, 2018), and emotional understanding (Farkas et al., 2018). Reading fictional stories in particular may increase empathy (Bal & Veltkamp, 2013; Djikic et al., 2013; Sherr & Beise, 2015), and lower racial bias in children (Johnson et al., 2014). Children who watch a lot of movies have better creative thinking abilities compared to their peers (Kete et al., 2021). Moreover, McLean et al. (2007) suggests that stories help people make connections between their experiences and their self-concept. Similarly, Mar et al. (2006) proposes that fiction helps children develop real-world skills and social understanding. In fact, Zunshine (2011) theorizes that if we did not possess the ability to put ourselves in other peoples’ shoes, stories would not hold as much importance as they do in human societies. Whatever the reason for it, humans of all ages seek out, learn from, and get pleasure from narratives.

Mimesis is the idea that literature is reflective of the world around it (Oatley, 1999). Much of our knowledge about the world is shared knowledge; for example, most of us have a similar representation of what a bicycle is. Stories rely on this shared knowledge, which allows different people to have a similar understanding when listening
to a narrative. In fact, when different adults listen to the same story, their brain activity will often synchronize; specifically, the time course of their brain activity correlates with other people’s brain activity. Hasson et al. (2004) first showed neural synchrony in five participants who watched a clip of the movie *The Good, the Bad, and The Ugly* while in the fMRI scanner. While participants watched this movie, their brains showed significant correlated activity in approximately 30% of the brain, including the visual and auditory cortex, the superior temporal and lateral sulcus, the cingulate, the frontal gyrus, and the postcentral sulcus. This correlated activity was not present when participants were in a resting state. Moreover, participants’ brains did not synchronize if they were watching different segments of the same film, nor did participants show significant synchrony in non-sensory regions when they watched an unstructured video clip of people walking in Washington Square Park (Hasson, Landesman, et al., 2008). More recent work has shown that scrambling the movie still produces synchrony in regions associated with auditory and visual processing, but not in higher-order associative areas of the brain (Laforge et al., 2020; Lerner et al., 2011; Naci et al., 2014). This suggests that correlated brain activity is time-locked to the events that occurred in the narrative, and the plot appears to be driving synchrony in many regions of the brain.

Since Hasson et al.’s (2004) ground-breaking study, numerous studies have been conducted to investigate what types of stimuli lead to neural synchrony. People show synchronized brain activity with others when they listen to the same political speeches (Schmälzle et al., 2015), audiobooks (Hakonen et al., 2020; Thiede et al., 2020; Yeshurun et al., 2017), podcasts (Thiede et al., 2020), and personal narratives (Grall et al., 2021). Neural synchrony also occurs when different individuals watch boxing matches (Nummenmaa, Smirnov, et al., 2014), television episodes such as *The Office* (Byrge et al., 2015) and *Desperate Housewives* (Lahnakoski et al., 2014), and films such as *Bang! You’re Dead* (Naci et al., 2014). Correlated activity across different people is greater during more engaging political speeches and emotional narratives compared to those that are less interesting (Grall et al., 2021; Hasson, Landesman, et al., 2008; Nummenmaa, Saarimäki, et al., 2014; Schmälzle et al., 2015). However, when individuals listen to a narrative in a language that they do not understand, significant synchrony is only observed in sensory regions of the brain (Honey et al., 2012), and individuals under
anesthesia presented with a narrative do not synchronize to other participants (Naci et al., 2018). In contrast, when participants are told to explicitly simulate the feelings of one of the boxers while watching a boxing match, synchrony is greater in the sensorimotor cortices, superior temporal gyrus, intraparietal sulcus, and frontal eye fields compared to when they passively watch the same boxing match (Nummenmaa, Smirnov, et al., 2014). Similarly, when participants watching the same TV show were told to take one of two different perspectives, that of a detective or that of an interior decorator, they showed systematic differences in brain activity time courses across the anterior cingulate, the orbitofrontal cortex, the superior temporal sulcus, the parahippocampal gyrus, the lateral occipital cortex, and the posterior parietal cortex. These findings have led some to propose that neural synchrony in higher-level associative areas measures shared contents of conscious experiences (Naci et al., 2014; Nummenmaa et al., 2018; Zadbood et al., 2017).

While the brains of individuals synchronize when processing audio and visual stimuli of various sorts (Dikker et al., 2017; Hasson, Yang, et al., 2008; Lerner et al., 2011; Schmälzle et al., 2015; Stephens et al., 2010; Yeshurun et al., 2017), films may be especially effective at leading to synchrony across different people (Hasson, Landesman, et al., 2008). Narratives that combine auditory and visual information, such as films, are proposed to reduce the degree of intersubjectivity in interpretation, since different individuals may imagine the visual aspects of a narrative differently during audio-only stories (Levin et al., 2013). Furthermore, processing a movie has many parallels to what occurs in real-world experiences. Mast (1977) describes films as persuasive illusions of reality and claims that the viewer has an experience that is equivalent to what they encounter in the real world. Although it may feel as though watching a film is an automatic process that does not involve top-down cognition, in fact, a listener must integrate perceptual and cognitive systems to understand the plot of a movie, with some calling it a ‘super-cognitive experience’ (Nadaner, 1984). When we are particularly interested in a narrative, we become absorbed, which is the experience of intense awareness in a story world (Balint & Tan, 2015; Tan et al., 2017; Tan, 2018). Balint & Tan (2018) describe this experience as a change in conscious state, such that the listener feels as though they are part of the narrative. Others have described it as a dream-like or
hypnotic state (Nadaner, 1984). Although absorption can occur during many types of narratives, films are particularly effective at leading to absorption (Levin et al., 2013; Tan, 2018) and driving synchronized brain activity across different viewers (Hasson, Landesman, et al., 2008).

Previous work has shown that watching a movie leads to significant neural synchrony in regions associated with high-level cognition, including the frontoparietal and default mode networks. Synchrony in these networks is thought to be dependent on different individuals having a similar interpretation, or experience, of the movie (Chen et al., 2017; Naci et al., 2014; Nguyen et al., 2019). For example, Nguyen et al. (2019) had participants watch a movie that included no spoken dialogue, and then had them interpret what they believed was happening. Participants with a more similar interpretation of the movie had significantly greater synchrony in the right supramarginal gyrus, bilateral anterior superior temporal gyrus, bilateral dorsolateral and dorsomedial prefrontal cortex, as well as across the default mode network. Similarly, Ames et al. (2015) presented participants with short vignettes that were difficult to understand without contextual background; half of the time, participants were given a contextual cue needed to understand the vignettes (the valid context condition), and the other half they were not given this information (the invalid context condition). Compared to the invalid context trials, participants in the valid context trials had greater synchrony in many regions of the default mode network, including the medial prefrontal cortex, posterior cingulate cortex, and the temporal parietal junction. The invalid context condition did not show any regions with significantly greater synchrony compared to the valid context condition. Using a similar behavioral paradigm, Smirnov et al. (2014) found that the frontoparietal network showed greater functional connectivity during valid context compared to invalid context trials. Additionally, Naci et al. (2014) found that neural synchrony in the frontoparietal network was greater during periods of a movie that were rated as more, compared to less, suspenseful. The Attentional Theory of Cinematic Continuity proposes that viewing a film is an active cognitive process, with the viewer directing their eye gaze to seek out information, attending to objects that are no longer on the screen, creating representations of the important facets of the plot, and making predictions about future
events (Smith, 2012). I propose that these cognitive systems must work together for an individual to understand the plot of a movie in a similar way to others.

1.5.1 Socio-cognitive processing associated with movie watching

When watching a movie, a viewer must create meaning from complex visual and auditory information (Nadaner, 1984). They must make sense of the auditory information being presented, whether it is human voices, background music, or sound effects. They must perceive the moving shapes, lines, colors, and animate and inanimate objects in a movie, as well as the depth of the objects being presented, and how the images come together to create a specific scene (Tan, 2018). Previous work has shown that viewers of films often direct their eyes to the same visual cues (Dorr et al., 2010; Loschky et al., 2015; Smith & Mital, 2013; Wang et al., 2012). The ‘eye-mind hypothesis’ proposes that where someone looks is directly related to how they comprehend a narrative (Just & Carpenter, 1980; Loschky et al., 2015; Reichle et al., 1998; Reilly & Radach, 2006), although Loschky et al. (2015) found that even when viewers had a different understanding of a film, they still showed a high degree of synchrony in their eye gazes. Viewers must also integrate the visual and auditory information to make sense of what is happening in the context of the rest of the plot. For example, if a viewer incorrectly links a line of dialogue to a character that did not deliver that line, they likely will have trouble keeping track of the plot. Processing the complex visual and auditory stimuli of a movie is the first step in understanding the plot.

Viewers must also integrate sensory information across time. Lerner et al. (2011) presented participants with stories that were scrambled at the word, sentence, and paragraph level. They found that early auditory regions had neural synchrony across all conditions. In contrast, the sentence trials showed greater synchrony in areas associated with lexical processing compared to the word trials. Furthermore, the trials with full paragraphs showed greater synchrony in higher-level areas, including the precuneus, posterior superior temporal sulcus, the temporal parietal junction, and the frontal cortex compared to the other two trials. Using a similar paradigm, Hasson, Yang, et al. (2008)
scrambled silent films at short, intermediate, and long time scales. All trials led to similar amounts of synchrony in the primary visual cortex, but the shorter time scales had significantly less synchrony in the superior temporal sulcus, posterior lateral sulcus, frontal eye fields, and temporal parietal junction, and in fact, had no synchrony in the precuneus, compared to longer time scales. These findings suggests that synchrony in higher-order regions is dependent on the integration of sensory information from prior timepoints.

Once a viewer has processed the incoming sensory information, they must link this with their previous knowledge and mental representations (Tan, 2018). For example, in the movie *Rear Window*, the main characters, Lisa and Jefferies, suspect their neighbor of killing his wife, and to find proof of their suspicions, Lisa breaks into the neighbor’s apartment while Jefferies is watching through his window. As the suspected murderer comes home, Lisa finds an engagement ring and puts it on. When leaving the apartment, Lisa shows her hand with the engagement ring to Jefferies, but the killer sees her do it. This is the moment that the killer discovers that Jefferies knows what he has done. To understand what is happening in this scene, the viewer must understand what an engagement ring is and why it would be suspicious for Lisa to find one in the suspected murderer’s apartment. If the viewer did not know what an engagement ring represents, they would not understand that Jefferies was in trouble and thus, suspense would not be built. Film makers take advantage of the knowledge that is shared between most people in a culture to drive the plot.

Not only must viewers connect the events of the movie to previous knowledge, but they must also link it to what has already happened in the film. They must keep track of the timeline, which often spans much longer than the actual length of the movie. They must create a mental representation of each character in the movie, and continuously update these representations as new information is presented (Nadaner, 1984). This likely requires executive processes, including working memory, inhibition, and cognitive flexibility. For example, a viewer must direct their attention to the salient events occurring in the scene, while filtering out distractions (Naci et al., 2014). They must encode this information in their working memory to relate it to what has previously
happened. Then, they must store the most relevant information in their long-term memory. When the scene changes, they must switch their attention to what is currently happening and start this process all over. To a viewer, this may seem like an automatic process, but in fact, it requires significant mental resources. For instance, Naci et al. (2014) had participants perform a taxing executive function task (The Sustained Attention to Response Task) while watching a movie. Participants’ performance decreased during the points in the movie that were rated as the most suspenseful, at which time there was also the greatest neural synchrony across individuals. If watching a movie was an automatic process, participants’ performance on The Sustained Attention to Response Task would not be impacted by the movie.

Most movies center around several characters, whether they are humans, animals, or cartoons. To comprehend a plot involving animate beings, one must understand the actions, plans, goals, and emotions of the characters involved (Levin et al., 2013; Tan, 2018; Zunshine, 2008). For example, in the short film *Bang! You’re Dead*, which has previously been shown to invoke a high degree of neural synchrony across individuals (Naci et al., 2014), a child finds a loaded gun in their uncle’s suitcase but believes it is a toy gun. Suspense is built up as the child starts pointing the gun at people they encounter and reaches a climax when the child finally starts to pull the trigger. To follow the plot, the viewer must understand that the gun is real, but that the child and the other characters do not know it is real. Similar to the classic Sally-Anne task used to measure the development of theory of mind, a viewer must realize the boy does not know what the viewer knows. In fact, false beliefs are commonly used in narratives and films, for example in dramatic irony, when the audience knows something that a character does not. Most films involve a mismatch between what the characters know and what the audience knows, and the resolution involves everyone finding out (Levin et al., 2013). Moreover, many films involve complex relationships between characters, and often, different characters have dissimilar or even opposing perspectives or emotions, requiring recursive theory of mind.

Research has shown that individuals with poor theory of mind, such as autistic children, do indeed process movies differently. Studies that have compared narrative
comprehension in autistic and non-autistic individuals have found that those with autism have difficulty answering questions about characters’ mental states (Golan et al., 2006), spend more time describing aspects of the narrative unrelated to the characters (Barnes et al., 2009), and are less likely to understand sarcasm and deception (Dziobek et al., 2006). Autistic children show reduced brain activation compared to participants without autism in the theory of mind network when watching movies (Kana et al., 2015). Moreover, they spend less time looking at faces and more time looking at objects in the background (Klin et al., 2002). When describing events of a story, autistic and neurotypical adults are equally able to explain the events of the story, but autistic individuals have more difficulty differentiating relevant and irrelevant parts of the plot (Barnes, 2012). Moreover, typically developed adults tend to show a preference for narratives about people over objects, however, autistic individuals show no such preference (Barnes, 2012). Taken together, these results suggest that social abilities are associated with differences in how someone follows the plot of a movie.

In summary, understanding the plot of a movie involves various cognitive processes, including memory, executive functions, and theory of mind. If a viewer does not understand the events, dialogue, or mental states of the characters, they will not interpret the plot in the same way as someone who does. Even differences in how a viewer directs their attention or how well they remember the events of the narrative may lead to differences in interpretation. Given neural synchrony in associative areas of the brain is thought to be driven by different people understanding the plot of a movie in a similar way, it stands to reason that variations in these cognitive processes would lead to differences in neural synchrony. Furthermore, as cognitive abilities mature, neural synchrony may differ across development.

### 1.5.2 Individual differences in neural synchrony

Previous work has shown that individual variation in neural synchrony is predictive of a range of different behaviours and outcomes. For example, neural synchrony is predictive of the severity of depressive symptoms a participant is currently experiencing (Gruskin et al., 2020). Correlated activity between two individuals during a social interaction, which has also been termed brain-to-brain coupling, is predictive of
how successful the interaction was rated as (Dikker et al., 2017; Kinreich et al., 2017; Reindl et al., 2018; Stephens et al., 2010), perhaps even in non-primate animals (Kingsbury et al., 2019). Individual differences in synchrony when watching videos is associated with ones’ later memory of its content (Chen et al., 2017; Cohen & Parra, 2016; Hasson, Furman, et al., 2008; Zadbood et al., 2017). Meshulam et al. (2021) found that students who showed greater neural alignment to other students in the default mode network when they watched their first-year computer science lectures performed better on the final exam compared to those who showed less synchrony. This pattern was also evident in the hippocampus, ventrolateral prefrontal cortex, and the premotor cortex. In fact, Hasson et al. (2012) asserts that brain-to-brain synchronization is essential for learning skills such as language development or becoming proficient at a musical instrument.

These individual differences in synchrony are likely, at least in part, due to differences in interpretations of what the viewer is experiencing. Yeshurun et al. (2017) experimentally manipulated what participants believed about a narrative they were listening to and found this changed the degree of neural synchrony in several brain networks that are associated with social and executive processing. Specifically, they randomly assigned participants to be told either that they were listening to a story about a paranoid husband, or about a cheating wife. Then, all participants listened to the exact same story as their brain activity was measured by fMRI. They found that the groups did not differ in their neural responses in the auditory network; however, the time course of brain activity in voxels across the default mode network, hippocampus, inferior frontal gyrus, ventrolateral prefrontal cortex, superior temporal sulcus, and premotor cortex differed significantly between the groups. These differences in activity time courses could reliably classify individual participants into the two groups with an accuracy between 66% to 88% depending on the voxel. Voxels in the right temporo-parietal junction, precuneus, and bilateral ventrolateral prefrontal cortex showed the greatest classification accuracy. This is causal evidence that changing someone’s interpretation of a narrative leads to differences in neural synchrony in higher-order brain areas.
There is mounting evidence that neural synchrony in associative regions of the brain measures shared experiences (Naci et al., 2014, 2018; Nummenmaa et al., 2018; Yeshurun et al., 2017; Zadbood et al., 2017). However, a question within this literature that remains unanswered is why some individuals in a group synchronize more than others (Hasson et al., 2012). Investigating the relationship between cognitive development and neural synchrony may be able to shed light on this question; though, much less is known about how children’s brains respond to naturalistic stimuli.

The few studies that have investigated neural synchrony during movie watching in children often use a measure of neural maturity, which is the degree to which a child’s brain activity correlates with a group of adults. Cantlon and Li (2013) used functional magnetic resonance imaging (fMRI) to investigate the relationship between academic scores and how much children aged 4 to 10 synchronized with adults when observing clips from Sesame Street. They found that the degree to which children’s brain activity in the left and right intraparietal areas (areas that have previously been implicated in mathematical processing) synchronized with a group of adult brains was correlated with their mathematic scores. Similarly, the degree of synchronization between children’s and adult’s brain activity in Broca’s area, an area implicated in language processing, was correlated with verbal ability in children. Moraczewski et al. (2018) found that younger children (aged 4 to 6) showed less synchrony in several regions of the theory of mind and visual networks when compared to adults while watching the movie Toy Story, suggesting that children have more variable and individualized responses to movies compared to adults. Lastly, Richardson et al. (2018) measured the degree to which children aged 3 to 12 synchronized to adults while they watched a Pixar movie and found that children who had greater neural maturity also had greater functional connectivity within the theory of mind network, and less connectivity between the theory of mind network and the pain network. They also found that this measure of neural maturity predicted theory of mind performance. They then replicated this finding in an independent dataset (Richardson, 2019). These studies suggest that children who synchronize more with adults while processing naturalistic stimuli have more advanced, or matured, cognitive abilities than those who show less synchronization. Nevertheless, the degree to which children synchronize with their peers has yet to be characterized. Do
children vary in the degree they synchronize with other children? If so, is this variation related to differences in cognitive and social abilities?

1.6 Research goals and hypotheses

The overarching aim of this project was to investigate if we can better understand how cognitive and social abilities support naturalistic processing of children and adolescents by measuring how their brains respond to movies. As children learn more about their world, they become better at linking what they are experiencing to their previous knowledge. Their attention improves and they have more control over their mind and actions. They also become increasingly able to reflect on what they are experiencing. Zelazo (2004) proposes that these developmental changes to cognition cause information to be processed at a deeper level, resulting in more complex conscious experiences. To test this theory, one would need to investigate the relationship between cognitive development and real-world experiences. However, measuring differences in peoples’ naturalistic processing is challenging given the subjective nature of people’s experiences (Overgaard, 2015). One way we can better understand how different people process the same event is to measure neural synchrony; the more similar a participant’s brain responses are to another person’s, the more similar their experience of that event is said to be (Chen et al., 2017a; Hasson, Furman, et al., 2008; Nguyen et al., 2019; Nummenmaa et al., 2018; Zadbood et al., 2017).

Movies often lead to similar interpretations across participants (Levin et al., 2013), and therefore, are effective at driving neural synchrony across subjects. Based on findings that neural synchrony in the frontoparietal and default mode networks is dependent on having a similar understanding of the movie plot, researchers have proposed that neural synchrony in these regions may be a measure of shared contents of conscious experiences (Naci et al., 2014; Nummenmaa et al., 2018; Zadbood et al., 2017). For instance, when adults interpret an ambiguous video in a similar way, they have greater synchrony in the frontoparietal and default mode network compared to adults who interpreted the video differently (Nguyen et al., 2019). These findings suggest that neural synchrony is a measure of how similarly two individuals are processing an external stimulus, such as a movie, and thus may be a measure of how similar their
experience of the stimulus is. However, individuals differ in the degree of neural synchrony they produce even when watching a highly engaging film. This leads to an important question: why do some individuals synchronize more than others (Hasson et al., 2012)?

Watching a movie requires the viewer to process the incoming sensory information, use their previous knowledge and memories to make sense of what is happening, and to take on the perspectives of the different characters. To have a similar experience of a movie, viewers must use these various cognitive abilities to understand the plot in a similar way to others. Therefore, differences in the abilities required to follow the plot of a movie should lead to differences in neural synchrony. Investigating how neural synchrony relates to cognitive abilities across development may clarify what processes are required for different individuals to have a similar interpretation when processing complex stimuli. For instance, do social and cognitive abilities relate to differences in how much a group of children will synchronize to each other during a movie? If so, this would support the use of neural synchrony to investigate how different children and adolescents process real world events.

A major goal of this thesis was to investigate the link between cognition and neural responses during movies. A secondary goal of this thesis was to compare neural responses during movie watching and resting state. Specifically, I addressed the following questions: 1) Do differences in autism and autistic traits in childhood predict neural synchrony during movie watching? 2) Do children and adolescents with different IQ scores differ in their neural responses to movies? 3) Do functional brain networks differ during movie and rest in children?

In Chapter 2, I examined how neural synchrony during movie watching differs in autistic and non-autistic children (aged 7 to 12) with different levels of autistic traits. Autism is associated with worse performance on traditional theory of mind tasks (Andreou & Skrimpa, 2020; Baron-Cohen, 1991, 2000; Kana et al., 2009; Pedreño et al., 2017), but whether autistic children show less synchrony during a movie has yet to be investigated. Levin et al. (2013) proposes that theory of mind is a key component of
understanding a complex movie plot; accordingly, children with worse social cognitive abilities should have a more dissimilar understanding of a movie plot compared to children who are better at understanding the perspectives of the characters. As neural synchrony in the frontoparietal network has been implicated in shared comprehension of a narrative (Naci et al., 2014), I hypothesized that autistic children and those with higher autistic traits will synchronize less than children with lower autistic traits within this network when watching the same movie. Performance on traditional theory of mind tasks is associated with greater activation in the social brain (Blakemore, 2008, 2012; Kana et al., 2015; Schurz et al., 2020). Consequently, I also predicted differences in neural synchrony in the theory of mind network will be associated with autism and high autistic traits.

In Chapter 3, I investigated how neural synchrony during a movie relates to IQ scores in children (aged 7 to 11) and adolescents (aged 11 to 15). As discussed above, theory of mind is one of several abilities that are required to understand the plot of a movie. Differences in general cognitive abilities also have the potential to lead to differences in how someone interprets a movie, especially across development since children tend to have less general knowledge to draw from to develop an understanding of what is happening. However, neural synchrony has yet to be compared within children who have differing cognitive abilities. Yeshurun et al. (2017) showed that experimentally manipulating participants’ interpretations of an identical narrative leads to differences in neural synchrony, specifically in the default mode network. Similarly, Naci et al. (2014) showed that synchrony in the frontoparietal network was associated with the executive processing of a movie. Based on these findings, I predicted that children and adolescents with different general cognitive abilities, as measured by IQ scores on the WISC, will differ in the degree of neural synchrony they have with each other in the default mode and frontoparietal networks.

In Chapter 4, I compared the functional connectivity of brain networks while children and adolescents watched a movie versus when they were in a resting state. To investigate neural synchrony differences in the frontoparietal and default mode networks in Chapters 2 and 3, I parcellated the brain based on adult resting state data (specifically
using the Yeo et al. (2011) parcellation). This assumed the spatial topography of functional brain networks during movie watching and rest are comparable, and that brain networks in children and adults are similar. There are several areas of research that suggest this is a reasonable assumption. Previous work has shown that by age two, brain networks in children resemble those in adults (Gao et al., 2015; Grayson & Fair, 2017; Marek & Dosenbach, 2018; van den Heuvel et al., 2015), although they continue to mature throughout childhood and adolescence (Bassett et al., 2011; Baum et al., 2017; Grayson & Fair, 2017). Cole and colleagues (2014) compared functional connectivity during rest versus tasks (not including movies) and found that these states are highly correlated. However, there is evidence that some features of functional brain networks do differ across different states, with studies finding both increases and decreases in connectivity during rest compared to tasks (Cole et al., 2014; Finn et al., 2015; Geerligs et al., 2015). In Chapter 4, I used a data-driven method to explore how functional brain networks in children (aged 7 to 13) watching a movie differ from those when they are in a resting state. Specifically, I compared the spatial topography of brain networks, the patterns of functional connectivity, and the degree of neural synchrony while children watched a movie and while they were at rest.

1.7 Division of data across chapters

All studies referenced this thesis were based on data from the Healthy Brain Network Biobank collected by the Child Mind Institute (described in Alexander et al., 2017), which is an ongoing initiative to collect neuroimaging, medical, and behavioural data on 10,000 participants between the ages of 5 to 21. The Chesapeake Institutional Review Board approved this study. Detailed information on the dataset can be found at [http://fcon_1000.projects.nitrc.org/indi/cmi_healthy_brain_network/](http://fcon_1000.projects.nitrc.org/indi/cmi_healthy_brain_network/)

The Healthy Brain Network Biobank used a community-referred recruitment model to generate a heterogeneous and transdiagnostic sample. Briefly, recruitment involved advertising the study to community members, educators, local care providers, and parents who were on email lists or at events. Potential participants were screened, and were excluded if there were safety concerns, impairments that would interfere with
the study procedure (such as being nonverbal or having an IQ of less than 66), and/or medical concerns that could potentially impact brain related findings (for a full description, see Alexander et al., 2017).

The study protocol included, where possible, the acquisition of T1 weighted anatomical MRI scans and functional MRI data acquired while the participants watched a ten-minute clip of *Despicable Me* (from 1:02:09 to 1:12:09) and during two five-minute resting state scans. All MRI data was collected on a 3T Siemens scanner using a Siemens 32-channel head coil. Functional images were acquired with a gradient-echo planar imaging pulse sequence (TR = 800 ms, TE = 30 ms, Flip Angle = 31 degrees, whole brain coverage 60 slices, resolution 2.4 x 2.4 mm⁴). High-resolution T1-weighted MPRAGE structural images were acquired in 224 sagittal (TR = 2500 ms, TE = 3.15 ms, resolution .8 x .8 mm). The first five volumes of the movie and resting state scan were discarded. The studies described in Chapter 2-4 used identical imaging preprocessing scripts. Specifically, the MRI data were preprocessed and analyzed using the Automatic Analysis (AA) toolbox (Cusack et al., 2015), SPM8 (Ashburner et al., 2012), and in-house MATLAB and Python scripts. Figures were created using R and MRIcroGL (*NITRC*, 2021).
2 Examining the relationship between measures of autistic traits and neural synchrony during movies in children with and without autism.


2.1 Introduction

Autism spectrum disorder (ASD) is a complex developmental condition characterised by a variety of neurological and psychological features; however, the most prominent feature of ASD is a marked deficit in ‘social cognition’. Social cognition refers to understanding what other people believe, how they will react in situations, and why they feel the way they do, and is a core element of successful human interactions. Autistic individuals perform poorly on tasks that assess social cognition, such as face perception (Spencer et al., 2011), perspective taking (Hamilton et al., 2009), and theory of mind (ToM), or the ability to attribute mental states to oneself and others (Pedreño et al., 2017). One of the most common tools to screen for deficits associated with ASD is the Social Responsiveness Scale, which measures aspects of social awareness, communication, and motivation (Constantino & Gruber, 2012).

The brains of autistic individuals often show differences when compared to those of typically-developing individuals. These include differences in structural (Barnea-Goraly et al., 2004; Brieber et al., 2007) and functional connectivity (Cherkassky et al., 2006; Kana et al., 2015; Monk et al., 2009; Weng et al., 2010), and in brain activation patterns during task-based fMRI (Bölte et al., 2008; Gilbert et al., 2008; Just et al., 2007; Mason et al., 2008; Solomon et al., 2009). Many of the brain regions that show differences in autistic individuals have been linked to ToM in healthy individuals, including the temporal parietal junction (Saxe & Kanwisher, 2003; Saxe & Wexler, 2005), the medial prefrontal cortex (Hartwright et al., 2013; Krause et al., 2012; Völlm et
Evidence has recently emerged that autistic adults process social information in naturalistic, or ‘real-life’ contexts differently than typically-developing individuals. Several studies have investigated social processing differences between those with and without ASD by examining brain activity in response to watching movies (Bolton et al., 2018; Byrge et al., 2015; Hasson et al., 2009; Salmi et al., 2013). Movie watching mimics real-world experiences by requiring the viewer to integrate perceptual and cognitive systems in order to follow the complexities of the plot. It is known that the brains of healthy individuals become highly synchronized (or correlated) when viewing the same movie (Hasson, Landesman, et al., 2008). This measure of synchronization across different brains is termed *inter-subject correlation* (ISC) and high levels of synchrony suggest that individuals are experiencing the movie in much the same way. For example, Naci et al. (2014) noted a high degree of synchrony in frontoparietal regions when healthy individuals watched “Bang You’re Dead!” by Alfred Hitchcock and this was shown to relate to how suspenseful and engaging viewers found the movie. The brains of autistic adults have been shown to be less synchronized than those of typically-developing adults during movie watching (Bolton et al., 2018; Byrge et al., 2015; Hasson et al., 2009; Salmi et al., 2013). However, this has not been examined in autistic children.

Richardson et al. (2018) have shown that in typically-developing children, those with poorer social cognition have reduced synchrony during movie watching in areas known to be involved with ToM, suggesting that lower synchrony in these areas may also be a feature of autistic children. In the current study, this question was investigated in three groups of children who differed with respect to their degree of autistic traits and whether or not they had been diagnosed with ASD. Specifically, a data-driven approach was used to examine differences in the degree of inter-subject correlation during movie watching in children aged 7 to 12, who had either been diagnosed with ASD, or did not have ASD but their scores on the Social Responsiveness Scale – revised (SRS-2) indicated a high degree of autistic traits, or did not have ASD and had typical SRS-2 scores for their age.
On the basis of the existing literature, it was predicted that group differences would emerge in ISC within brain networks associated with social cognition. Specifically, it was hypothesized that brain activity within both frontoparietal (Naci et al., 2014), and the ToM networks (Richardson et al., 2018) would be less synchronized in children without ASD but who had higher SRS-2 scores (higher degree of autistic traits) compared to those with lower SRS-2 scores (lower degree of autistic traits). Furthermore, it was hypothesized that the brains of children with ASD would be the least synchronized of all, based on their known impairments in many aspects of social cognition.

2.2 Methods

2.2.1 Participants

From the Healthy Brain Biobank database (described in Chapter 1 and in Alexander et al., 2017), participants were included in the current analysis if they were between the ages of 7-12 and both anatomical and functional MRI data during movie watching had been successfully acquired. Everyone included in the current study had written consent obtained from their legal guardians and written assent obtained from the participant. Participants were not excluded based on their handedness or if they had any diagnoses. All participants also had scores on the Social Responsiveness Scale Revised (SRS-2), which is a measure of social reciprocity and communication associated with deficits in ASD (Constantino & Gruber, 2012). Specifically, the SRS-2 assesses deficits associated with social awareness, social cognition, social communication, social motivation, and restrictive interests and repetitive behavior, and is rated by parents or caregivers of the child. A score of 59 or below on the SRS-2 scale suggests that the child does not exhibit autistic traits. A score above 59 is suggestive of impairments in social functioning.

As part of this study, all participants completed a computerized version of the Schedule for Affective Disorders and Schizophrenia - Children’s version (KSADS) in addition to the social responsiveness scale - revised (SRS-2). The KSADS is a semi-structured diagnostic interview used to assess current and past psychopathology according to the DSM-IV criteria, and is rated by a research clinician or social worker (Alexander et al., 2017; Kaufman et al., 1997). Participants who were suspected to have
ASD were then assessed in person by a clinician. These participants were assessed using the Autism Diagnostic Observation Schedule – 2nd edition (Lord, Rutter, DiLavore, Risi, Gotham & Bishop, 2012) and the Autism Diagnostic Interview – Revised (Rutter, Le Couteur & Lord, 2003) and those who met the relevant criteria were diagnosed with autism.

Participants were divided into three groups based on their SRS-2 Total scores: The “Low SRS-2 score” (L-SRS) group included those who had an SRS-2 score $\leq 59$; the “High SRS-2 Score (H-SRS)” group included participants who had an SRS-2 score of $\geq 60$ (the ASD screener cut-off), but were not diagnosed with ASD; and the Autism Spectrum Group (ASD) included participants who were diagnosed with ASD by a clinician as part of the HBN protocol (for details, see Table 2.1).

Because the groups differed with respect to sample size, age and sex, the L-SRS and H-SRS groups were resampled to produce three demographically matched subgroups. Specifically, for each participant in the ASD group, an L-SRS and an H-SRS individual who had the same sex and was closest in age (to the month) were selected for inclusion where possible (see Table 2.1). This resulted in three groups of 28 participants, ensuring sufficient power for acquiring reliable inter-subject correlation results (Pajula & Tohka, 2016). The matched sample was used to statistically compare the groups in the whole brain and network of interest analyses. All but one of the participants in the High SRS-2 group were assessed in person by a clinician. All but one participant also completed the Weschler Intelligence Scale for Children (WISC; Wechsler, 2014)
Table 2.1. A summary of participant demographics.
Means, standard deviations, and ranges of the ages, SRS-2 Total scores, and the WISC full scale IQ scores, as well as the number of females and males (F/M) are displayed for each group in the full and matched sample. The full sample of participants was used to create the matched groups. The matched sample was then used for all group comparisons (i.e. the whole brain analysis, the network of interest analysis, and the percentage of synchronized cortex). Only the pairwise cluster-based analysis used the full sample of participants.

<table>
<thead>
<tr>
<th>Measure</th>
<th>L-SRS</th>
<th>H-SRS</th>
<th>ASD</th>
<th>Test of difference</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Full Sample:</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>N</td>
<td>64</td>
<td>34</td>
<td>28</td>
<td></td>
</tr>
<tr>
<td>Mean Age (SD) and range</td>
<td>9.9 (1.7)</td>
<td>9.2 (1.6)</td>
<td>9.4 (1.5)</td>
<td>F_{(2,123)} = 1.99, p = .141</td>
</tr>
<tr>
<td>Sex (F/M)</td>
<td>27/37</td>
<td>13/21</td>
<td>2/26</td>
<td>X^2 (2) = 11.27, p = .003</td>
</tr>
<tr>
<td>SRS-2 scores</td>
<td>49.6(4.8)*</td>
<td>67.5 (6.0)*</td>
<td>76.6 (10.5)*</td>
<td>F_{(2,123)} = 180.98, p &lt; .001</td>
</tr>
<tr>
<td>Mean IQ scores (SD) and range</td>
<td>103 (17)</td>
<td>98 (16)</td>
<td>93 (18)</td>
<td>F_{(2,123)} = 3.77, p = .026</td>
</tr>
<tr>
<td><strong>Matched Sample:</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>N</td>
<td>28</td>
<td>28</td>
<td>28</td>
<td></td>
</tr>
<tr>
<td>Mean Age (SD) and range</td>
<td>9.4 (1.5)</td>
<td>9.6 (1.6)</td>
<td>9.4 (1.5)</td>
<td>F_{(2,81)} = .155, p = .857</td>
</tr>
<tr>
<td>Sex (F/M)</td>
<td>3/25</td>
<td>7/21</td>
<td>2/26</td>
<td>X^2 (2) = 4.08, p = .129</td>
</tr>
<tr>
<td>SRS-2</td>
<td>48.6 (4.8)*</td>
<td>67.2 (5.7)*</td>
<td>76.6 (10.5)*</td>
<td>F_{(2,81)} = 101.79, p &lt; .001</td>
</tr>
<tr>
<td>Mean IQ scores (SD) and range</td>
<td>103 (18)</td>
<td>96 (15)</td>
<td>93 (18)</td>
<td>F_{(2,81)} = 2.71, p = .073</td>
</tr>
</tbody>
</table>

2.2.2 MRI preprocessing

Functional and structural scans were co-registered and normalized to the Montreal Neurological Institute (MNI) template. Pre-processing of functional data included motion correction (using six motion parameters: left/right, anterior/posterior, superior/inferior, chin up/down, top of head left/right, nose left/right). Functional data were then spatially smoothed using a Gaussian filter (8 mm kernel), and low-frequency noise (e.g., drift) was removed by high-pass filtering with a threshold of 1/128 Hz. The data was denoised using Bandpass filter regressors, with cerebrospinal fluid, white matter signals, motion
parameters, their lag-3 2nd-order volterra expansion (Friston et al., 2000), and “spikes” (based on mean signal variance across volumes) as nuisance regressors.

2.2.3 Exploratory whole brain synchronization

To determine the degree of synchronization separately for each group, the degree of ISC across the whole brain was calculated using a leave-one-out approach within the matched sample. That is, the pre-processed time course of every voxel was correlated (Pearson and then Fisher z-transformed) between each participant and the mean time course of every voxel from the rest of the group (N-1). A one-sample t-test was calculated on the resulting individual brain-wide correlation values. Multiple comparisons were corrected with a false discovery rate (FDR) of .05 to generate group maps of significantly correlated voxels. To identify where in the brain inter-subject correlation differences existed between the three groups, t-tests were performed on the correlation values at each voxel derived for all of the individuals within each group. Multiple comparisons were corrected with an FDR of .05.

2.2.4 Network of interest inter-subject correlation

The degree of synchronization within eight previously defined functional networks was calculated. To address our specific hypotheses, a map for the ToM network was used (Dufour et al., 2013) as well as the frontoparietal network from the Yeo et al., (2011) parcellation. Six additional networks (Visual, Dorsal Attention, Ventral Attention, Somatomotor, Limbic, Default Mode Network) from Yeo et al. (2011) were also included in an exploratory analysis to examine potential differences in other areas of the brain. The 8 network parcellations are displayed in Figure 2.1. Similar to the whole brain ISC analysis, the intra-group inter-subject correlation for each of these eight networks was calculated using a leave-one-out approach within the matched sample. Specifically, the time course of each network (based on the average time course of each voxel within the network) for each participant was correlated with the average time course of each network for the remaining participants in the group, minus that participant (N-1). Finally, we used a general linear model to determine if group membership was a significant
predictor of intra-group synchronization across the 8 networks. The model included inter-
subject correlation values as the predicted variable and group as the predictor variable.
This was done separately for each network. The networks that showed a significant effect
of group were followed up with Welch t-tests (all results were FDR corrected to .05).

To better understand the results from the intra-group analysis, the degree of inter-
group inter-subject correlation was then calculated, by taking the mean time course for
each individual in one group and correlating it with the mean of the two other groups.
This generated a correlation value that reflected how similar each participant’s time
course was to the two other groups. For instance, we calculated how correlated each ASD
participant was to the mean of the other two groups. Finally, we calculated three separate
general linear models to determine if participants correlated significantly more with their
own group than the mean of the other two groups.

2.2.5 Percent synchronization across the cortex

The percent of significant voxels across the cortex was calculated, for descriptive
purposes, to quantify the number of synchronized voxels common across all individuals
in each of the three matched sample groups. To calculate the total percentage of cortex
that was synchronized, the number of voxels that were significant per group were divided
by the total number of voxels in grey matter. To calculate the total percentage of each
network that was synchronized, the number of voxels that were significant per group
were divided by the total number of voxels in the network of interest.
2.2.6 Cluster-based inter-subject correlation analysis

To explore the relationship between SRS-2 scores (as a continuous variable) and neural synchrony, pairwise correlations were calculated between each participant and that of every other participant in the ToM and frontoparietal networks. This was done by calculating the mean time course (i.e. by averaging across all voxels in the network) in both networks for each participant, and then correlating it with every other participant’s mean time course. Because SRS-2 scores were skewed (upwards) in the ASD and H-SRS groups, this analysis included all participants (N = 126), rather than the smaller matched groups. These pairwise correlations were then plotted in a matrix by ranking each participant by their SRS-2 score (from low to high) for descriptive purposes. Finally, a clustering analysis was conducted to determine whether groups of participants could be
identified based solely on their neural synchronization, rather than group membership or SRS-2 scores. To do this, a k-means clustering algorithm was used to group together participants using the time series of neural activity in the ToM and frontoparietal networks. The MATLAB evalclusters function was used to identify the optimal number of clusters based on the variance in the data using the Calinski-Harabasz Index computed over 1000 iterations to minimize the fitting parameter. Based on the groupings generated from this cluster analysis, a logistic regression analysis was computed to investigate which factors (SRS-2 total and subscale scores, age, sex, and group membership) best predicted the cluster-generated groupings.

2.3 Results

There was a total of 267 eligible participants who met the inclusion criteria (see Methods). Of this sample, 141 participants were removed because of excessive motion or issues with imaging data quality. There was a significant difference between the three groups in terms of SRS-2 scores ($F_{(2,81)} = 101.76, p < .001$) and post-hoc t-tests showed that the H-SRS group had significantly higher scores than the L-SRS group ($t_{(51.9)} = 12.96, p < .001$) and significantly lower scores than the ASD group ($t_{(42.54)} = 4.12, p < .001$). There were no significant differences between the groups on the WISC full scale IQ scores ($F_{(2,80)} = 2.71, p = .073$), or any of the WISC subscales except for working memory; ($F_{(2,80)} = 3.29, p = .042$). The ASD group had significantly lower working memory scores compared to the L-SRS group ($t_{(52.10)} = 2.35, p = .023$) but not the H-SRS group ($t_{(50.24)} = 1.05, p = .30$).

Differences in correlated motion within each group were examined, in order to ensure that this did not inflate the inter-subject correlation results. Correlated motion was calculated separately for each group, by taking each participant’s 6 motion parameters for each frame and correlating the time course with that of the mean of the rest of the group (N-1). No significant differences were found between the groups in their degree of correlated motion ($F_{(2,80)} = .181, p = .835$).
2.3.1 Exploratory whole brain synchronization

Whole brain synchronization was characterized in the three groups. All groups showed significant synchronization in the auditory and visual areas (Figure 2.2a). In fact, synchronization in these areas was stronger than in any other brain areas, replicating previous inter-subject correlation findings during movie watching (Hasson et al., 2008). The H-SRS and L-SRS groups also showed significant inter-subject correlation in areas associated with ToM and executive processing, including parts of the right and left temporal parietal junction, the precuneus, the intraparietal sulcus, the superior parietal lobe, and portions of the medial and lateral prefrontal cortex. In contrast, the ASD group had very little significant inter-subject correlation outside of visual and auditory areas (see Figure 2.2a, bottom row).

Next, whole brain contrasts were conducted (Figure 2.2b) to examine whether the magnitude of synchronization differed between the three groups. When the L-SRS group was contrasted to the H-SRS group, only tiny areas of difference were observed after multiple comparisons corrections, in the inferior temporal gyrus (MNI coordinates $x,y,z = -46,-37,-17$, $t_{(54)} = 4.61$, $p_{\text{corrected}} = .030$), and white matter (see Figure 2.2b, top row). The H-SRS group did not show any voxels that were more significantly correlated than the L-SRS group. The L-SRS group showed significantly greater inter-subject correlation than the ASD group (Figure 2.2b, middle row) in the bilateral temporal parietal junction (MNI coordinates (left) = $-57,-61,30$, $t_{(54)} = 3.97$, $p_{\text{corrected}} = .011$, MNI coordinates (right) = $49,-67,31$, $t_{(54)} = 5.07$, $p_{\text{corrected}} = .002$), precuneus (MNI coordinates = 4, -51, 41, $t_{(54)} = 4.14$, $p_{\text{corrected}} = .009$), right superior temporal sulcus (MNI coordinates = 60, -11, -16, $t_{(54)} = 4.47$, $p_{\text{corrected}} = .005$), right hippocampus (MNI coordinates = 32, -14, -19, $t_{(54)} = 3.52$, $p_{\text{corrected}} = .026$), and in regions of the lateral (MNI coordinates = 39, 54, -9, $t_{(54)} = 3.61$, $p_{\text{corrected}} = .022$), and the right medial prefrontal cortex (MNI coordinates = 22, 42, 37, $t_{(54)} = 3.89$, $p_{\text{corrected}} = .014$). The H-SRS group had significantly greater synchronization than the ASD group in the precuneus (MNI coordinates = -3, -55, 45, $t_{(54)} = 4.00$, $p_{\text{corrected}} = .017$), right hippocampus (MNI coordinates = 28, -5, -21, $t_{(54)} = 3.37$, $p_{\text{corrected}} = .043$), and in regions of the lateral (MNI coordinates = 46, 44, 12, $t_{(54)} = 6.30$, $p_{\text{corrected}} < .001$), and medial prefrontal cortex (MNI coordinates = -5, 65, -7, $t_{(54)} = 4.27$, $p_{\text{corrected}} = .012$) (Figure 2.2b, bottom row). The ASD
group did not have more significantly correlated voxels in any part of the brain when contrasted with L-SRS and H-SRS groups.

Figure 2.2. Exploratory whole brain inter-subject correlation analysis. a) Voxels displayed in red showed significant inter-subject correlation during movie watching in the L-SRS group. Voxels displayed in violet showed significant inter-subject correlation in the H-SRS group. Voxels displayed in blue showed significant inter-subject correlation in the ASD group. All p values were FDR corrected to an alpha of .05. b) Whole brain contrasts were calculated by conducting one-tailed t-tests on the inter-subject correlation values between each group (p values corrected to an FDR of .05). Voxels displayed in yellow showed significantly greater inter-subject correlation values based on this contrast, voxels displayed in red show the ToM network parcellation. c) Voxels displayed in yellow showed significantly greater inter-subject correlation values based on the same contrast displayed in b, overlaid on top of the Yeo et al. (2011) 7-network parcellation. (Frontoparietal = orange, Visual = dark blue, Somatomotor = light blue, Dorsal attention = dark green, Ventral attention = light green, Limbic = mustard, Default mode = red).
2.3.2 Network based synchronization

Group differences in the magnitude of intra-group synchronization revealed a main effect of group in the ToM (F\_\text{(2,81)} = 4.94, p = .009) and the limbic (F\_\text{(2,81)} = 3.93, p = .023) networks (Figure 2.3), but not in any of the others examined, including the frontoparietal network (F\_\text{(2,81)} = 2.02, p = .140, Cohen’s d ranged from .037 to .476). Post-hoc analyses of neural synchronization revealed that the ASD group had significantly lower ISC values compared to the L-SRS group within the ToM (t\_\text{(50.11)} = 3.50, p\_\text{corrected} = .006, Cohen’s d = .934) and limbic networks (t\_\text{(50.00)} = 2.48, p\_\text{corrected} = .044, Cohen’s d = .664). The ASD group also had significantly lower ISC values compared to the H-SRS group in the limbic network (t\_\text{(50.21)} = 2.18, p\_\text{corrected} = .044, Cohen’s d = .631), although differences in inter-subject correlation just failed to meet the corrected alpha level in the ToM network (t\_\text{(52.13)} = 2.36, p\_\text{corrected} = .0504, Cohen’s d = .584). Moreover, no significant differences in inter-subject correlation were observed between the L-SRS and H-SRS groups within the ToM (t\_\text{(57.72)} = .488, p\_\text{corrected} = .628, Cohen’s d = .130) or limbic networks (t\_\text{(57.20)} = .417, p\_\text{corrected} = .628, Cohen’s d = .111).
Figure 2.3. Intra-group network of interest analysis. Inter-subject correlations, based on a leave one out correlation analysis conducted separately for each group, is displayed as dots for each participant in the eight networks. Boxplots indicate the median inter-subject correlation value and interquartile range for each group (blue = L-SRS, yellow = H-SRS, red = ASD). The ASD group had significantly lower ISC in the limbic and ToM networks compared to the L-SRS group. The ASD group also had significantly lower ISC in the limbic network compared to the H-SRS group, while in the ToM network this difference narrowly missed statistical significance (corrected p value = .0504). The groups did not differ significantly in any of the six other networks.
An inter-group inter-subject correlation network analysis was performed to investigate whether individuals in one group had significantly greater neural synchronization with their own group than that of the other two groups. The results revealed that the degree of inter-subject correlation was not significantly different between any of the groups in any of the examined networks, including the frontoparietal and ToM networks.

2.3.3 Percent synchronization across the cortex

When looking at the percentage of synchronized voxels across the whole brain, the ASD group had nearly one-third less (38%) than the L-SRS (56%) and H-SRS (52%) groups (see Figure 2.4). The percentage of significant voxels in each of the eight networks of interest was also calculated (see Figure 2.4). The difference in percentage across the whole brain between the groups was not accounted for by less synchronization in any one network; rather, the ASD group had fewer synchronized voxels in every network, including in the ToM and frontoparietal networks.

![Figure 2.4. Percentage of correlated voxels.](image_url)

The percent of significant voxels across the cortex was calculated, for descriptive purposes, to quantify the number of synchronized voxels common across all individuals in each of the three matched sample groups. This was calculated by dividing the number of voxels with significant inter-subject correlation by the total number of voxels in the whole brain or network for each group separately (blue = L-SRS, yellow = H-SRS, red = ASD).
2.3.4 Cluster-based inter-subject correlation analysis

To explore whether SRS-2 scores predicted inter-subject correlation values when used as a continuous measure (instead of a categorical variable), pairwise inter-subject correlations were calculated between each participant (N=126) in the frontoparietal and ToM networks. The entire sample was used so that the SRS-2 scores were more normally distributed and to increase statistical power. Pairwise correlations were conducted to reduce any influence the groupings may have had on the mean time course originally used to calculate inter-subject correlation. For instance, if those with low SRS-2 scores and those with high SRS-2 scores both correlated with their own group to a similar degree, but the pattern of activations was different, using these groupings would obfuscate any differences. For descriptive purposes, the matrix of pairwise correlation values was plotted by ranking each participant by their SRS-2 score, from low to high (see Figure 2.5a). A k-means clustering analysis was conducted on the pairwise correlations to explore potential factors that predicted groups of participants who have the most similar degree of synchrony in these two networks. The best fit was achieved by dividing the data into two clusters in both the frontoparietal and ToM networks; cluster 1 included individuals with similar neural responses to the movie (large positive correlations) and cluster 2 included individuals with unrelated neural responses to the movie (Figure 2.5b). Moreover, there was also a large overlap between the participants who were in cluster 1 in the ToM and frontoparietal networks. Specifically, of the 58 participants who had high similarity in the ToM network (cluster 1), 45 of them also had high similarity in the frontoparietal network.
Figure 2.5. Matrices of pairwise inter-subject correlations. Yellow squares indicate a higher positive correlation (i.e. high similarity in time series), blue squares indicated a low or negative correlation (i.e. low similarity in time series). a) Pairwise correlations in time series in the frontoparietal and ToM networks between each pair of participants are ordered by SRS-2 scores (from low to high). b) Pairwise correlations in time series are ordered based on the K-means analysis in the frontoparietal and ToM networks. Black boxes display cluster 1 (the high similarity group) for each network.

Logistic regression was run to determine whether the probability of being in cluster 1 versus cluster 2 could be predicted by age, sex, full scale IQ, SRS-2 total and subscales, or group membership (i.e., L-SRS, H-SRS and ASD). None of these factors significantly predicted cluster membership in the frontoparietal network. However, in the ToM network, group membership significantly predicted cluster membership. Cluster 1 comprised 35 participants (60%) in the L-SRS group, 17 individuals (29%) from the H-SRS groups, and 6 individuals (10%) who were diagnosed with ASD. In contrast, cluster 2 consisted of 29 individuals (45%) from the L-SRS group, 17 individuals (20%) from the H-SRS group, and 22 individuals (35%) diagnosed with ASD. There were
significantly more participants from the ASD group in cluster 2 than in cluster 1 in the ToM network ($X^2 = 7.5, p = .006$), while there was no significant difference in the number of H-SRS participants between the two clusters ($X^2 = .11, p = .73$), and although there were more L-SRS participants in cluster 1, this difference did not reach significance ($X^2 = 3.25, p = .072$).

### 2.4 Discussion

In the current study, a group of ASD participants had significantly less neural synchronization when watching a movie compared to the L-SRS and H-SRS groups across the whole brain, including the ToM and limbic networks. These regions have been shown previously to be associated with elements of ‘plot following’ during movie watching (Hasson, Furman, et al., 2008; Hasson, Landesman, et al., 2008; Naci et al., 2014; Nguyen et al., 2019), suggesting that the children in the ASD group were experiencing the movie qualitatively differently than the participants in the other two groups. These results, in particular the fact that the ToM network was less synchronized in the ASD group, are intriguing given that regions within this network are associated with social cognition (Dufour et al., 2013; Mills et al., 2014; Richardson et al., 2018; Rilling et al., 2004), which is known to be affected in ASD (Hamilton et al., 2009; Pedreño et al., 2017; Spencer et al., 2011). While aspects of social cognition are usually discussed in the context of inter-personal relationships, they are also essential components of movie-watching, allowing one to become immersed in the plot by taking the perspective of the characters appropriately, understanding their motives, and following their verbal and nonverbal communication cues. Yeshurun et al. (2017) have reported previously that manipulating an individual’s understanding of a plot reduces neural synchrony in ToM regions, including the precuneus, temporal parietal junction, and medial prefrontal cortex. Thus, these findings support the idea that autistic children process social stimuli in a distinct way, as they have different neural responses in the ToM network during a movie, when compared to children without ASD.

It is also interesting that participants in the ASD group had significantly less synchrony in the lateral prefrontal cortex, a region within the frontoparietal network, when compared to those in the other two groups. Understanding a complex narrative
(such as a movie’s plot) requires a viewer to remember previous events, pay attention to what is currently happening, make predictions about the future consequences of current events, and integrate this information over time, all of which depends on frontoparietal executive processing (Naci et al., 2014). In previous studies, reduced synchrony in this network has been associated with ‘losing the plot’ during deep sedation (Naci et al., 2018), and in patients with severe brain damage (Naci et al., 2014). Thus, this decrease in inter-subject correlation in the lateral prefrontal cortex may suggest that participants in the ASD group are also failing to grasp elements of the plot in the way that the other participants do.

Despite finding that inter-subject correlation was reduced in prefrontal regions using a whole brain analysis, no differences in the degree of ISC were found in the frontoparietal network when a network of interest analysis was used. One potential reason is that the parcellation used for the frontoparietal network was based on adult resting state data and may not accurately capture this network in children while they watch a movie. Previous work has shown that the frontoparietal network continues to develop into early adulthood (Baum et al., 2017; Peters et al., 2016), and so the parcellation masks from Yeo et al. (2011) may have led us to average neural activity from regions that are not yet fully integrated in children.

While not part of our hypotheses, it is interesting that the ASD group showed less inter-subject correlation in the right hippocampus in the whole brain analysis as well as in the limbic network, when examined using the parcellation by Yeo et al. (2011). Similar findings have been reported in autistic adults watching movies (Byrge et al., 2015). Moreover, Chen et al. (2017) found that, in healthy adults, the degree of inter-subject correlation within the hippocampus during movie watching predicted events that were later recalled, although this has not been examined during development. Nevertheless, differences in long-term memory have been reported in ASD; specifically, autistic individuals tend to perform worse on episodic, but not semantic, memory tasks (Crane & Goddard, 2008; Lind, 2010)

Contrary to our hypothesis, no meaningful differences in neural synchrony were found between the L-SRS and H-SRS groups. This contrasts with the results of Richardson et al., (2018) who found that social cognition in typically-developing children
was related to the degree of inter-subject correlation within the ToM network during movie-watching. One potential reason for this difference is that Richardson et al., (2018) calculated inter-subject correlation based on how similar each child’s time course was to a group of adults watching the same movie, whereas in the current study, inter-subject correlation was calculated by correlating each participant’s time course to the mean of their own group. Moreover, the measure of social cognition used by Richardson et al. (2018) focused specifically on comprehension of a social narrative, which has many things in common with how people follow the plot of a movie. It is perhaps not surprising then, that the two things correlated. In the current study, a measure that captures autistic traits was used – the SRS-2, which measures an individual’s motivation to engage in social interactions, their use of social communication, their ability to understand social cues, and restrictive and repetitive behaviors (Constantino & Gruber, 2012). Thus, while the H-SRS and L-SRS groups differed in terms of their autistic traits as measured by the SRS-2 scale, these mechanisms may be unrelated, or only moderately related, to those that are involved in plot following. Moreover, it is also possible that creating categorical groups based on the SRS-2 scores may have obscured subtle differences in individuals with differing levels of autistic traits, such as social impairment. To investigate this possibility, the exploratory pairwise correlation analysis was conducted, which found that SRS-2 scores as a continuous measure did not predict whether participants had similar patterns of neural activity in the ToM or frontoparietal networks. Taken together, these results suggest that it is only when autistic traits are in the clinical range, as is seen in ASD, that differences in conscious processing of naturalistic stimuli emerge.

As a group, autistic participants had less inter-subject correlation compared to those without ASD, but these differences did not apply uniformly to each individual. The clustering analysis indicated that the majority of ASD participants had low similarity in their time courses compared to all other participants. However, six out of 28 of those diagnosed with ASD clustered with the ‘high similarity’ group (comprising about 10% of the group) according to their synchronization in the ToM network. Using a similar clustering analysis, Byrge et al. (2015) found that in a sample of 17 high functioning autistic adults, five showed idiosyncratic patterns of inter-subject correlation compared to typically-developing individuals, while the other 12 clustered with the control group.
Moreover, Byrge et al. (2015) found that these five individuals were significantly worse than the control group and the other 12 ASD participants when asked to explain elements of a movie plot. Together, these findings suggest that lower synchronization during movie-watching may be common, but not a uniform characteristic of either autistic children or adults. Indeed, heterogeneity in clinical features, cognitive profiles, and differing genetic and environmental risk factors has plagued research in ASD (Betancur, 2011; Jeste & Geschwind, 2014; Lenroot & Yeung, 2013). For example, within the neuroimaging literature, some studies have reported underconnectivity across the brains of autistic individuals (Cherkassky et al., 2006; Di Martino et al., 2014; von dem Hagen et al., 2013), while others find hyperconnectivity (Supekar et al., 2013; Uddin et al., 2010, 2013).

Finally, it is important to keep in mind the exploratory nature of the current study when interpreting these findings. This is a step towards a better understanding of how children with and without ASD process naturalistic stimuli, but replication and further investigation is needed to better understand the nature of the differences observed. For instance, one potential mechanism underlying our results could be that participants in the ASD group had more variable neural responses to the movie. However, it would be valuable for future studies to directly examine if more variable neural responses to movies are driving reduced neural synchronization in those diagnosed with ASD. Additionally, a major limitation of this study is that no memory test, or measure of how well the movie clip was understood, was collected. A behavioral measure of movie comprehension may help to explain the nature of the neural differences observed in this study. It is possible that individuals were attending to different features of the movie, which has been shown to influence the degree of neural synchrony (Nguyen et al., 2019), although previous work has confirmed that movies similar to Despicable me maintain the viewers’ attention (Hasson, Landesman, et al., 2008; Naci et al., 2015). It is also unlikely that participants were asleep during the movie, as most of the visual network was synchronized across the three groups during the movie, which is not observed when individuals are sedated (Naci et al., 2018).

In sum, the current results suggest that autistic children, as a group, process movies in a unique way compared to those without ASD. Interestingly, a minority of
these children had time courses that were highly correlated with a group of children without ASD in the ToM network. Future research should investigate factors that underlie this heterogeneity, as this may be one avenue to better understand how autistic individuals process the world around them.
3 Examining the relationship between shared experiences during movie watching and cognitive ability in late childhood and early adolescence

3.1 Introduction

The period between late childhood and adolescence is marked by tremendous physical, social, and intellectual development. During this time, the brain undergoes widespread structural and functional changes in regions associated with high-level cognition, including the frontal and parietal cortices (Baker et al., 2015; Blakemore, 2012; Giedd et al., 1999; Sowell et al., 1999; Tamnes et al., 2017). These neural changes coincide with improvements in higher-level cognitive abilities, such as working memory, attention, and reasoning (Crone et al., 2004; Gur et al., 2012; Kwon et al., 2002; Luca et al., 2003; Luciana et al., 2005; Theodoraki et al., 2020). Cognitive development is unique for every child, such that these abilities improve at different rates for different children (Ayoub & Fischer, 2006). This individual variation is predictive of many important outcomes, including academic success (Best et al., 2011; Morgan et al., 2019; Rohde & Thompson, 2007; Zaboski et al., 2018), health (Brown & Landgraf, 2010; Reimann et al., 2020; Stautz et al., 2016), and well-being (Luerssen & Ayduk, 2017; Nieto et al., 2020; Stern et al., 2017, 2017). Zelazo (2004) has proposed that while different cognitive systems develop, the conscious experiences of children and adolescents also become more elaborate. If cognitive development is associated with more complex conscious experiences, do individual differences in cognitive abilities influence how children experience their world?

Investigating individual differences in conscious experiences is a challenge, as many of the measures currently available do not reflect how children and adolescents process complex information within the real world. Naturalistic stimuli, such as movies, offer a potentially powerful way to characterize the relationship between individual differences in cognitive development and shared experiences. Movie watching has many parallels to real-world experiences; for instance, both require the integration of perceptual and cognitive systems to make sense of complex information that changes across time.
When individuals watch the same movie, their brains become highly synchronized (as measured by inter-subject correlation, or ISC) with each other (Hasson, Landesman, et al., 2008). Previous work has shown that movies with a narrative lead to greater ISC across the entire brain compared to video clips without a plot (Hasson, Landesman, et al., 2008) and synchrony across participants is absent when they are at rest (Simony et al., 2016). The degree of ISC in adults is predictive of individual differences in emotional processing (Guo et al., 2015), theory of mind (Richardson et al., 2018), memory (Baldassano et al., 2017; Chen et al., 2017; Meshulam et al., 2021). Neural synchrony has also been used to assess conscious awareness in clinical populations (Laforge et al., 2020; Naci et al., 2014). These findings have led some to propose that neural synchrony is a measure of shared experiences, particularly when occurring in the frontoparietal and default mode networks (Naci et al., 2014; Nummenmaa et al., 2018; Zadbood et al., 2017).

The frontoparietal network, which is composed of regions in the lateral PFC and intraparietal sulcus, (Cui et al., 2020; Dosenbach et al., 2006; Marek & Dosenbach, 2018; Yeo et al., 2011), is associated with executive processes including working memory, cognitive flexibility, and reasoning (Burzynska et al., 2011; Peters et al., 2016; Satterthwaite et al., 2013; Wendelken et al., 2017). Previous work has shown that synchrony in the frontoparietal network is associated with the degree of suspense and the executive demands of the movie (Naci et al., 2014), and disappears during sedation (Naci et al., 2018). The default mode network includes regions in the medial prefrontal cortex, posterior cingulate cortex, and inferior parietal cortices (Yeo et al., 2011; Yeshurun et al., 2021), and is associated with cognitive processes involving task switching, autobiographical memory, theory of mind, and thinking about the future (Crittenden et al., 2015; Mars et al., 2012; Philippi et al., 2015; Smith et al., 2018; Xu et al., 2016; Yeshurun et al., 2021). Regions within the default mode network show significantly more synchrony when participants are listening to an intact version of a story compared to a scrambled version (Simony et al., 2016), and greater ISC in this network is predictive of how well the movie is later remembered (Chen et al., 2017; Nguyen et al., 2019, 2019; Zadbood et al., 2017). Yeshurun et al. (2017) experimentally manipulated how participants interpreted a narrative they were listening to by priming them to believe they
were listening to a story about either a cheating wife or a jealous husband. Participants across the two groups did not differ in the degree of synchrony in the auditory cortex. However, despite listening to an identical story, those with a different interpretation of the narrative did not synchronize to each other in the default mode network.

There is also natural variability in how much participants synchronize to each other while processing the same narrative, even when they have not been primed to interpret the story differently (Gruskin et al., 2020; Hasson & Honey, 2012; Meshulam et al., 2021; Moraczewski et al., 2018; Salmi et al., 2013). That is, some individuals show more synchrony, while others show less. Since participants are processing the same stimuli, these differences are not likely due to the properties of the narrative or movie. Why some people in a group synchronize more than others is still an outstanding question (Hasson & Honey, 2012).

Given the cognitive processes that are required to follow the plot of a film, differences in intellectual abilities may be a significant factor in predicting the degree of neural synchrony between individuals watching the same movie. Moreover, this relationship may be stronger during different developmental stages. For instance, as children’s cognitive abilities mature, those with more similar capacities may have more similar experiences of their environment. In support of this idea, Cantlon & Li (2013) found that the degree of synchrony between individual children to a group of adults in response to educational movie clips predicted academic abilities in each child. However, this is one of only a few studies examining neural synchrony in children, and most have focused on the degree to which a child’s brain synchronizes with a group of adults processing the same narrative, a measure known as neural maturity. While neural maturity has been found to correlate with brain development, social cognition, and academic scores (Cantlon & Li, 2013; Moraczewski et al., 2018; Richardson, 2019; Richardson et al., 2018), this may be a biased measure of shared processing. First, the perspectives, abilities, and preferences often differ qualitatively between children and adults (Carey, 1985; Chandler & Helm, 1984; Goldberg & Thompson-Schill, 2009; Gopnik et al., 2004; Jonauskaite et al., 2019; Luca et al., 2003; Salles et al., 2016), which likely influences how one’s brain responds to complex narratives. Second, previous work
has shown that children who have more ‘adult-like’ brains, thought to be due to accelerated development, are more likely to have experienced adverse childhood events and tend to have poorer cognitive abilities (Callaghan & Tottenham, 2016; Ellis et al., 2022; Shaw et al., 2006; Tooley et al., 2021). Calculating ISC between similarly aged participants may be a more appropriate measure of shared experiences, but how synchrony within children and adolescents is related to cognitive abilities has yet to be investigated. For instance, higher synchrony in the default mode and frontoparietal networks in adults has been shown to be associated with a similar understanding a narrative, however, whether children synchronize with each other in these networks has yet to be explored. It is possible that the patterns of synchrony in these networks differ in children compared to adults, given the structural and functional changes that occur in these regions across development (Baker et al., 2015; Baum et al., 2020; Power et al., 2010; Uddin et al., 2011).

The current study investigated whether the degree of neural synchrony during movie watching in children aged 7 to 15 related to individual differences in cognitive performance, as measured by IQ. Specifically, a data-driven approach was used to examine if participants with different scores on the Weschler’s Intelligence Scale for Children (WISC) differ in their degree of inter-subject correlations during movie watching. On the basis of the existing literature, it was predicted that participants with higher scores on the WISC would have greater neural synchrony in brain networks associated with plot following, including the frontoparietal network (Naci et al., 2014) and the default mode network (Chen et al., 2017; Nguyen et al., 2019, 2019; Zadbood et al., 2017).

3.2 Methods

3.2.1 Participants

From the Healthy Brain Biobank database (described in Chapter 1 and in Alexander et al., 2017), participants were included in the current analysis if they were between the ages of 7 and 15 and both anatomical and movie fMRI data had been successfully acquired. Everyone included in the current study had written consent
obtained from their legal guardians and written assent obtained from the participant. Participants were not excluded based on their handedness or if they had any diagnoses. All participants included in this study had completed the Weschler Intelligence Scale for Children (WISC; Wechsler, 2014), and were excluded if their full-scale IQ score was less than 70. Participants (N = 301) were also excluded because of failed registration, excessive motion, or if 25% or more of the data contained large ‘spikes’ (significant fluctuations in signal intensity).

Participants included in the final sample (N = 309, see Table 3.1 for participant demographics) were grouped into two age cohorts (Children and Adolescents) and four IQ bins (Highest, Middle High, Middle Low, and Lowest). Figure 3.1 displays the distribution of ages and IQ scores. To assess the relationship between ISC and IQ within similarly aged children and adolescents, participants were split (using a median split of their ages) into two equal sized aged groups. Participants in the children group (N = 155) were below the age of 11.2 years, participants in the adolescent group (N = 154) were above the age of 11.2 years. The IQ bins were created using an inter-quartile split of the IQ data, creating a Lowest, Middle Low, Middle High, and Highest IQ group for each age cohort, which ensured equal sample sizes in each group. Based on a chi-square test of independence run separately for the age cohorts, the IQ groups did not differ significantly in the number of participants with anxiety/mood disorders, autism, or ADHD (all uncorrected p > .30), except for the adolescent Middle High IQ group (N = 1) who had significantly fewer autistic participants compared to the adolescent Lowest IQ group (N = 11, p = .005). The Lowest IQ group in either age cohort did not statistically differ significantly from any other groups in the number of autistic participants (N ranged from 5 to 8). The Lowest IQ groups in both age cohorts had significantly more participants with learning disabilities (N = 17 in both age cohorts) compared to the three other IQ groups (p < .001, N range from 5 to 9).
Table 3.1. Summary of participant demographics.

<table>
<thead>
<tr>
<th>Group</th>
<th>N</th>
<th>Mean Age (SD)</th>
<th>Mean IQ (SD)</th>
<th>% Female</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Children</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Lowest IQ</td>
<td>39</td>
<td>9.5 (1.3)</td>
<td>81.8 (5.8)</td>
<td>28.2%</td>
</tr>
<tr>
<td>Middle Low IQ</td>
<td>39</td>
<td>9.2 (1.3)</td>
<td>96.5 (2.9)</td>
<td>33.3%</td>
</tr>
<tr>
<td>Middle High IQ</td>
<td>39</td>
<td>9.2 (1.2)</td>
<td>106.9 (2.8)</td>
<td>46.2%</td>
</tr>
<tr>
<td>Highest IQ</td>
<td>38</td>
<td>8.9 (1.2)</td>
<td>121.4 (8.0)</td>
<td>47.4%</td>
</tr>
<tr>
<td><strong>Adolescents</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Lowest IQ</td>
<td>39</td>
<td>13.7 (1.4)</td>
<td>79.2 (4.5)</td>
<td>33.3%</td>
</tr>
<tr>
<td>Middle Low IQ</td>
<td>39</td>
<td>13.2 (1.5)</td>
<td>92.1 (3.6)</td>
<td>30.8%</td>
</tr>
<tr>
<td>Middle High IQ</td>
<td>38</td>
<td>13.6 (1.3)</td>
<td>103.1 (3.6)</td>
<td>34.2%</td>
</tr>
<tr>
<td>Highest IQ</td>
<td>38</td>
<td>13.6 (1.3)</td>
<td>120.5 (8.2)</td>
<td>34.2%</td>
</tr>
</tbody>
</table>

Figure 3.1. Histogram displaying the distribution of a) age cohorts and b) IQ scores across the four groups.

3.2.2 MRI Pre-processing

Functional and structural scans were co-registered and normalized to the Montreal Neurological Institute (MNI) template. Pre-processing of functional data included motion
correction (using six motion parameters: left/right, anterior/posterior, superior/inferior, chin up/down, top of head left/right, nose left/right). Functional data were then spatially smoothed using a Gaussian filter (8 mm kernel), and low-frequency noise (e.g., drift) was removed by high-pass filtering with a threshold of 1/128 Hz. The data were denoised using Bandpass filter regressors, with cerebrospinal fluid, white matter signals, motion parameters, their lag-3 2nd-order volterra expansion (Friston et al., 2000), and "spikes" (based on mean signal variance across volumes) as nuisance regressors.

3.2.3 Exploratory whole brain inter-subject correlation analysis

The degree of inter-subject correlation across the whole brain was calculated using a leave-one-out approach, and this analysis was conducted separately for each group. That is, the pre-processed time course of every voxel was correlated (Pearson and then Fisher z-transformed) between each participant and the mean time course of every voxel from the rest of the group (N-1). A grey matter mask was used to extract r values within grey matter. One-sample t-tests were calculated on the resulting individual brain-wide correlation values. Multiple comparisons were corrected with a false discovery rate (FDR) of 0.05 to generate group maps of significantly correlated voxels. To identify where in the brain inter-subject correlation differences existed between the IQ groups, t-tests were performed across the different groups on the correlation values at each voxel derived for all the individuals within each group (FDR corrected).

3.2.4 Network-based inter-subject correlation analysis

The degree of synchronization was computed within seven previously defined functional networks based on the Yeo et al. (2011) parcellation. Hypothesis driven analyses focused on the frontoparietal and default mode networks, however, five additional networks (Visual, Dorsal Attention, Ventral Attention, Somatomotor, Limbic) were included as exploratory analyses. The intra-group inter-subject correlation (ISC) for each of these seven networks was calculated using a leave-one-out approach. Specifically, the time course of each network (based on the average time course of each voxel within the network) for each participant was correlated with the average time course of each network for the remaining participants in the group, minus that participant
(N-1). Finally, using the rstatix package in R (Kassambara, 2020), a mixed model ANOVA was conducted to determine if group membership was a significant predictor of intra-group synchronization across the two networks of interest, as well as the five exploratory networks. This was done separately for both age cohorts. The model included ISC values as the predicted variable and group (a between subject factor) and network (a within subject factor) as the predictor variables. The networks that showed a significant effect of group were followed up with Welch t-tests (all results were FDR corrected to 0.05).

3.2.5 Cluster-based inter-subject correlation analysis

To ensure the method of grouping participants did not bias the results of the current study, pairwise correlations were calculated in the default mode and frontoparietal networks. This was done by calculating the mean time course (i.e. by averaging across all voxels) separately in both networks for each participant, and then correlating it with every other participant’s mean time course. Finally, a k-means clustering analysis was conducted to determine whether groups of participants could be identified based solely on the degree of neural synchronization, and whether cluster-based group membership was associated with differences in cognitive abilities. The MATLAB function evalclusters was used to identify the optimal number of clusters based on the variance in the data using the Calinski-Harabasz Index, computed over 1000 iterations to minimize the fitting parameter. Based on the groupings generated from this cluster analysis, a logistic regression analysis was computed to investigate which factors, if any, (i.e. age, full scale IQ, and scores on the five subscales of the WISC) significantly predicted the cluster-generated groupings.

3.3 Results

3.3.1 Whole brain ISC

All age cohorts (Child and Adolescent) and IQ groups (Highest, Middle High, Middle Low, Lowest) showed significant synchrony across the entire cortex (see Figure 3.2), including much of the visual and auditory cortex, as well as associative regions of the brain. Despite finding widespread synchrony across the brain for each group, it is
unclear whether groups differed in the degree of synchrony. To address this, whole brain contrasts were conducted separately for the child and adolescent cohort. First, this analysis revealed that no other IQ group had greater synchrony in any voxels compared to the Highest IQ group. Second, no significant differences were observed across any of the group contrasts for the child cohort, except for the contrast between the Lowest IQ and the Highest IQ groups. This contrast revealed the Highest IQ group had significantly greater ISC in a few small clusters in the right supplementary motor area, supramarginal gyrus, and posterior cingulate, as well as the bilateral paracentral lobule and left superior frontal cortex compared to the Lowest IQ group. For the adolescent cohort, the Highest IQ group had significantly greater synchrony compared to all three other IQ groups. In particular, the Highest IQ group had significantly greater ISC in regions of the bilateral paracentral lobule, precuneus, insula, superior frontal cortex, inferior frontal cortex, and cingulate compared to the Lowest IQ group, and showed greater synchrony compared to the Middle Low and Middle High groups in regions of the superior frontal cortex, temporal cortex, and cingulate.
Figure 3.2 Whole brain spatial maps with significant intra-group ISC displayed for (a) the child and (b) adolescent cohorts.

All age cohorts and IQ groups had significant synchrony in sensory and associative regions of the brain. Whole brain ISC contrasts were conducted to investigate group differences (FDR corrected for multiple comparisons). ISC contrasts for the child cohort between the Highest and Lowest IQ groups are displayed in c). The Highest IQ group in the child cohort showed a few small clusters in the right supplementary motor area, supramarginal gyrus, posterior cingulate, and the bilateral paracentral lobule, and the left superior frontal cortex that had significantly greater synchrony compared to the Lowest IQ group, with no regions showing greater synchrony in the Lowest IQ group. The Highest, Middle Low, Middle High IQ groups had no voxels with significantly different ISC. ISC contrasts for the adolescent cohort comparing the Highest and Lowest IQ groups are displayed in d). The Highest IQ group in the adolescent cohort had significantly greater ISC in regions of the bilateral paracentral lobule, precuneus, insula, superior frontal cortex, inferior frontal cortex, and cingulate compared to the lowest IQ group, with no regions showing greater synchrony in the Lowest IQ group. The Highest IQ group also showed greater
synchrony compared to the Middle Low and Middle High groups in regions of the superior frontal cortex, temporal cortex, and cingulate (not shown here), and no voxels showed significantly more synchrony in the Middle Low and Middle High groups compared to the Highest group.

3.3.2 Network based ISC

A mixed effects ANOVA was conducted on both age cohorts separately. ISC values were normally distributed (assessed using Shapiro’s test, p-values ranged from .17 to .72), except for in the dorsal attention network for the child cohort (p = .007) and adolescent cohort (p = .04), and the limbic network for the adolescent cohort (p = .025). There were no significant deviations in the assumption of equal variances in ISC values across groups (assessed using Levene’s test, p-values ranged from .12 to .99). The Greenhouse-Geisser sphericity correction was applied to correct for violations in sphericity. In the child cohort, there was no main effect of group (F(3,151) = 1.6, p = .19), but there was a main effect of network (F(4,444,8) = 181.3, p < .001) and a significant interaction between group and network (F(13,444,8) = 1.9, p = .02). This significant interaction suggested that the pattern of group differences in ISC values differed across the seven networks. When each network was investigated separately, only the somatomotor network showed a significant group effect (F(3,151) = 5.7, p(adj) = .007, see Table 3.2). Post-hoc comparisons indicated that children in the Lowest IQ group had significantly less ISC compared to the Middle Low (t(74.5) = 2.94, p = .009), Middle High (t(69.0) = 3.21, p = .006) and Highest IQ group (t(63.8) = 3.90, p = .001).

The adolescent cohort showed a main effect of group (F(3,150) = 5.0, p = .002), a main effect of network (F(3.8,575.9) = 144.5, p < .001), but no significant interaction between group and network (F(11.5,575.9) = 1.3, p = .22). These results suggested that the groups differed significantly in their degree of ISC, but that the pattern of group differences was not significantly different across the seven networks. When each network was investigated separately, all but the dorsal attention and limbic networks showed a significant group effect (see Table 3.2 for statistics for each network). Post-hoc comparisons indicated that for the networks that showed a significant group effect, the Highest IQ group had greater ISC compared to the Lowest and Middle Low IQ groups, although some of these differences failed to reach significance after multiple comparison correction (uncorrected
p values ranged from .019 to < .001, corrected p values ranged from .056 to .001, see Figure 3.3)

Table 3.2. Results from separate ANOVAs calculated to compare ISC in the four IQ groups across the seven networks.
Uncorrected p-values displayed as p, FDR corrected p-values displayed as \( p_{adj} \).

<table>
<thead>
<tr>
<th>Network</th>
<th>df</th>
<th>F</th>
<th>p</th>
<th>( p_{adj} )</th>
<th>Generalized Eta²</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Child</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Visual</td>
<td>3, 151</td>
<td>2.62</td>
<td>0.053</td>
<td>0.186</td>
<td>0.049</td>
</tr>
<tr>
<td>Somatomotor</td>
<td>3, 151</td>
<td>5.69</td>
<td>0.001</td>
<td>0.007*</td>
<td>0.102</td>
</tr>
<tr>
<td>Dorsal Attention</td>
<td>3, 151</td>
<td>0.13</td>
<td>0.943</td>
<td>0.943</td>
<td>0.003</td>
</tr>
<tr>
<td>Ventral Attention</td>
<td>3, 151</td>
<td>2.10</td>
<td>0.103</td>
<td>0.189</td>
<td>0.040</td>
</tr>
<tr>
<td>Limbic</td>
<td>3, 151</td>
<td>0.17</td>
<td>0.916</td>
<td>0.943</td>
<td>0.003</td>
</tr>
<tr>
<td>Default mode</td>
<td>3, 151</td>
<td>2.06</td>
<td>0.108</td>
<td>0.189</td>
<td>0.039</td>
</tr>
<tr>
<td>Frontoparietal</td>
<td>3, 151</td>
<td>0.46</td>
<td>0.709</td>
<td>0.943</td>
<td>0.009</td>
</tr>
<tr>
<td><strong>Adolescent</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Visual</td>
<td>3, 150</td>
<td>3.13</td>
<td>0.028</td>
<td>0.039*</td>
<td>0.059</td>
</tr>
<tr>
<td>Somatomotor</td>
<td>3, 150</td>
<td>3.69</td>
<td>0.013</td>
<td>0.023*</td>
<td>0.069</td>
</tr>
<tr>
<td>Dorsal Attention</td>
<td>3, 150</td>
<td>2.62</td>
<td>0.053</td>
<td>0.062</td>
<td>0.050</td>
</tr>
<tr>
<td>Ventral Attention</td>
<td>3, 150</td>
<td>4.98</td>
<td>0.003</td>
<td>0.011*</td>
<td>0.091</td>
</tr>
<tr>
<td>Limbic</td>
<td>3, 150</td>
<td>1.01</td>
<td>0.392</td>
<td>0.392</td>
<td>0.020</td>
</tr>
<tr>
<td>Default mode</td>
<td>3, 150</td>
<td>5.95</td>
<td>0.001</td>
<td>0.005*</td>
<td>0.106</td>
</tr>
<tr>
<td>Frontoparietal</td>
<td>3, 150</td>
<td>4.37</td>
<td>0.006</td>
<td>0.014*</td>
<td>0.080</td>
</tr>
</tbody>
</table>
Figure 3.3. Boxplots displaying ISC for each IQ group across every network for the child cohort (displayed in panel a) and the adolescent cohort (displayed in panel b). Reported p-values have been FDR adjusted for multiple comparisons. Middle line represents the median ISC value for each group. The color boxes indicate the interquartile range for each group. Dots indicate outlier ISC values.
3.3.3 Cluster-based inter-subject correlation analysis

To assess the robustness of the intra-group ISC analysis, pairwise inter-subject correlations were calculated between each participant and every other participant in the default mode and frontoparietal network (see Figure 3.4). A k-means clustering analysis indicated that the data best clustered into two groups for both networks: one group with high pairwise correlations and a group with low pairwise correlations (see Table 3.3 for participant demographics of each group). A logistic regression analysis indicated that cluster membership in the default mode network was significantly predicted by IQ scores ($p = .041$), and scores on the visual spatial ($p = .025$), verbal comprehension ($p = .036$), and working memory ($p = .038$) subscales of the WISC. Specifically, those with higher scores were more likely to be part of the high similarity cluster. Age was not a significant predictor of cluster membership in the default mode network. The results of a logistic regression analysis also indicated that cluster membership in the frontoparietal network was significantly predicted by age ($p = .006$), with participants in the high similarity group being slightly younger than participants in the low similarity group. However, cluster membership in the frontoparietal network was not predicted by full scale IQ or any of the WISC subscale scores.

![Figure 3.4](#) Pairwise correlation matrices across all subjects from all age and IQ groups for the default mode and frontoparietal networks.
Table 3.3. Mean age and WISC scores for the high similarity and low similarity clusters.
WMI = Working memory index, VSI = Visuospatial index, VCI = Verbal comprehension index, FRI = Fluid reasoning index, PCI = Processing speed index.

<table>
<thead>
<tr>
<th></th>
<th>Default mode</th>
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<th>Frontoparietal</th>
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<tbody>
<tr>
<td></td>
<td>High</td>
<td>Low</td>
<td>High</td>
</tr>
<tr>
<td>N</td>
<td>Similarity</td>
<td>Similarity</td>
<td>Similarity</td>
</tr>
<tr>
<td>138</td>
<td>171</td>
<td>168</td>
<td>141</td>
</tr>
<tr>
<td>Mean Age (SD)</td>
<td>11.2 (2.4)</td>
<td>11.4 (2.6)</td>
<td>11.0 (2.5)</td>
</tr>
<tr>
<td>Mean IQ (SD)</td>
<td>102 (16)</td>
<td>98 (15)</td>
<td>101 (16)</td>
</tr>
<tr>
<td>Mean WMI (SD)</td>
<td>100 (14)</td>
<td>96 (15)</td>
<td>98 (14)</td>
</tr>
<tr>
<td>Mean VSI (SD)</td>
<td>104 (17)</td>
<td>99 (16)</td>
<td>102 (17)</td>
</tr>
<tr>
<td>Mean VCI (SD)</td>
<td>106 (15)</td>
<td>102 (15)</td>
<td>105 (15)</td>
</tr>
<tr>
<td>Mean FRI (SD)</td>
<td>103 (15)</td>
<td>100 (16)</td>
<td>102 (16)</td>
</tr>
<tr>
<td>Mean PSI (SD)</td>
<td>96 (15)</td>
<td>95 (15)</td>
<td>96 (15)</td>
</tr>
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</table>

3.4 Discussion

The current study found that adolescents (between the ages of 11 and 15) with higher IQ scores showed greater neural synchrony, as measured by inter-subject correlation, compared to those with lower IQ scores. Several of the brain regions that showed this pattern, including the frontoparietal and default mode networks, have previously been found to be associated with following the plot of a movie. For instance, Nguyen et al. (2019) found that adult participants who had a more similar interpretation of a movie had significantly greater synchrony in regions within these two networks. Yeshurun et al. (2017) found that experimentally manipulating an adult participant’s understanding of a narrative led to systematic differences in neural synchrony within these networks. Additionally, Naci et al. (2014) found that synchrony in the frontoparietal network was associated with the executive load of a movie; that is, time points during movies that are the most engaging were also the periods that show the greatest synchrony in this network. Based on this work in adults, the current study’s findings suggest adolescents with higher cognitive scores likely had a more similar experience of the movie compared to those with lower IQs.
However, differences in the degree of neural synchrony between groups of adolescents based on IQ scores were not specific to the default mode and frontoparietal networks. Individuals in the Highest IQ group had significantly greater synchrony in the visual, somatomotor, and ventral attention networks compared to the groups with lower scores. This was an unexpected result, since synchrony in sensory areas has been shown to occur in the absence of plot following (Hasson et al., 2004; Hasson, Landesman, et al., 2008; Honey et al., 2012; Lerner et al., 2011; Naci et al., 2014). However, this is not to suggest synchrony in sensory areas may not be important for plot following. For instance, several studies have found that individual differences in neural synchrony in the premotor cortex, sensorimotor cortices, and frontal eye fields is predictive of comprehension and memory of the narrative being processed (Meshulam et al., 2021; Yeshurun et al., 2017). Given the exploratory and correlational nature of this analysis, it is difficult to explain why these differences are present. Could it be that differences in high-level cognition influence lower-level sensory processing during naturalistic stimuli, or, are sensory processes the necessary foundation on which high-level cognitive abilities are built off of? Future research should investigate the reliability and nature of the potential relationship between neural synchrony in sensory regions and cognitive performance within longitudinal developmental samples.

In contrast to the study’s hypothesis, the pattern observed between adolescents’ IQ scores and neural synchrony in the default mode and frontoparietal networks was not evident in children between the ages of 7 and 11. The only differences in neural synchrony between IQ groups was primarily in the somatomotor network. There are several potential reasons for why the current study failed to find evidence for the hypothesized differences in children. One reason might be that children rely less on high-level cognitive processes when watching movies. It seems unlikely that they were not paying attention however, since significant synchrony across the entire cortex was observed for all four IQ groups in this age cohort in response to the movie. Moreover, the movie in the study, Despicable Me, is a popular movie for children in this age range, and is in fact, part of the highest grossing animated film franchise ever (Jesus, 2017).
Another potential explanation of these null results could be that the parcellation (based on the Yeo et al. (2011) spatial maps) used in this study may not accurately capture these functional networks in children. Children’s brains undergo considerable change throughout development, and the parcellated spatial maps used were based on adult brains at rest, consequently, they may not accurately capture how those networks are parcellated in children. Because of this, the current study’s measure of ISC in the default mode and frontoparietal networks may be computed between brain regions that are functionally distinct, and this may have unintentionally understated the degree to which children’s brains were synchronized during movie-watching.

Alternatively, perhaps the current study did not find that IQ was predictive of neural synchrony in children because the method used to group participants may have masked potential differences. The groups were divided arbitrarily based on an inter-quartile/median split, but IQ scores and age are continuous in nature; is it possible that this was not the best way to investigate the relationship between IQ and ISC?

To explore the robustness of the association between IQ scores and neural synchrony, pairwise correlations were calculated across all subjects. Specifically, the time courses in the default mode and frontoparietal networks for each participant were correlated with every other participant’s time course. This analysis revealed that the data best fit a model with two clusters in both networks: a cluster of high similarity, and a cluster of low similarity. The results of the logistic regression analysis in the default mode network were consistent with the findings from the IQ grouping analysis in adolescents; participants with more similar time courses were more likely to have higher scores on the WISC (on average, approximately 4 IQ points higher), and on the working memory, verbal, and visuospatial subscales. The two default mode clustering groups did not differ significantly in their age. These results suggest that IQ scores are predictive of synchrony in the default mode network, regardless of the age of participants. Specifically, participants with lower IQ scores, as well as verbal, visuospatial, and working memory abilities, have more idiosyncratic neural responses to a movie compared to those with higher IQs.
Previous work has consistently shown that synchrony in the default mode network is dependent on how someone is engaging with and understanding a movie plot (Ames et al., 2015; Chen et al., 2017; Hasson, Landesman, et al., 2008; Hasson, Yang, et al., 2008; Lerner et al., 2011; Nguyen et al., 2019; Yeshurun et al., 2017). The current study’s findings within the default mode network support the idea that having more matured cognitive abilities allows adolescents, and perhaps children, to process the movie in a more similar fashion. Higher cognitive abilities may help participants stitch together different nuances in the plot, which may lead to understanding the movie in a more comparable way. It is plausible that having better working memory, verbal, and visuospatial abilities would make following a movie plot less effortful. Though, a limitation of the current study is that a measure of movie comprehension was not collected, which could have helped tease apart why those with higher IQs have more synchrony in the default mode network.

The results of the clustering analysis in the frontoparietal network revealed that IQ scores were not predictive of clustering group in this network. These results contrast with previous findings within the adolescent cohort, that the Highest IQ group had greater synchrony in the frontoparietal network compared to those with lower scores. One possibility for this conflicting result could be that this effect was subtle in the adolescent group, and therefore was lost when younger participants were included in the analysis.

Conversely, the logistic regression revealed that age was a significant predictor of clustering group in the frontoparietal network. Those in the high similarity cluster were slightly younger, on average by 10 months, than those in the low similarity group. The current sample was skewed towards a slightly younger group (see Figure 3.1), which may explain why the high similarity cluster in the frontoparietal network is younger as well, since similar aged children likely experience a movie in a more similar way. As such, this finding could be an artifact of the movie used in this study; younger children may be more interested in the movie *Despicable Me*, and thus pay more attention when watching the movie. However, the high similarity cluster included 15-year-old participants, the oldest age cohort included in this study, suggesting that this was not the case for all older participants. *Despicable Me* was released in the year 2010, so another possibility could be
that fewer young children may have seen this movie compared to adolescents, leading to greater interest and potentially greater synchrony in those who had not seen the movie. A limitation of the current study was that participants were not asked whether they had seen the movie before, although previous work suggests that familiarity with a stimulus leads to a decrease in neural synchrony (Aly et al., 2018; Dmochowski et al., 2012; Sternin, 2021). Future studies should investigate how neural synchrony changes across development in a longitudinal design, which would be the best way to disentangle cohort effects from developmental changes.

The current study’s sample was highly heterogeneous; participants were not excluded for their handedness or having a DSM diagnosis, and the range in IQ scores was approximately 70 points. Despite this heterogeneity, only two clusters emerged from the pairwise correlations in both networks of interest. Participants in the high similarity cluster had similar patterns of brain activation while watching a movie, whereas those in the low similarity cluster had unique patterns of activation. Although participants in the high similarity cluster in the default mode network were, on average, 4 IQ points higher than the low similarity cluster, the range of IQ scores were nearly identical. Moreover, the range in age was also almost identical (approximately 7 to 15 for both groups). This suggests that in addition to IQ being a significant predictor of neural synchrony in the default mode network, there are other factors that likely predict whether children and adolescents have unique versus similar patterns of brain activation during movie watching. For instance, what explains why a 7-year-old child with an average IQ shows a high degree of similarity in brain activity in the default mode network to a 15-year-old adolescent with a high IQ? Why do two 10-year-old children with similar IQ scores show distinct activation patterns in the default mode network (as is seen in the low similarity cluster)? A logical next step would be to investigate whether these clustering differences are associated with a different interpretation of the naturalistic stimuli; however, this was not possible in the current study because it used existing data that did not contain information about how the participants interpreted the movie.

Overall, the current study found that adolescents with higher IQ scores show greater neural synchrony when watching a movie, compared to those with lower scores.
These differences appeared within the default mode network, suggesting adolescents with more mature cognitive abilities have similar experiences of naturalistic stimuli. This pattern was not found in children when participants were grouped by their age participants, nor was it reliably found within the frontoparietal network, which may suggest children are less reliant on the prefrontal cortex to process movies. To investigate this possibility, future studies should investigate how neural synchrony changes across development, which the current study cannot speak to as it was not longitudinal. Future studies should also expand on how cognitive abilities are quantified. Although IQ scores are often treated as a proxy for general cognitive ability, they are also thought to be biased towards certain groups and influenced by socioeconomic factors (Brinch & Galloway, 2012; Capron & Duyme, 1989; Hanscombe et al., 2012; Marks, 2010; Zoref & Williams, 1980). For instance, differences in access to education, home environment, and adverse life events influence a child’s performance on IQ tests (Brinch & Galloway, 2012; Capron & Duyme, 1989; Clearfield & Niman, 2012; Hanscombe et al., 2012; Kira et al., 2012; Ritchie et al., 2013; Ronfani et al., 2015; Saltzman et al., 2006; van Os et al., 2017). It is possible that similar factors may influence the degree of neural synchrony unrelated to cognitive ability, for example, if children from different socioeconomic backgrounds are exposed to different types of movies and stories in their household. An interesting next step would be to investigate the relationships between naturalistic processing, socioeconomic factors, and cognitive abilities in children and adolescents. Finally, future studies should include objective measures of movie comprehension to link with neural synchrony and cognition. If synchrony in the default mode network is critical to have a similar experience of the movie, including a comprehension measure may explain why some children and adolescents showed a high degree of synchrony in the default mode network, whereas others did not, even among participants with similar ages and cognitive scores. Moreover, investigating the links between differences in IQ scores, neural synchrony, and movie comprehension may help explain why adolescents with higher IQ scores showed greater synchrony in brain regions associated with sensory processing.
4 Investigating differences in functional brain networks during movie watching and resting state in children

4.1 Introduction

To investigate differences in neural synchrony in Chapter 2 and 3 of this thesis, brain networks were parcellated from maps developed on adult resting state data (from the Yeo et al. (2011) network maps). This assumed that the spatial topography of functional brain networks during movie and rest conditions are comparable, and that brain networks in children and adults are similar. However, it is possible that these parcellations may not accurately capture functional networks in children during movie watching. To address this question, the current study sought to compare the brains of children while they were watching a movie and while they were at rest.

The human brain is interconnected by white matter tracts. The physical connection formed by these myelinated axon fibres are the foundation on which different parts of the brain functionally communicate (Babaeeghazvini et al., 2021; Honey et al., 2009; Supekar et al., 2010; Uddin et al., 2011). Brain regions that “work” together to perform tasks show correlated neural activity (known as functional connectivity) and can be grouped to create functional brain networks (Finn et al., 2015; Geerligs et al., 2015; Yeo et al., 2011). However, task completion is not a necessary requirement for brain activity to cluster into distinct functional networks; even brains at rest organize along similar functional networks (Bijsterbosch & Beckmann, 2017; Elliott et al., 2019). While it is a matter of debate as to why the brain inherently contains a functional architecture (Pezzulo et al., 2021), individuals have unique and reliable connectivity profiles, similar to human fingerprints (Finn et al., 2015). These individual differences in functional connectivity patterns are predictive of many behavioral outcomes, such as fluid intelligence scores (Elliott et al., 2019; Finn et al., 2015), theory of mind ability (Spreng & Mar, 2012; Zemánková et al., 2018), and language development (Xiao et al., 2016).

However, the functional architecture of an individual’s brain is not static, in fact, functional connectivity changes across development. As children age, within-network connectivity increases, between-network connectivity decreases (Fair et al., 2009; Power
et al., 2010; Xiao et al., 2016), and the coupling between structural and functional connectivity increases (Baum et al., 2020). These changes are associated with improvements in cognitive abilities across development (Anandakumar et al., 2018; Baum et al., 2017; Emerson & Cantlon, 2012; Finn & Bandettini, 2021; Shah et al., 2016) and are thought to improve the efficiency of mental processes (Baum et al., 2020).

Functional brain networks are often obtained using fMRI when participants are in a ‘resting state’ (i.e., not doing an explicit task). Once the scan is finished, there are several ways to estimate functional brain networks from fMRI data, such as independent components analysis and node-based functional connectivity analyses. Independent components analysis (ICA) is a data-driven method that decomposes the brain into independent components based on correlated signals across voxels. Each resulting independent component includes a timeseries, which reflects changes in signal across time, and a spatial map, which reveals where in the brain this signal is detected (Bijsterbosch & Beckmann, 2017; Calhoun et al., 2008). Importantly, these spatial maps are highly consistent across participants (Bijsterbosch & Beckmann, 2017; Calhoun & Adali, 2012; Yeo et al., 2011). While ICA is a powerful model-free technique to better understand the spatial topography of large-scale brain networks, it generally is not used to investigate connectivity changes between networks. Estimating functional connectivity between parcellated regions allows for more fine-grained analysis of regional connectivity changes (Bijsterbosch & Beckmann, 2017). First, the brain is parcellated into separate brain regions (termed nodes). Second, the activity time course in each node is extracted. Third, the correlation between each node and every other nodes’ time-courses is estimated; this measure of connectivity between two nodes is termed an edge. The magnitude and direction of each edge represents the strength of the connection and whether the connection is correlated or anti-correlated. Once each edge is estimated for each subject, the patterns of connectivity can be compared across participants or across conditions.

There are several challenges to estimating functional brain networks in developmental samples. One of the biggest challenges is that children tend to move more in the scanner when they are asked to do nothing (Vanderwal et al., 2019), which greatly reduces data quality (Power et al., 2012; Satterthwaite et al., 2012). Vanderwal et al.
(2019) found that children moved significantly more in the fMRI scanner during a resting state scan compared to when they watched a video specifically created to obtain neuroimaging data in children called *Inscapes*. This video contains abstract moving shapes without a narrative. Similarly, Greene et al. (2018) found that children moved significantly more during a resting state scan compared to when they watched video clips of cartoons. Based on these findings, it has been proposed that videos and/or movies can be used to reduce motion and increase data quality when obtaining resting state data in younger participants (Vanderwal et al., 2019).

If functional connectivity is estimated while participants are watching a movie compared to when they are at rest, are these brain states comparable? This is important if one wants to compare functional connectivity findings across studies that may have used different paradigms. In fact, studies have previously reported collecting resting state scans even though participants were watching video clips during the scan session (Blankenship et al., 2019; Riggins et al., 2016; Xiao et al., 2016), and others have proposed using movies to investigate resting state networks based on the assumption that they are similar states (Long et al., 2017).

There is evidence that functional connectivity patterns obtained during movie watching and resting state are similar. For instance, Vanderwal et al. (2017) compared functional connectivity patterns in adults during rest, and while they watched *Inscapes* or the movie *Ocean’s Eleven*. Although the two video clips led to stronger within-subject correlations compared to rest, participants’ functional connectivity patterns could be accurately identified (using a classifier) based on their movie and rest scans. This was true even for cross-condition matching (with accuracies between 87% to 97% between the two conditions), which suggests that individual patterns of functional connectivity in movies and rest are highly consistent. Additionally, Kim et al. (2018) found that adults functional connectivity profiles obtained while participants watched short movie clips and while participants were in a resting state were highly correlated ($r = .87$). Similar results have been found in developmental samples. For instance, Vanderwal et al. (2015) found that mean functional connectivity patterns while children watched *Inscapes* versus while they were in a resting state are highly correlated. Similarly, no significant differences in within-network functional connectivity patterns between movie watching
and resting state were found in children using a seed-based hypothesis driven approach (Greene et al., 2018) and a data-driven ICA approach (Emerson et al., 2015). Furthermore, functional connectivity measures obtained during movie scans are similarly predictive of behavior as those obtained during resting state. For instance, functional connectivity obtained while children watched cartoons was correlated with mathematical ability (Emerson & Cantlon, 2012), and attentional and executive function measures (Rohr et al., 2018). These preliminary findings suggest that estimates of functional connectivity during movie watching and rest share many similarities.

Using movies to obtain functional connectivity estimates is a relatively new technique, and much more is known about how brain networks differ during active tasks versus resting state. While functional brain networks during tasks (excluding those using naturalistic stimuli) and resting state show some similarities, they also differ in several important ways. For instance, overall mean connectivity tends to be stronger during rest and weaker during task states (Geerligs et al., 2015). Connectivity patterns across networks also tend to differ, with tasks being associated with both increases and decreases in connectivity across several functional networks (Cole et al., 2014). For instance, the frontoparietal network shows dynamic changes in connectivity to other networks depending on task demands (Cole et al., 2013; Finn et al., 2015; Shi et al., 2018). Functional connectivity during tasks may also heighten individual differences, often leading to better prediction of behavioral outcomes compared to rest (Elliott et al., 2019; Geerligs et al., 2015). Despite these differences, when functional connectivity patterns are compared between different cognitive tasks and resting state, the correlations range from approximately .55 to .93 depending on the task and study (Bolt et al., 2007; Cole et al., 2014; Finn et al., 2015; Geerligs et al., 2015; Shah et al., 2016). These findings suggest that there is a stable intrinsic functional architecture of the brain during active tasks and rest (Cole et al., 2014).

Is processing a movie more similar to being in a resting state, or is it more like performing an explicit task? When participants are asked about what they are doing during a resting state scan, they tend to report spending their time engaged in inner dialogue, imagery, feeling emotions, thinking of or remembering an event, or paying attention to a particular sensory aspect of the environment (Hurlburt et al., 2015).
Together, these processes form the basis of daydreaming (Singer, 1975). Intriguingly, the process of watching a movie has been compared to a dream-like state (Nadaner, 1984).

In many ways, however, daydreaming and watching a movie are not the same thing. For instance, watching movies involves incoming sensory information and an external narrative that the viewer must follow. This is an important distinction and may account for results showing that some features of functional brain networks differ between movies and rest. For instance, Kim et al. (2018) estimated functional connectivity patterns while adults watched short movie clips using an inter-subject functional connectivity analysis (i.e., calculating the correlation between region A’s time course in one group of participants to the time course in region B in a second group of participants), and compared the resulting correlation matrix to functional connectivity obtained during rest. They found that movies were associated with reduced connectivity between the visual network and several other networks, and increased connectivity within the dorsal attention, frontoparietal, and cingulo-operculum networks. Similarly, other studies have found that although functional connectivity patterns in rest compared to movie conditions were highly consistent, several regions showed significant differences, especially in the visual network and the frontoparietal network (Emerson et al., 2015; Greene et al., 2018).

Differences in the functional connectivity profiles of participants' brains while they watch movies compared to when they are at rest may be even greater than the differences found between movie watching and active task completion. For instance, Geerligs et al. (2015) found functional connectivity patterns were more correlated during resting state and a sensorimotor task than during resting state and movie watching in adults. Certainly, movies also differ from resting state in that they lead to a high degree of neural alignment across subjects (Hasson et al., 2004, 2008).

Functional connectivity patterns during a movie, compared to a resting state, may also better predict individual differences in behavioural outcomes. For instance, Finn and Bandettini (2021) found that functional connectivity estimated while adults watched movie clips predicted cognitive performance significantly better than when it was estimated during a resting state scan. It was also found that movies with engaging interpersonal narratives led to better prediction over movies without dialog. The
researchers propose that movies, especially those with an interesting plot, enhance individual differences in functional connections that are associated with behaviour. Moreover, the test-retest reliability of the functional connectivity estimates obtained while adults watch a movie may be greater than during resting state (Shah et al., 2016).

In summary, there are several potential advantages to using movies to investigate brain networks, including that they reduce motion and potentially increase prediction accuracy and reliability of the functional connectivity estimates obtained. Due to these advantages, movie paradigms in fMRI studies are becoming more popular not just to investigate neural synchrony, but also to obtain functional connectivity measures. However, there is still much to learn about the intrinsic functional architecture of children’s brains while they are in a resting state compared to when they are watching a movie. The few studies that have compared brain networks in children using resting state and naturalistic stimuli often use video clips without a plot, or a series of very short clips of cartoons. These studies found the functional connectivity profiles during these video clips compared to resting state were highly similar (Greene et al., 2018; Vanderwal et al., 2015). Based on the findings in adults (Finn & Bandettini, 2021; Vanderwal et al., 2017), videos that involve an engaging plot may be more likely to lead to differences in functional connectivity patterns in children compared to short video clips lacking a plot. Investigating differences in functional brain networks during movie watching compared to at rest in children may help characterize what types of stimuli are best to use when obtaining fMRI data in developmental samples. Moreover, understanding the differences between these two states may help explain why functional connectivity features could be leading to greater prediction of behavioral outcomes during movie watching compared to rest.

The current study explored how spatial network topography, functional connectivity patterns, and neural synchrony differed during movie watching and resting state in children aged 7 to 13. A group-ICA was conducted to estimate subject specific networks when participants were at rest and while they watched a 10-minute clip from the movie Despicable me. These spatial maps were then compared within subjects across the two conditions to assess whether the topography of the networks differed. A node-based approach was used to investigate within and between network functional
connectivity patterns during the movie and rest. Lastly, neural synchrony within each component obtained from the ICA was compared during rest and movie viewing.

4.2 Methods

4.2.1 Participants

The current study used data from the Healthy Brain Biobank (described in Chapter 1). Participants (N = 55) were included in the current analysis if they were between the ages of 7 and 13 and both anatomical and functional MRI data had been successfully acquired. Functional MRI data was collected during a 10-minute clip of Despicable Me and a 5-minute resting state scan. Written consent was obtained from legal guardians and written assent was obtained from each participant included in the current study. Exclusion criteria for this study included any DSM-5 diagnoses, failed registration, excessive motion, or if 25% or more of the data contained large ‘spikes’ (significant fluctuations in signal intensity). Participants were not excluded based on their handedness. The final sample included 20 participants (mean age = 10.4, mean IQ = 105, 7 females).

4.2.2 MRI Pre-processing

Pre-processing of functional data included motion correction (using six motion parameters: left/right, anterior/posterior, superior/inferior, chin up/down, top of head left/right, nose left/right), then functional and structural scans were co-registered and normalized to the Montreal Neurological Institute (MNI) template. Functional data were then spatially smoothed using a Gaussian filter (8 mm kernel), and low-frequency noise (e.g., drift) was removed by high-pass filtering with a threshold of 1/128 Hz. For all other analyses (excluding the ICA), the data was then denoised using Bandpass filter regressors, with cerebrospinal fluid, white matter signals, motion parameters, their lag-3 2nd-order volterra (Friston et al., 2000), and ‘spikes’ (based on mean signal variance across volumes) as nuisance regressors.
4.2.3 Independent component analysis (ICA)

Using the Group ICA of fMRI Toolbox (GIFT), GIG-ICA (Du et al., 2015; Du, Fryer, Fu, et al., 2018; Du, Fryer, Lin, et al., 2018) was applied to the preprocessed fMRI data to estimate each subject’s intrinsic functional networks during rest and movie watching. First, the data was concatenated across all subjects and conditions, and then an ICA with the Infomax algorithm was conducted to estimate group-level independent components. The number of components was set to 30 (Du, Fryer, Lin, et al., 2018). Each group level independent component was Z-scored, with larger positive Z-scores representing voxels with a greater contribution to that component, and negative Z-scores indicating that the timeseries in that voxel is anticorrelated to the timeseries for that component. Each component was visually inspected to identify meaningful networks based on whether the spatial maps were restricted to grey matter and low spectral and amplitude time courses of activity. Components containing motion or noise artefacts were removed. The final set of group level components were used to calculate subject specific components based on a multi-objective functional optimization algorithm. This resulted in spatial maps of Z-scores for each participant in each condition, which were then used to calculate one-sample right-tailed t-tests to create a network mask for the rest and movie-watching conditions separately. To identify differences in the spatial maps of the components associated with the two conditions, paired sample t-tests were conducted between movies and rest on the Z-scores for each voxel within each component map. The resulting p-values were FDE corrected to .05. A significant p-value in a voxel would indicate that Z-scores were significantly higher in one condition over the other.

4.2.4 Node-based functional connectivity

Using the nilearn and scikit-learn package (Abraham et al., 2014; Pedregosa et al., 2011) in Python, the preprocessed fMRI data were parcellated into 264 separate nodes based on the Power Atlas parcellation (Power et al., 2011). The mean activity for each node was calculated separately for each participant and each condition, and a Pearson correlation (fisher z transformed) was taken between all pairs of nodes, resulting in a 264 by 264 functional connectivity (FC) matrix for each subject during the movie and resting
state scans. To get rid of redundant data, the values that were above and right of the diagonal were retained, while all other values were discarded (resulting in a 34,716 x 1 vector). Then, a Pearson correlation was calculated between the mean functional connectivity vector for each condition to compare similarity in the functional connectivity profiles between the two conditions. Lastly, paired sample two-tailed t-tests were conducted to investigate which edges were significantly different during movie and rest. Statistical threshold based on p-values obtained from the t-tests were FDR corrected.

4.2.5 Inter-subject correlation

The degree of inter-subject correlation (ISC) within the spatial maps of each component estimated from the ICA was calculated using a leave-one-out approach within each condition separately. That is, the time course for each component was correlated (Pearson and then Fisher z-transformed) between each participant and the group-wise mean time course from the rest of the group in that condition (N-1). Paired sample two-tailed t-tests were then used to compare the degree of ISC in rest and movies for each component.

4.3 Results

4.3.1 Independent components analysis

Out of the 30 components obtained from the group-ICA, 12 were identified as noise-related components and were excluded. The remaining 18 components (shown in Figure 4.1) were included for the following analyses. Many of the included components resembled intrinsic functional networks obtained in adults during rest. For instance, component 17 was located within regions of the visual cortex, resembling visual networks obtained in other studies (Yeo et al., 2011). Component 5 showed significant overlap within the bilateral superior and middle temporal gyrus, resembling previously obtained auditory networks (Kuiper et al., 2020). Component 1 and 15 involved regions of the medial PFC and cingulate and component 14 showed significant overlap within the precuneus and cingulate. These brain areas are typically seen as part of the default mode.
network (Yeo et al., 2011). Components 11, 12, and 16, encompassed regions of the lateral PFC, overlapping with much of the frontal regions included in Yeo et al.’s (2011) frontoparietal network. Similarly, component 4 included bilateral regions of the dorsolateral PFC and a small cluster in the left intraparietal sulcus.

After estimating the subject and condition specific spatial maps, paired sample t-tests were conducted on the z-scored spatial maps for each of the 18 components to compare rest and movie conditions. Only two of the components showed any voxels with significant differences. Specifically, component 1 had one small cluster (cluster size was 1 voxel, MNI coordinates: -4, 38, 24) in the left anterior cingulate with significantly greater involvement during movie compared to rest. Component 5 showed two small clusters in the left superior temporal gyrus (MNI coordinates of the peak difference in the largest cluster: -54, -14, 6; MNI coordinates of the peak difference in the second largest cluster: -66, -10, -2) and one cluster in the right superior temporal gyrus (cluster size was 1 voxel, MNI coordinates: 60, -6, 2) with significantly more involvement during movie compared to rest.
Figure 4.1. Intrinsic network maps for the 18 components obtained from the ICA for the rest and movie scan separately. Each map was obtained by performing voxel-wise right-tailed one-sample t-tests on the corresponding subject and condition specific spatial maps. Voxels that showed significant z-values in the rest condition are displayed in red, and voxels in blue indicated significant z-values in the movie condition. Purple voxels indicated overlap between the two conditions.
4.3.2 Node-based analysis

To investigate more fine-grained differences in functional connectivity patterns that the ICA may have missed, FC matrices were estimated for the rest and movie conditions based on a parcellation of the brain using the Power Atlas (Power et al., 2011; see Figure 4.2a for functional connectivity matrices). Functional connectivity patterns were highly consistent between movie and rest ($r = .892, p < .001$). Two-tailed paired-sample t-tests revealed that the majority of edges showed no significant differences between rest and movies. After FDR correction, 3.6% of edges showed a significant difference between the two conditions, with almost all significant edges (99.1%) showing greater FC during rest compared to movie watching, predominately between nodes from different networks (see Figure 4.2b). The most common edges to show significant differences included nodes within the visual and sensory/somatomotor regions of the brain (see Figure 4.2b).
Figure 4.2. Functional connectivity matrices estimated for the movie and rest conditions. a) Mean FC matrices for the movie and rest conditions, respectively, based on the Power et al. (2011) parcellation. A Pearson r correlation revealed that the mean FC matrices were highly correlated ($r = .892, p < .001$) between the rest and movie conditions. Colour coding indicates where each region is located in relation to previously defined brain networks. b) Matrices display results from a two-tailed paired-sample t-test conducted on the FC values for each edge. The matrix in the left bottom corner displays the t values for each contrast. Blue cells indicate where the FC values in rest were greater than in the movie condition. Orange cells indicate cells where FC values in movies were greater than in the rest condition. The matrix in the right bottom corner displays which edges (the cells in purple) showed a significant difference between the two conditions after FDR correction. White cells indicate edges that were not significantly different between the two conditions.
4.3.3 Inter-subject correlation

Using the component spatial maps obtained from the ICA, ISC for each participant during their movie and rest scans was calculated and compared between the conditions for all 18 intrinsic networks. There was significantly greater synchrony during movies, compared to rest, in all components except for component 16 (see Table 4.1). This component included regions of the left and right anterior and dorsolateral prefrontal cortex (PFC). Five of the six components (component 1, 11, 12, 15, 16) with the lowest mean ISC during movie watching were comprised of regions of the lateral and medial PFC (see Figure 4.3). Component 3, which had the third lowest overall mean ISC during movie watching, encompassed regions in the left intraparietal sulcus and angular gyrus. The bottom six components all had significantly less synchrony compared to component 6, which had the seventh lowest mean ISC value (paired sample t values ranged from 10.3 to 14.3, all p-values < .001).

The components with the greatest neural synchrony predominately encompassed sensory regions, including components resembling an auditory network (component 5) and visual networks (component 9 and 17), and components comprised of sensorimotor regions (component 8, 10, and 18). Component 2, which had the greatest mean ISC during the movie condition, predominately encompassed regions of the left and right supramarginal gyrus. Component 13, which had the second greatest mean ISC, included regions of the precuneus and angular gyrus. Component 14, which covered regions of the precuneus and posterior cingulate cortex, was the 7th network with the greatest mean ISC during movie watching. These top 7 components showed significantly greater synchrony compared to component 6 (paired sample t values ranged from 11.0 to 23.5, all p-values < .001), and compared to the ten components with the lowest mean ISC values (components 9, 17, 4, 6, 1, 11, 12, 3, 15, 16).
Table 4.1. Results from paired sample t-tests comparing neural synchrony during the rest and movie conditions in the 18 intrinsic functional networks obtained from the ICA. P values were FDR corrected across all contrasts, displayed under the \( p \) adj column.

<table>
<thead>
<tr>
<th>Component</th>
<th>df</th>
<th>( t )</th>
<th>( p )</th>
<th>( p ) adj</th>
<th>Cohen’s d</th>
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<tr>
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</tr>
<tr>
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</tr>
<tr>
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<td>&lt;0.001*</td>
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<tr>
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</tr>
<tr>
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<tr>
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<tr>
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<td>&lt;0.001*</td>
<td>4.55</td>
</tr>
</tbody>
</table>
Figure 4.3. **Mean ISC calculated for each component for the movie and rest conditions.** All components showed significantly greater synchrony during movie compared to rest except for component 16. Components on the x-axis are ordered based on greatest to lowest mean ISC during the movie scan. Error bars indicate standard deviations.

### 4.4 Discussion

Finn (2021) recently asserted that ‘it is time to put rest to rest’ because brain activity during movie paradigms predicts behaviour better than during resting state scans. To better characterize differences and similarities in the developing brain in these two states, the current study compared functional brain networks in a group of children between the ages of 7 and 13 while they watched a movie and while they were in a resting state. Specifically, the current study investigated whether the spatial topography, connectivity patterns, and neural synchrony in functional brain networks differed between these two conditions. These analyses revealed many similarities, but also several
differences, in the brains of children while they watched movies compared to when they were at rest.

The results of the ICA revealed that the rest and movie conditions had nearly indistinguishable network-level spatial topographies. Out of the 18 components investigated, only two showed statistically significant differences between the two conditions. Specifically, component 1 overlapped with regions of the medial PFC and cingulate and showed one voxel that had greater co-activation during movie compared to rest. Component 5 was composed of regions of the bilateral superior and middle temporal gyrus, and had three small clusters in the left and right superior temporal gyrus that showed significantly more involvement during movie watching compared to rest. Movies have been proposed as a method to obtain resting state data in developmental samples to prevent motion, with some studies suggesting resting state and movie watching are comparable enough states to claim they are the same (Blankenship et al., 2019; Long et al., 2017; Riggins et al., 2016; Xiao et al., 2016). The ICA results from the current study suggest spatial topography of functional brain networks do not differ substantially during rest and movies in a developmental sample, supporting the use of resting-state data to parcellate the brain when investigating network differences in children watching movies.

Although the spatial topographies of networks obtained from the ICA were highly consistent between the two conditions, it is possible that children’s brains differ in the degree of between network connectivity during movie watching and rest. To investigate whether patterns of functional connectivity across networks differed between rest and movies, a node-based analysis approach was used. This approach allowed for more fine-grained analysis of inter-regional connectivity changes (Bijsterbosch & Beckmann, 2017). The current study found that patterns of functional connectivity were highly correlated between the two conditions, and the majority of edges (connections between nodes) did not differ significantly. Interestingly, of the edges that did differ, most were connections involving visual and sensory/somatomotor regions, and almost all had greater connectivity strength in the resting state compared to the movie condition. This result is consistent with findings in adult samples comparing rest and movie states (Emerson & Cantlon, 2012; Greene et al., 2018; Kim et al., 2018), including Geerligs et al. (2015), who found that overall mean functional connectivity was stronger during rest
and weaker during tasks. The results from the node-based analysis suggest that although functional connectivity patterns are similar when a child watches a movie compared to when they are in a resting state, there are several differences that may be driven by sensory aspects of the film.

Given that the current study found very few differences in functional connectivity patterns between movie watching and resting state, what could be driving the finding that FC measures during movie watching lead to better prediction accuracy compared to during rest? It is possible that idiosyncratic patterns of differences appear on the individual level, while the current study compared group-level differences between movie watching and resting state. It is also possible that the few differences observed between the two conditions in the current study, in particular connections involving visual and sensorimotor areas, may be the edges that lead to better prediction of behavioural outcomes. A final possibility is that the differences between movie-watching and resting state grow larger as children age, as Finn & Bandettini (2021) compared the prediction accuracy of FC during movie and resting states in an adult sample and the current study was conducted in children. Future work could investigate these possibilities by measuring how individual differences in FC patterns during movie watching and resting state change across development.

Although the current study found that functional brain networks in children are highly comparable during movie watching and rest, there is one measure that should differ substantially during these two conditions: neural synchrony. Previous work has consistently found that during movie watching, the brains of different individuals become highly correlated, which is not the case during rest (Hasson et al., 2004, 2008; Naci et al., 2014, 2018). This pattern of results was also true in the current study; almost every component showed significant synchrony during the movie condition, and minimal to no synchrony during resting state.

Only one component (component 16) did not differ significantly in the degree of ISC during the two conditions. This component included regions of the anterior and dorsolateral PFC. This result is surprising, since research done in adults shows that synchrony in the lateral prefrontal cortex during movie watching is greater than during resting state and is associated with plot following (Naci et al., 2018, 2018; Nguyen et al.,
Could this mean that the current study’s participants are not paying attention to the plot? It is likely that many participants in the current study were watching, as this *Despicable Me* is a highly popular movie for children (Jesus, 2017). Additionally, participants showed significant synchrony in other regions shown to be dependent on plot following. For example, components 13 and 14, which showed a high degree of ISC during the movie condition, overlapped with several regions that have been shown to be especially dependent on plot comprehension, including the precuneus and posterior cingulate (Ames et al., 2015; Lahnakoski et al., 2014; Nguyen et al., 2019).

Another possibility for why component 16 did not differ significantly in ISC during the rest and movie conditions could be that children do not rely on the dorsolateral PFC as much as adults to process naturalistic stimuli. In support of this, five other components that were made up of regions of the PFC showed significantly less synchrony compared to all other components investigated in this analysis except one. Development is associated with substantial changes to the function and structure of brain networks, especially in the frontoparietal network (Baum et al., 2017; DeSerisy et al., 2021; Power et al., 2010). Moreover, late childhood and early adolescence is associated with a process termed ‘frontalization’, which is when the PFC becomes increasingly involved in executive functions as developing brains mature (Baker et al., 2015; Lewis and Todd, 2007). Is it possible that the minimal synchrony observed during movie watching in these frontal components is because children are less reliant on the PFC to process movies?

One way to assess the hypothesis that children are less reliant on the PFC to process naturalistic stimuli would be to correlate the degree of synchrony during movie watching within the PFC with a measure of narrative comprehension across different developmental periods. If it is true that children are less reliant on the PFC when processing movies, there would likely not be a significant correlation between synchrony in this brain area and the measure of comprehension. As adolescents become more reliant on the PFC to process movies, the correlation between synchrony and comprehension would likely increase. A limitation of the current study is that it did not have a measure of movie comprehension.
In summary, the current study found functional connectivity patterns during movie watching and rest in children were highly consistent. Regions that did show significant changing FC patterns during these two conditions were mostly between different functional networks. Almost all of the edges that showed a significant difference had greater functional connectivity during the rest compared to the movie condition. The one measure that did differ substantially between the two conditions was neural synchrony; children showed significantly more neural synchrony during movie watching compared to rest in almost all networks measured, except for a network that was comprised of the anterior and dorsolateral PFC. Moreover, several other networks that included the PFC showed minimal synchrony during movie watching compared to most other components included in this analysis. This could suggest that children may be less reliant on the PFC when processing complex naturalistic stimuli compared to adults, though much more work is needed to better understand the nature of this finding.
5  Discussion

5.1  Summary and Key Findings

The developmental period between late childhood to early adulthood is marked by significant improvements in social and cognitive abilities (Blakemore et al., 2007; Davidson et al., 2006; Dumontheil, 2014; Luna et al., 2004). These systems are interconnected (Breiner et al., 2018; Carlson et al., 2004; Hughes, 1998; Marcovitch et al., 2015; Vetter et al., 2013), and may follow similar developmental trajectories (Blakemore & Mills, 2014; Larsen & Luna, 2018). However, social-cognitive development is frequently studied by looking at different abilities in isolation, even though real-world experiences often involve the ongoing integration of numerous mental processes. For instance, when a child is sitting in their Mathematics class, they are making sense of the visual, auditory, and tactile information within their environment. They may be focusing their attention on what their teaching is saying while reasoning through how to solve the problem being presented on the chalkboard, storing the relevant information in memory, and ignoring potential distractions in the environment. This student may also be feeling an emotion, perhaps anxiety or excitement. Their friend sitting next to them may be focusing on the same information, and may be having a similar experience of the classroom environment. Other students in this class may be having a different experience; they may be focused on the students playing outside the classroom window, or daydreaming about what they will do once school is over. Why some children experience events more or less similarly than others remains poorly understood. The primary focus of my thesis was to better understand how social and cognitive abilities support children’s processing of naturalistic events.

Cognitive development is a dynamic and complex process that is unique to every child (Blakemore, 2008; Foulkes & Blakemore, 2018). Late childhood and adolescence are associated with substantial improvements in higher-level abilities, including social cognition, executive functioning, and reasoning (Anderson et al., 2001; Burnett et al., 2009; Chapman et al., 2011; Davidson et al., 2006; Dumontheil et al., 2010; Dumontheil Iroise et al., 2010; Theodoraki et al., 2020). As children mature, they process information at a deeper level and their conscious experiences likely become richer and more elaborate
Differences in these abilities have the potential to influence how a child processes real-world experiences. In this thesis, I investigated this possibility by characterizing neural responses during naturalistic processing and resting state in children and adolescents who differed in their general cognitive ability and autistic traits.

In Chapter 2, I examined whether autism and autistic traits were associated with the degree of neural synchrony children showed while watching a movie. I found that autistic children showed less similar brain activation patterns with each other, as measured by inter-subject correlation, compared to those without autism in the social brain, a network that has previously been shown to be associated with theory of mind tasks and narrative processing (Blakemore, 2008; Byrge et al., 2015; Fletcher et al., 1995; Paunov et al., 2021; Richardson et al., 2018; Saxe & Kanwisher, 2003). These results suggest that autistic children have more distinct experiences when watching a movie that involves complex social interactions like Despicable Me. However, autistic children did not show significantly less neural synchrony compared to those without autism in the frontoparietal network, a region previously shown to be associated with executive functions and plot following (Burzynska et al., 2011; Naci et al., 2014, 2018; Nguyen et al., 2019; Spreng et al., 2010). Moreover, children who did not have a diagnosis of autism, but who differed in their degree of autistic traits, showed a similar amount of neural synchrony in the theory of mind and frontoparietal networks. Although autistic traits are present in children on a continuum (Abu-Akel et al., 2019; Bölte et al., 2011; Mandy et al., 2018; Robertson & Simmons, 2013; Robinson et al., 2011), these results suggest that these traits in children who do not have autism are not associated with significant differences in shared experiences of naturalistic stimuli.

In Chapter 3, I investigated if general cognitive abilities were associated with differences in neural synchrony in children and adolescence. I found that adolescents between the ages of 11 to 15 with higher intellectual scores synchronized more with each other within the default mode network, as well as several other regions across the brain, compared to those with lower cognitive scores. However, I did not find the same pattern of results in younger children. Instead I found that in a group of 7 to 11 year olds, those with higher cognitive scores did not show greater synchrony compared to those with
lower scores in regions associated with plot following. These results suggest that adolescents with more mature cognitive abilities have a more similar experience during movie watching, and perhaps, younger children may be less reliant on higher-level cognitive abilities to process the complexities of the plot.

Contrary to my prediction, I did not find that neural synchrony in the frontoparietal network was associated with differences in cognitive and social abilities in children. Furthermore, the group of participants who showed more similar patterns of brain activation (based on the clustering analysis) in the frontoparietal network did not significantly differ in the number of autistic participants (Chapter 2) nor in their WISC scores (Chapter 3) compared to those who did not have similar activity in this network. Even within the participants who clustered together, pairwise inter-subject correlations tended to be lower in the frontoparietal network compared to the default mode and theory of mind networks.

There are several potential reasons for why I did not find a relationship between autism/IQ scores and neural synchrony in the frontoparietal network in children. One potential reason could be due to the fact that this network continues to mature into adolescence (Baker et al., 2015; Baum et al., 2017; Chai et al., 2017; Cui et al., 2020; DeSerisy et al., 2021; Wierenga et al., 2018), and the network parcellations used in Chapters 2 and 3 are based on adult resting-state data (Yeo et al., 2011). This led to an important question: could the lack of significant differences within the frontoparietal network be related to the use of these parcellations?

In Chapter 4, I compared functional brain networks when children were at rest and while they watched the film Despicable Me. The results from this study suggested that children’s brain networks during movie watching and resting state have a similar functional architecture, although a small number of between-network connections showed stronger functional connectivity during rest. When inter-subject correlations were calculated based on the spatial components obtained from the ICA, I found that movies elicited significant neural synchrony in almost all of the networks, whereas there was little to no neural synchrony in any of the networks while at rest. More neural synchrony
During movie watching relative to rest in much of the cortex is consistent with what has been shown in adult populations (Hasson et al., 2009; Naci et al., 2014; Nguyen et al., 2019). However, compared to similar work in adult populations, my results differ in which brain regions were least synchronized during movie watching. I found the networks that had very little neural synchrony in this sample of children during movie watching overlapped with the lateral and medial PFC. When adults are processing a narrative, these prefrontal regions tend to be highly synchronized across participants (Baldassano et al., 2018; Hasson et al., 2010; Hasson, Furman, et al., 2008; Lerner et al., 2011; Naci et al., 2014, 2018). The results from Chapter 4 may suggest that children are less reliant on the prefrontal cortex when processing naturalistic stimuli compared to adults.

In Chapters 2 and 3, I found that brain activation patterns across participants in three networks of interest showed a reliable pattern: some participants had similar brain activity during movie watching, while other participants’ brain activity did not correlate highly with other participants. An exploratory analysis revealed that different variables predicted whether participants would show similar or dissimilar activity patterns in each network of interest; specifically, autism diagnosis for the theory of mind network, cognitive scores for the default mode network, and age for the frontoparietal network. Although these factors significantly predicted which pattern of inter-subject correlation a participant showed, there was also a lot of heterogeneity within the groups that had highly correlated activity. For instance, the high similarity cluster in the theory of mind network included six autistic participants, the high similarity cluster in the default mode network included eleven participants with an IQ under 80, and the high similarity cluster in the frontoparietal network included sixteen participants who were 15 years old (the oldest age cohort included). Although differences in autism, age, and cognitive ability explained some of the variance in who is more likely to show similar brain activation patterns during movie watching, there are likely other factors that were not investigated in this thesis that can help explain these clustering patterns. I believe differences in a participant’s interest in, attention to, and comprehension of the movie are likely all important factors in explaining differences in the degree of neural synchrony present.
5.2 Contributions to the Field

The use of naturalistic stimuli, such as movies, to better understand brain development is growing in popularity because of several advantages these types of paradigms have over traditional task or resting state study designs. Specifically, children tend to move less when watching a movie compared to when they are at rest, which improves fMRI data quality (Vanderwal et al., 2019). Naturalistic stimuli also allow for greater experimental control over what a participant is doing compared to rest, while providing a paradigm that is more similar to what children experience in the real-world compared to traditional cognitive tasks (Finn, 2021; Hasson & Honey, 2012; Vanderwal et al., 2019). Moreover, neural responses to movies also appear to be more predictive of individual differences in behavioural outcomes compared to rest (Finn, 2021; Finn & Bandettini, 2021). For instance, naturalistic paradigms have been used to better understand social and cognitive processing in developmental samples (Cantlon & Li, 2013; Gruskin et al., 2020; Richardson et al., 2018) and in clinical groups, including disorders of consciousness patients (Laforge et al., 2020; Naci et al., 2018), individuals with depression (Gruskin et al., 2020; Guo et al., 2015; Komulainen et al., 2021), and in adults who have been diagnosed with schizophrenia (Patel et al., 2021; Yang et al., 2020). Disentangling the factors that predict neural synchrony during naturalistic processing may have important clinical implications. If we know which social and cognitive processes are required for two people to synchronize with each other, we can better understand the abilities that are preserved in patients who show significant synchrony during naturalistic processing. By characterizing how children’s brains respond to movies, the results of my thesis contributed to the field of developmental neuroscience in five unique ways.

First, I showed that children as young as 7 years old showed significant neural synchrony in both sensory and associative brain regions when watching a movie. The majority of studies that have investigated neural synchrony in developmental samples have used a measure of how similar a child’s brain activation is to a group of adults
(termed *neural maturity*). This thesis showed that many children between the ages of 7 and 15 show significant synchrony with other children across the entire cortex, in many of the same regions observed in adult participants. In fact, Chapter 2 found that approximately 50% of the cortex showed significant synchrony across participants between the ages of 7 to 11. These findings support the use of measuring neural synchrony within developmental samples to better understand how children process naturalistic stimuli.

Second, I showed that movies can be used as a clinical tool to better understand differences in naturalistic processing in children. In Chapter 2, I found evidence that autistic children show less neural synchrony in the theory of mind network compared to those without autism. These differences were specific to regions associated with social and emotional processing and were not present in sensory or attentional networks of the brain. To my knowledge, the study in Chapter 2 was the first to show that autistic children show less neural synchrony in regions thought to be important for social processing.

Autism is associated with worse performance on traditional theory of mind tasks (Baron-Cohen, 1991, 2000; Baron-Cohen et al., 1985; Frith, 2001), but there is controversy over the nature of these differences since some autistic individuals perform equally as well on social cognition tasks compared to those without autism (Bowler, 1992; Gernsbacher & Yergeau, 2019; Ozonoff et al., 1991). Moreover, how these tasks relate to real-world processing of social stimuli is not always straightforward. For instance, for children who do poorly on traditional theory of mind tasks, it is not always clear if it is because they do not have theory of mind, or because they did not understand the instructions or could not keep the task goals in their mind (Boucher, 2012; Gernsbacher & Yergeau, 2019; Grant et al., 2001; Loukusa et al., 2014). Additionally, false belief tasks, such as the Sally-Anne Task, are often scored as ‘pass’ or ‘fail’, but children may differ substantially in their social cognitive abilities even among those who can pass these tasks (Boucher, 2012; Grant et al., 2001). Since the values obtained from neural synchrony during movie watching are continuous, this may offer a more nuanced measure of real-world social processing compared to false-belief tasks. Additionally,
following the plot of a movie is likely more similar to the experiences we have in our everyday lives compared to performing traditional theory of mind tasks.

The findings from Chapter 2 resemble results obtained using other social cognitive tasks. First, when comparing neural responses of autistic and non-autistic children during theory of mind tasks, differences are predominately detected in the social brain. Second, this study observed several autistic children who showed similar brain activation patterns in the theory of mind network to a group of participants without autism during the movie, which is consistent with previous findings that show some autistic children perform similarly to those without autism on social cognitive tasks (Bowler, 1992; Gernsbacher & Yergeau, 2019; Ozonoff et al., 1991). These results support the use of movies to better understand naturalistic social processing in neurotypical and neurodivergent children.

A third contribution of this thesis to the field of developmental neuroscience was showing that cognitive ability is predictive of neural synchrony in adolescence, but may not be predictive in childhood. Zelazo (2004) proposes that as children’s cognitive abilities mature, their conscious experiences also become more complex. To test this theory, we need a measure of naturalistic processing. One tool we can use to understand naturalistic processing is neural synchrony; the more correlated a participant’s brain patterns are to another person’s, the more similar their experience of that event is said to be (Chen et al., 2017a; Hasson, Furman, et al., 2008; Nguyen et al., 2019; Nummenmaa et al., 2018; Zadbood et al., 2017). Neural synchrony is present when students listen to classroom lectures (Dikker et al., 2017; Meshulam et al., 2021), when adults watch a political speech (Schmälzle et al., 2015), and when two people socialize with each other (Bevilacqua et al., 2019; Nguyen et al., 2020). Movies are particularly effective at producing neural synchrony. However, even when participants are watching the same movie, there are individual differences in the degree of neural synchrony present. Why do some individuals synchronize more than others (Hasson et al., 2012)? This thesis suggests that differences in general cognitive ability may partially explain this, at least in adolescence. Better cognitive abilities may allow an adolescent to pay attention to what is
happening in a movie, pick up on nuances of the plot, and link different events in the film together more easily.

A fourth contribution of this thesis was finding that neural responses to movies within a developmental sample show several similarities to findings within the adult literature. Across Chapters 2 to 4, I found neural synchrony was greatest in sensory areas and regions of the default mode network. This is consistent with what is shown during movie watching in adult samples (Chen et al., 2017; Hasson, Landesman, et al., 2008; Lerner et al., 2011; Nguyen et al., 2019; Yeshurun et al., 2017). Regions of the brain that showed significant differences in functional connectivity during movie watching compared to resting state in Chapter 4 predominately involved regions of the visual network, which is similar to what has been found in adults (Emerson et al., 2015; Greene et al., 2018). These findings suggest that the brains of children and adolescents respond to movies in many similar ways to adults, at least during a movie that is of interest to younger viewers.

However, one substantial difference in the findings of this thesis compared to the adult literature was that I found evidence that children may not show meaningful neural synchrony in brain networks that encompass much of the PFC. This is in contrast to what has been shown in adult participants; synchrony in the frontoparietal network in adults has been shown to be significantly greater than during resting state, and is correlated with how engaging a movie is (Naci et al., 2014; Nguyen et al., 2019). The frontalization theory of development proposes that children are less reliant on the prefrontal cortex to perform executive function tasks compared to adolescents (Baker et al., 2015; Lewis and Todd, 2007). The results from this thesis are in line with this, and lead to an interesting question: are children also less reliant on the PFC to process naturalistic stimuli?
5.3 Limitations and Future Directions

The current thesis suggests that although social and cognitive abilities are predictive of neural synchrony in regions thought to be important for plot following, these factors do not discount a child from synchronizing with other children while watching a movie. For instance, about half of the participants in Chapters 2 and 3 showed low pairwise correlations with other participants in the theory of mind, default mode, and frontoparietal networks, including those who had above average IQ scores and those who did not have a clinical diagnosis of autism. I suspect what explains these findings is that children and adolescents who had more similar brain activation patterns with other participants (based on the clustering analysis in Chapters 2 and 3) are paying attention to and understanding the narrative in a similar way; those with low pairwise inter-subject correlations may be focused on irrelevant aspects of the narrative or may not understand the plot in a similar way to other participants. A major limitation of the current thesis is that it did not include a measure of how participants understood the movie. I believe that what will best predict whether a child shows similar or dissimilar patterns of activity during movie watching will be whether or not they understood the plot in a similar way to other children. Cognitive and social abilities may be one of many factors that could influence how a child makes sense of a movie plot. To investigate these possibilities, future work should examine the links between cognitive abilities, neural synchrony, and movie comprehension in children and adolescents.

For a final study in this thesis, I planned to conduct a study investigating neural synchrony and movie comprehension in children, but due to restrictions placed on data collection during the COVID-19 pandemic, I was unable to complete this study. The plan for this study was to collect fMRI data while children and adolescents watched Despicable Me. After the fMRI scan, participants would be asked to describe what happened in the movie, and then they would be asked a series of questions regarding specific details about the plot. Lastly, participants would also complete cognitive tasks from the Cambridge Brain Science battery, which is a battery of 12 tasks that measure various aspects of cognition. First, this study would investigate if the findings from Chapter 3 replicate in an independent sample. Second, this study would investigate
whether movie comprehension mediates the relationship between cognition and neural synchrony during movie watching.

The current thesis suggests that a substantial number of children and adolescents included in Chapters 2 and 3 showed minimal neural synchrony (based on the clustering analysis) to other participants in networks associated with high-level processing while watching a movie intended to be engaging for children. An interesting next step would be to investigate if a similar pattern emerges when children are in the classroom, and whether this relates to how much a student is learning. Success in school is associated with physical and mental health outcomes, incomes, and career attainment as adults (Borghans et al., 2016; French et al., 2015; Kretschmann et al., 2019; Moran et al., 2012). If we can better understand what aspects of the classroom children are paying attention to, we may be able to promote better learning experiences for those who are experiencing academic difficulties. Previous work has shown that students who display greater synchrony with other classmates during course lectures report higher engagement (Dikker et al., 2017), and perform better on the final exam (Meshulam et al., 2021). Bevilacqua et al. (2019) found that student-teacher synchrony was predictive of student engagement and teacher likeability in secondary school students. Understanding the factors that increase synchronization between students and their teachers may help improve educational outcomes for children experiencing academic difficulties.

Although knowledge attainment is an important goal of education, going to school also allows children to gain important social expertise (Elliott et al., 2015; Wentzel, 2015). For instance, school-aged children learn how to respond appropriately to their peers and adjust their behaviour based on the social dynamics and demands of the classroom (Walker et al., 1994). Social cognitive abilities allow us to successfully navigate our environment, and are associated with job success and satisfaction, physical health, and well-being (Davenport Sypher et al., 1989; Demir et al., 2012; Morgeson et al., 2005; Ray & Elliott, 2006; Rovniak et al., 2002). Peer rejection at school, especially during adolescence, is thought to have damaging long-term effects on the physical and mental health of the excluded child (Lynn Mulvey et al., 2017). It also increases the likelihood of depression, anxiety, and low self-esteem (Bijstra et al., 1994; Dill et al.,
Neural synchrony during social interactions may help us better understand how to promote positive social interactions in school settings. For example, Dikker et al. (2017) found that closeness ratings and brain-to-brain synchrony in secondary school students during class lessons were highly correlated; that is, students who felt closer to each other had more similar brain responses. They also found that brain-to-brain synchrony was increased in classrooms that promoted social interactions and classroom discussion. A more recent study found pairs of participants that were friends showed more similar neural responses in the default mode network while watching video clips compared to pairs of acquaintances and strangers (Baek et al., 2022). Similarly, lonely individuals show more idiosyncratic neural responses during naturalistic processing compared to those that do not report being lonely (Baek et al., 2021). These results suggest that neural synchrony may be an effective tool to better understand social dynamics in schools and assess interventions aimed at promoting prosocial behaviors in the classroom.

Understanding how different children experience their world can also help support parents, teachers, and other adults involved in a child's life. Children and adolescents often feel that 'parents just don’t understand'. Similarly, adults often have difficulty understanding the decisions, motivations, and perspectives of teenagers; this is in spite of the fact that all adults were previously children and adolescents. The current thesis suggests that children may be less reliant on high-level processes, mediated by the PFC, during naturalistic experiences compared to adults; could this explain why children and adults often feel they are on different pages? Measuring how neural synchrony changes across development longitudinally (i.e. within the same participants) may be able to better explain the surprising results from this thesis. For instance, does synchrony in the PFC and/or the frontoparietal network increase within the same individual as they age? Are these changes associated with a more adult-like understanding of the world?

Investigating how a child’s brain synchronizes with their own parents during movie watching or even real-life social interactions may also be able to elucidate the factors that allow for children and parents to be on the same page. For instance, is brain-to-brain coupling associated with parents and children getting along? If so, can we use
synchrony to help parent-child dyads find ways to understand each other? Recently, Nguyen et al. (2020) found that neural synchrony between parent-child dyads doing puzzles together (as measured by fNIRS) was predictive of problem solving success. An interesting avenue of future research would be to investigate the factors that promote child-parent synchrony, which in the longterm, may help support families experiencing interpersonal difficulties.

Lastly, many of the analyses conducted in this thesis were data-driven and led to several surprising results. For instance, Chapter 3 found that participants with higher IQ scores had greater synchrony in sensory brain regions. Given the exploratory nature of these studies, direct replication is an important next step to assess the reliability of these finding. Open access developmental neuroimaging databases, like the Healthy Brain Biobank, are becoming more common (Alexander et al., 2017; Casey et al., 2018; Volkow et al., 2018), and allow for exciting opportunities to replicate findings in large independent datasets. Currently, the Healthy Brain Biobank is the only developmental database that includes fMRI during movie watching (to the best of my knowledge). With the use of naturalistic stimuli becoming more popular in developmental neuroscience, it is possible that more open-access databases will start collecting neuroimaging data while children process narratives. Once this becomes available, investigating the replicability of the findings from this thesis in a large independent dataset would be straightforward.

5.4 Conclusions

In summary, this thesis found that autistic children, and adolescents with poorer intellectual abilities, show more idiosyncratic brain responses when watching a movie compared to participants without autism and teenagers with higher cognitive scores, respectively. These findings suggest that, as a group, autistic children, and adolescents with lower IQs, are having more unique experiences when processing naturalistic stimuli compared to their peers without autism or those with above average IQ scores. However, there was significant heterogeneity in the group of participants who showed highly correlated neural responses. To better understand this variability, future work should
investigate how neural synchrony relates to plot comprehension during movie watching in children, and how these patterns change across time within the same participants.

Neural synchrony in the frontoparietal network, thought to be important for naturalistic processing in adults, was found not to be significantly related to autism, social cognition, or IQ scores in children. Participants also showed minimal to no synchrony in several networks that encompassed the PFC. Additionally, cognitive scores in children were not significantly predictive of neural synchrony in many regions previously shown to be associated with plot following in adults, including the default mode network. These set of results could suggest that children are less reliant on executive processes and the prefrontal cortex to process naturalistic stimuli, though much more work is needed to better understand these findings.

The series of studies presented in this thesis support the use of naturalistic stimuli to evaluate how children and adolescents experience their world, however, further research is needed to attain a full understanding of why some youngsters show highly similar patterns of brain activity during movie watching and others do not.
6 References


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Sternin, A. (2021). *Neural Markers of Musical Memory in Young and Older Adults.*


Curriculum Vitae

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<th>Name:</th>
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<tbody>
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Peer-Reviewed Publications


Selected conference presentations


**Professional Experience**

2019-2020: Member of the 2020 Inspiring Diversity in STEM conference committee

2018-2019: Member of the Western Psychology Colloquium Committee

2017-2019: Member of the Western Women in Neuroscience Group

**Teaching Experience**

2021-2022: Part-time faculty at King’s University College

*Courses:* Child Development & Research Methods in Psychology

2015-2016: Undergraduate Honours Thesis co-supervisor

*Alexandra Pearce, co-supervised with Dr. Adrian Owen & Dr. Bobby Stojanoski*

2014-2021: Graduate Teaching Assistant
Additional Training

2021: DataCamp’s Data Scientist career track
2021: DataCamp’s SQL Fundamentals skill track
2021: DataCamp’s Python Fundamentals skill track
2016-2017: Ph.D. coursework at the University of California, San Diego