# Brain Networks Involved in Higher Cognitive Functions in Adults with Autism Spectrum Disorder

by

Veronica Wai-Jong Yuk

A thesis submitted in conformity with the requirements for the degree of Doctor of Philosophy

> Department of Psychology University of Toronto

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### Abstract

People with autism spectrum disorder (ASD) experience difficulties with higher cognitive functions, including executive functions and theory of mind (ToM). They show atypical recruitment of brain regions involved in these functions, but functional connectivity among these areas within particular frequency bands has been less well characterized in ASD. Examining these factors is crucial to elucidating the neural mechanisms by which long-range underconnectivity and short-range overconnectivity reported in ASD influences their cognitive abilities. Therefore, this thesis used magnetoencephalography to explore the frequency-specific functional networks subserving executive functions and ToM in three studies of overlapping groups of 39 control adults and 40 adults with ASD aged 18–40 years old.

Study 1 demonstrated that during inhibitory control, lower alpha-band synchrony between the right inferior frontal gyrus (IFG) and areas not typically linked to inhibition was found in adults with ASD compared to controls and was associated with everyday inhibition, suggesting weaker suppression by the right IFG of extraneous brain activity. Study 2 revealed that while connectivity did not differ between groups when maintaining stimuli in working memory, adults with ASD showed reduced theta-band network synchrony involving the right IFG and left inferior parietal lobule when recognizing previously presented stimuli. Therefore, despite intact

maintenance, recognition in adults with ASD may be affected by diminished inhibition of irrelevant stimulus representations. Study 3 determined that during a ToM false-belief task, adults with ASD had lower theta-band synchrony among brain regions implicated in ToM and the right IFG, suggesting reduced inhibition of their own belief when inferring another's false belief. Adults with ASD reported difficulties in all three functions assessed by these three studies. Together, this work suggests that reduced connectivity impacts higher cognitive functions in ASD, and that atypical inhibitory control may be a common, key contributor to cognitive difficulties in adults with ASD.

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## Chapter 1 Introduction

## 1 Background and aims

## 1.1 Autism spectrum disorder (ASD)

Autism spectrum disorder (ASD) is a pervasive neurodevelopmental disorder that is diagnosed on the basis of two key symptoms: social communication/interaction impairments and restricted, repetitive behaviours (American Psychiatric Association, 2013). The worldwide prevalence of ASD is approximately 1% (Lai, Lombardo, & Baron-Cohen, 2014; Lord et al., 2020), and general awareness of this disorder is on the rise. ASD is typically diagnosed during childhood as early as the age of two to three years (Charman et al., 2005; Chawarska et al., 2014; Cox et al., 1999; Lord et al., 2006; Turner & Stone, 2007). However, symptoms can appear as early as in infancy (Ozonoff et al., 2015; Rogers, 2009; Zwaigenbaum et al., 2015), hence most research has focused on the behavioural and clinical profiles of ASD during childhood to identify early indicators of ASD. Nevertheless, there is a growing and urgent need to characterize ASD symptoms in adulthood; as ASD is a lifelong disorder, the number of adults with ASD is increasing as larger numbers of children being diagnosed with ASD grow up (Roux, Shattuck, Rast, Rava, & Anderson, 2015). Symptoms persist throughout life and affect the adults' quality of life (Henninger & Taylor, 2013; Howlin & Magiati, 2017; Levy & Perry, 2011; Simonoff et al., 2019; Taylor & Mailick, 2014), and the level of support from educational and healthcare systems typically diminishes as individuals with ASD transition into adulthood (Shattuck, Wagner, Narendorf, Sterzing, & Hensley, 2011; Smith, Greenberg, & Mailick, 2012).

In addition to the clinical symptoms, children and adults with ASD also experience deficits in a variety of cognitive domains (Narzisi, Muratori, Calderoni, Fabbro, & Urgesi, 2013; Rosa et al., 2017; Velikonja, Fett, & Velthorst, 2019; Wilson et al., 2014), and it has been hypothesized that these cognitive difficulties give rise to the symptoms of ASD. There are a few cognitive theories that are proposed to account for certain aspects of ASD symptomatology. In addition to the models of weak central coherence (Frith, 1989; Frith & Happé, 1994; Happé & Frith, 2006; Happé & Booth, 2008) and enhanced perceptual functioning (Mottron & Burack, 2001; Mottron, Dawson, Soulières, Hubert, & Burack, 2006), there are two theories that have been prominently

discussed in the literature: "mindblindness" and "executive dysfunction". The mindblindness account (Baron-Cohen, 1995; Frith, 2001; Tager-Flusberg, 1999) suggests that the social communicative deficits in ASD are mainly due to impairments in theory of mind (ToM), which is the ability to impute mental states to others (Premack & Woodruff, 1978). If an individual struggles with understanding or inferring the thoughts and emotions of others, it becomes difficult to act appropriately and accordingly in social situations. On the other hand, the executive dysfunction theory (Geurts, de Vries, & van den Bergh, 2014; Hill, 2004; Russell, 1997; Russo et al., 2007) attributes the restricted, repetitive behaviours to deficits in executive functions, which are cognitive functions that direct an individual's behaviour toward accomplishing their goals (Banich, 2009; Diamond, 2013). Deficits in cognitive control can lead to a person becoming fixated on certain actions that are not necessarily pertinent to a task at hand. However, these two theories are not completely independent from each other. Executive functions govern many aspects of behaviour and therefore certainly play a role in effective social communication and interactions. For instance, stopping one's impulsive reactions in a social situation is crucial to avoid potentially offending another person. Moreover, there is a substantial literature showing a strong influence of executive functions on the development of ToM (Apperly, Samson, & Humphreys, 2009; Jones et al., 2018; Joseph & Tager-Flusberg, 2004; Ozonoff, Pennington, & Rogers, 1991). Given the impact that these cognitive functions have on the clinical symptoms of ASD and their interrelatedness, there has been a wealth of behavioural and neuroimaging research investigating the nuances of ToM and executive function abilities and deficits in ASD. Although recent work has supported an emerging neuroscientific theory that the cognitive and clinical profiles in ASD may be explained by disrupted brain connectivity (Di Martino et al., 2014; Fishman, Keown, Lincoln, Pineda, & Müller, 2014; Just, Keller, Malave, Kana, & Varma, 2012; Kessler, Seymour, & Rippon, 2016), there has been relatively limited work demonstrating atypical connectivity patterns underlying ToM and executive functions in ASD. Of these, few studies, if any, have delved into the exact neural mechanisms underlying these connectivity differences, information that could be key to designing effective interventions for people with ASD. For instance, there has been little research describing the particular frequency bands in which these discrepancies occur, even though it is well established that populations of neurons selectively communicate through oscillations at different frequency bands to accomplish specific cognitive functions (Fries, 2015; Palva & Palva, 2012; Siegel, Donner, & Engel, 2012; Varela, Lachaux, Rodriguez, & Martinerie, 2001; Womelsdorf et al., 2007).

This thesis contributes to our current knowledge of cognition in ASD by exploring the frequency-specific differences in functional brain connectivity related to ToM and executive function impairments in adults with ASD using magnetoencephalography (MEG), a neuroimaging technique that is highly sensitive to the phase and timing of oscillations occurring in discrete brain regions (Baillet, 2017; Hämäläinen, Hari, Ilmoniemi, Knuutila, & Lounasmaa, 1993; Hari & Salmelin, 2012). The subsequent sections of this chapter provide an overview of the ASD literature pertaining to behavioural profiles of executive function and ToM deficits, followed by literature on functional connectivity, especially oscillatory synchrony, and finally on atypicalities in brain networks involved in executive functions and ToM. The subsequent chapters address the main aim of this thesis by detailing experiments in which functional brain connectivity within different frequency bands is compared between adults with and without ASD during tasks of executive functions and ToM. The concluding chapter draws together the key findings of these experiments and describes their implications for future work.

### 1.2 Executive functions in ASD

Executive functions are processes that guide one's behaviour to achieve certain goals. One prevailing model posits that three core functions comprise executive functions: inhibition, working memory, and cognitive flexibility (Diamond, 2013; Miyake et al., 2000). Inhibition occurs at different levels of cognitive processing to suppress internal tendencies or external salient stimuli that are extraneous or in opposition to one's goals. Working memory is the ability to temporarily maintain and manipulate meaningful information in mind in pursuit of a goal. Cognitive flexibility permits an individual to easily switch between tasks or behaviours when their goals change. While these executive functions appear to represent distinct processes, there is a large degree of overlap among them (Friedman & Miyake, 2017). For example, inhibition is thought to control access to and delete information that is irrelevant or no longer relevant from working memory (Hasher, Lustig, & Zacks, 2007), and inhibition and working memory together are believed to form the basis for cognitive flexibility (Dajani & Uddin, 2015; Davidson, Amso, Anderson, & Diamond, 2006; Garon, Bryson, & Smith, 2008; Zelazo, Muller, Frye, & Marcovitch, 2003).

Although there remains some discussion in the ASD literature regarding the specific executive processes affected, people with ASD demonstrate impairments in executive functions from

childhood to adulthood both during experimental tasks (Ambery, Russell, Perry, Morris, & Murphy, 2006; Geurts, Verte, Oosterlaan, Roeyers, & Sergeant, 2004; O'Hearn, Asato, Ordaz, & Luna, 2008; Pennington & Ozonoff, 1996) and in everyday life (Gardiner & Iarocci, 2018; Johnston, Murray, Spain, Walker, & Russell, 2019; Kenworthy, Yerys, Anthony, & Wallace, 2008; van den Bergh, Scheeren, Begeer, Koot, & Geurts, 2014; Wallace et al., 2016). These deficits are related to the core symptoms of ASD, but they also permeate several other aspects of behaviour, which can have negative repercussions for adaptive functioning in both children and adults with ASD (Gilotty, Kenworthy, Sirian, Black, & Wagner, 2002; Kercood, Grskovic, Banda, & Begeske, 2014; Nyrenius & Billstedt, 2020; Panerai, Tasca, Ferri, Genitori D'Arrigo, & Elia, 2014; Rosa et al., 2017; Wallace et al., 2016; Zimmerman, Ownsworth, O'Donovan, Roberts, & Gullo, 2017). Importantly, executive functions have been linked to ToM in both people with and without ASD (Carlson & Moses, 2001; Devine & Hughes, 2014; Hamilton, Hoogenhout, & Malcolm-Smith, 2016; Lukito et al., 2017; Oerlemans et al., 2013; Russell, Saltmarsh, & Hill, 1999; Sabbagh, Xu, Carlson, Moses, & Lee, 2006). Research involving children with and without ASD has demonstrated that executive functions predict ToM development (Brock, Kim, Gutshall, & Grissmer, 2019; Doenyas, Yavuz, & Selcuk, 2018; Kouklari, Tsermentseli, & Monks, 2019; Lecce, Bianco, Devine, & Hughes, 2017; Mutter, Alcorn, & Welsh, 2006), indicating that they support the maturation of ToM abilities. Executive functions may continue to play a role in some aspects of ToM during adulthood (Apperly et al., 2009; Klindt, Devaine, & Daunizeau, 2017). This relationship between executive functions and ToM is not surprising, given the roles of each of the three core executive functions in understanding others' mental states. For instance, during social interaction, one's mental representation of another person is being constantly held in working memory and updated based on that person's speech and behaviour. One's perception of another's mental state from their words and actions, however, is affected by the degree to which one can inhibit one's own viewpoint and flexibly switch to consider another person's perspective. Therefore, elucidating the precise aspects of executive functions that are impaired in ASD is essential to comprehend how they may impact ToM in this population. While all three core executive functions have been associated with ToM (Bock, Gallaway, & Hund, 2015; Carlson, Moses, & Breton, 2002; Chasiotis, Kiessling, Hofer, & Campos, 2006; Davis & Pratt, 1995; Leslie, Friedman, & German, 2004; Perner, Lang, & Kloo, 2002), this thesis will focus on inhibition and working memory, as

they are thought to be precursors to cognitive flexibility (Davidson et al., 2006; Garon et al., 2008).

#### 1.2.1 Inhibition

Inhibitory control is believed to encompass three different functions: prepotent response inhibition, interference control, and cognitive inhibition (Diamond, 2013; Friedman & Miyake, 2004). Prepotent response inhibition involves withholding a response that is dominant or automatic. Interference control selectively focuses attention by ignoring immediate distractors. Cognitive inhibition entails suppressing unwanted thoughts, as well as resisting interference from previously presented information (proactive interference) and from newly presented information (retroactive interference).

The extant literature has been mixed regarding the exact deficits in inhibitory control processes in ASD. Geurts and colleagues (2004) demonstrated that children with ASD had difficulties with prepotent response inhibition but were equally capable of executing interference control as typically-developing children. In contrast, Adams and Jarrold (2012) showed that children with ASD performed well on a prepotent response inhibition task, but poorly on an interference control task. Christ, Kester, Bodner, and Miles (2011) similarly reported that children with ASD had impaired interference control, but intact response inhibition and proactive interference resistance, even though in an earlier study they found that children with ASD had poorer performance on both a prepotent response inhibition and interference control task (Christ, Holt, White, & Green, 2007). On the other hand, one study did not observe any differences in either response inhibition or interference control between children with and without ASD (Ozonoff & Strayer, 1997). Aside from performance-based tasks, impaired inhibition in everyday life measured by behaviour rating scales in children with ASD has been reported (Gardiner & Iarocci, 2018; Yerys et al., 2009), although one study found that this effect was less prominent in older children and adolescents with ASD (van den Bergh et al., 2014). Schmitt, White, Cook, Sweeney, and Mosconi (2018), however, showed that deficits in response inhibition in terms of accuracy and slowing of responses did not improve with age.

Research into the inhibition abilities of adults with ASD also shows some inconsistency, though this population has been less well studied. Adults with ASD were reported to exhibit moderate or even no difficulties with response inhibition, as well as intact proactive and retroactive interference resistance, but they were generally slower in their responses (Johnston, Madden, Bramham, & Russell, 2011; Johnston et al., 2019; Lever, Ridderinkhof, Marsman, & Geurts, 2017). Conversely, a study by Luna, Doll, Hegedus, Minshew, and Sweeney (2007) of children, adolescents, and adults with ASD observed that while their response inhibition improved with age, they still showed more errors than controls in adulthood. Brady and colleagues (2017) also found that adults with ASD demonstrated worse performance on a prepotent response inhibition task compared to controls, though their scores were within the average range. However, adults with ASD still report significant deficits in inhibition in everyday life (Wallace et al., 2016).

Despite these conflicting findings, an early review by Hill (2004) speculated that individuals with ASD may be impaired in prepotent response inhibition. This suggestion has since been corroborated by meta-analyses which have revealed that across age, people with ASD show difficulties in response inhibition (Demetriou et al., 2018; Geurts, van den Bergh, & Ruzzano, 2014). Moreover, neuroimaging studies indicate that despite performing well on prepotent response inhibition tasks, children and adults with ASD exhibit atypical brain activation and connectivity during such paradigms (see Hlavatá, Kašpárek, Linhartová, Ošlejšková, & Bareš, 2018 for a review), signifying that experimental tasks may not be sensitive enough to the more subtle neural deficits in inhibition.

#### 1.2.2 Working memory

Working memory concerns the maintenance and manipulation of information in mind for a short period of time. A leading theory of working memory (Baddeley, 2012) postulates that its key components consist of a visuospatial sketchpad, phonological loop, episodic buffer, and central executive. The visuospatial sketchpad stores visual and (visuo)spatial information, while the phonological loop holds verbal and auditory stimuli. The episodic buffer integrates information from these two systems and from long-term memory into a single episodic representation, which is then brought to conscious awareness by the central executive and manipulated or altered as needed, then returned to the episodic buffer.

Though there are some reports of verbal or phonological working memory deficits (Alloway, Seed, & Tewolde, 2016; Andersen, Hovik, Skogli, Egeland, & Øie, 2013; Fried et al., 2016; Kiep & Spek, 2017; Minshew & Goldstein, 2001; Schuh & Eigsti, 2012), many studies find that children, adolescents, and adults with ASD show very consistent impairments in only visual and especially visuospatial working memory (Barendse et al., 2013; Corbett, Constantine, Hendren, Rocke, & Ozonoff, 2009; Funabiki & Shiwa, 2018; Geurts & Vissers, 2012; Goldberg et al., 2005; Morris et al., 1999; Sachse et al., 2013; Sinzig, Morsch, Bruning, Schmidt, & Lehmkuhl, 2008; Steele, Minshew, Luna, & Sweeney, 2007; Tse, Crabtree, Islam, & Stott, 2019; Verté, Geurts, Roeyers, Oosterlaan, & Sergeant, 2005; Williams, Goldstein, Carpenter, & Minshew, 2005). Whereas Happé, Booth, Charlton, and Hughes (2006) observed that spatial working memory differences in childhood were no longer present by adolescence, Luna and colleagues (2007) determined that spatial working memory maintenance was poorer in individuals with ASD across all ages relative to controls, even though their performance improved from childhood to adulthood. Conversely, Macizo, Soriano, and Paredes (2016) did not find any correlation between phonological working memory and age in children with ASD. Furthermore, children, adolescents, and young adults with ASD all exhibit impaired working memory in everyday life (Gardiner & Iarocci, 2018; Troyb et al., 2014).

Despite a few studies showing intact visual and visuospatial working memory in children and adults with ASD (Geurts et al., 2004; Lever, Werkle-Bergner, Brandmaier, Ridderinkhof, & Geurts, 2015; Yerys et al., 2009), recent meta-analyses have reported both visuospatial and verbal/phonological working memory deficits in the ASD population (Habib, Harris, Pollick, & Melville, 2019; Lai et al., 2017). However, other meta-analyses have demonstrated more severe difficulties with visuospatial than verbal working memory in ASD (Kercood et al., 2014) in terms of both maintenance and manipulation (Wang et al., 2017). Wang and colleagues (2017) speculate that since individuals with ASD tend to focus on local features of visual (but not verbal) stimuli rather than viewing them as an integrated whole, visuospatial patterns are processed in fragments and therefore become more challenging to retain in working memory.

## 1.3 Theory of mind (ToM) in ASD

ToM was first defined by Premack and Woodruff (1978) as the ability to impute mental states to others. If one has ToM, they can appreciate that others have sets of thoughts, beliefs, desires, feelings, etc. that are separate from one's own. With this knowledge, one can infer the intentions and beliefs of others in a variety of situations, without themselves being directly involved. ToM is related to social communication and social outcomes in people with and without ASD (Berenguer, Miranda, Colomer, Baixauli, & Roselló, 2018; Fink, Begeer, Peterson, Slaughter, &

de Rosnay, 2015; Hale & Tager-Flusberg, 2005; Happé, 1993; Hughes & Devine, 2015; Jones et al., 2018; Razza & Blair, 2009; Watson, Nixon, Wilson, & Capage, 1999), which in turn influences adaptive functioning and individual independence (Tillmann et al., 2019). As a result, there has been extensive research on the normal development of ToM, as well as on the precise ToM impairments observed in the ASD population.

One precursor of ToM that emerges in infancy is thought to be joint attention, in which individuals orient their attention to a common stimulus (Moore & Dunham, 1995; Mundy & Newell, 2007; Scaife & Bruner, 1975). It occurs either when a person signals to another to shift their attention to some item or event (e.g., pointing or shifting one's gaze to a novel object), or when a person responds to such cues (Mundy et al., 2007). Engaging in joint attention presupposes some understanding of differing perspectives, which then sets the foundation for the acknowledgement of diverse mental states necessary for ToM (Charman et al., 2000; Mundy & Jarrold, 2010; Tomasello, 2018). As infants and children with ASD have been consistently shown to initiate and respond less to bids for joint attention (Bruinsma, Koegel, & Koegel, 2004; Dawson et al., 2004; Franchini et al., 2019; Mundy, Sigman, & Kasari, 1994; Nyström, Thorup, Bölte, & Falck-Ytter, 2019; Sullivan et al., 2007), such deficits likely constrain the development of ToM in ASD.

ToM is a broad term that has been used to embody an assortment of social cognitive abilities, such as belief understanding, intention inference, emotion recognition, and mental state attribution. These behaviours begin to emerge during early childhood (Flavell, 1999; Meltzoff, 1999; Slaughter, 2015; Wellman, 2010; Wellman & Liu, 2004) and continue to mature throughout adolescence (Brizio, Gabbatore, Tirassa, & Bosco, 2015; Choudhury, Blakemore, & Charman, 2006; Dumontheil, Apperly, & Blakemore, 2010; Meinhardt-Injac, Daum, & Meinhardt, 2020; Valle, Massaro, Castelli, & Marchetti, 2015; Vetter, Leipold, Kliegel, Phillips, & Altgassen, 2013) and even into early adulthood (Hartshorne & Germine, 2015; Keysar, Lin, & Barr, 2003), although their developmental trajectory varies depending on the specific ToM function being examined (Tousignant, Sirois, Achim, Massicotte, & Jackson, 2017). While children with ASD demonstrate improvements in ToM over time, their performance on ToM tasks remains consistently below that of typically-developing children (Ellis et al., 2020; Peterson & Wellman, 2019). As a result, they exhibit impairments on a range of ToM tasks at several stages of development (Brent, Rios, Happé, & Charman, 2004; Kaland, Callesen, Møller-

Nielsen, Mortensen, & Smith, 2008; Kimhi, 2014; Klin, 2000; Margoni & Surian, 2016; White, Hill, Happé, & Frith, 2009), which continue into adulthood (Baron-Cohen, Wheelwright, Hill, Raste, & Plumb, 2001; Brewer, Young, & Barnett, 2017; Grainger, Williams, & Lind, 2014; Happé, 1994; Mathersul, McDonald, & Rushby, 2013; Spek, Scholte, & Van Berckelaer-Onnes, 2010; Velikonja et al., 2019; White, Coniston, Rogers, & Frith, 2011; Zalla, Barlassina, Buon, & Leboyer, 2011). Furthermore, their performance on ToM tasks is associated with ASD symptom severity and social communication skills (Hale & Tager-Flusberg, 2005; Hoogenhout & Malcolm-Smith, 2017; Jones et al., 2018; Joseph & Tager-Flusberg, 2004; Rosenthal, Hutcherson, Adolphs, & Stanley, 2019). Of these numerous methods designed to tap ToM, the most ubiquitous and well-studied paradigm in both the normative and ASD literatures has been the false-belief task.

#### 1.3.1 False belief (FB)

False-belief (FB) understanding is one aspect of ToM that refers to the ability to appreciate the fact that someone may have a belief that is false with regards to one's own belief or knowledge of a situation. For example, if a child places some chocolate into a kitchen cupboard, which is then moved by his mother to another cupboard without his knowledge, the child would falsely believe that his chocolate is still in the first cupboard. A person who has ToM and is viewing this situation would recognize that although they know that the chocolate has been moved to another cupboard, the child does not and would therefore look in the first cupboard for his chocolate. This exact scenario was first utilized by Wimmer and Perner in 1983 to investigate FB comprehension in young children. They found that three-year-old children would conflate their own beliefs with that of the child in the story and would incorrectly think that the child would look for his chocolate in the other cupboard. However, at around the age of four, children begin to consistently and correctly infer that the child would search in the first cupboard, thereby demonstrating an understanding of FB. This effect has since been replicated in several other studies of young children's belief development (Grosse Wiesmann, Friederici, Singer, & Steinbeis, 2017; Liu, Wellman, Tardif, & Sabbagh, 2008; Wellman, Cross, & Watson, 2001), suggesting that FB reasoning does not mature until about four years of age. This ability to recognize that another person can possess FB is also referred to as first-order FB understanding. Individuals are able to have FB not only regarding the reality of a situation, but also about another person's belief. Using the example above, if the child happens to witness his mother

moving the chocolate to another cupboard, unbeknownst to his mother, then one would expect that his mother would have a FB about the child's belief, as she would falsely think that the child believes his chocolate is still in the first cupboard. This concept is known as second-order FB understanding, as it involves comprehension that a person can have beliefs about others' beliefs. Second-order FB reasoning is thought to reflect more advanced ToM capabilities, since children do not consistently pass such second-order FB tasks until the age of six (Miller, 2009; Perner & Wimmer, 1985; Sullivan, Zaitchik, & Tager-Flusberg, 1994). As first- and second-order FB understanding requires the awareness of potentially differing mental states in others, it is considered one of the earliest markers of ToM, and FB tasks are now used as standard assessments of ToM.

Shortly after the initial experiment by Wimmer and Perner (1983), Baron-Cohen, Leslie, and Frith (1985) adapted their paradigm to investigate whether children with ASD had ToM, given their known difficulties with social communication and interaction. They demonstrated that children with ASD who were at roughly the same mental age or higher than typical four-yearolds could not pass this first-order FB task. Meanwhile, children with Down's syndrome who were at a lower mental age than the ASD group performed significantly better than those with ASD. These results indicated that the difficulty that children with ASD experienced in FB reasoning was not due to their intellectual capabilities but instead a fundamental impairment in ToM. Several studies have also established that young children with ASD have difficulties with FB understanding compared to their age-matched peers (Begeer, Bernstein, Van Wijhe, Scheeren, & Koot, 2012; Perner, Frith, Leslie, & Leekam, 1989; Peterson & Bowler, 2000; Rasga, Quelhas, & Byrne, 2017; Surian & Leslie, 1999; White et al., 2009). However, at around the verbal mental age of 11 years, children with ASD begin to pass first-order FB tests more reliably (Happé, 1995), indicating a protracted development of FB understanding (Baron-Cohen, 1989). Although adults with ASD are capable of FB reasoning (Bowler, 1997; Kimhi, 2014; Moran et al., 2011; Scheeren, de Rosnay, Koot, & Begeer, 2013), one study found that they made more errors than control adults on a first-order FB task (Bradford, Hukker, Smith, & Ferguson, 2018). There is also evidence that performance on more complex second-order FB tasks is correlated with social functioning in everyday life (Bishop-Fitzpatrick, Mazefsky, Eack, & Minshew, 2017). Moreover, adults with ASD who pass explicit FB tests may still fail on implicit tests of FB understanding (Schneider, Slaughter, Bayliss, & Dux, 2013; Schuwerk,

Vuori, & Sodian, 2014; Senju, 2012), where they are more likely to make anticipatory eye movements toward the actual location of an object, rather than where a character would mistakenly search for their item. As this atypical anticipatory looking pattern is thought to reflect a less spontaneous attribution of FB, these findings in implicit FB tasks suggest that the more automatic aspects of FB reasoning may be impaired in adults with ASD, an effect which may be more evident in neuroimaging studies of the underlying processes of FB understanding.

## 1.4 Neuroimaging of ASD

The clinical symptoms and cognitive deficits observed in ASD are inherently linked to differences in brain structure and function. Numerous studies have revealed considerable disparities in both grey and white matter in the brain between people with and without ASD, which have been associated with ASD symptomatology and behaviour (Amaral, Schumann, & Nordahl, 2008), though the specific morphological differences appear to vary with region and with age (e.g., Ameis et al., 2013; Cauda et al., 2011; DeRamus & Kana, 2015; Doyle-Thomas et al., 2013; Duerden, Mak-Fan, Taylor, & Roberts, 2012; Foster et al., 2015; Greimel et al., 2013; Jou et al., 2016; Lange et al., 2015; Mak-Fan, Taylor, Roberts, & Lerch, 2012; Mann et al., 2018; Smith et al., 2016; Sussman et al., 2015).

Recent work aggregating several large datasets of individuals with and without ASD aged 2-64 years established that overall, the frontal lobes show increased grey matter cortical thickness, while the temporal lobes exhibit decreased cortical thickness in ASD compared to controls (van Rooij et al., 2018), though there may be increased cortical thickness in the superior temporal gyrus specifically (Bedford et al., 2020; Haar, Berman, Behrmann, & Dinstein, 2016; Khundrakpam, Lewis, Kostopoulos, Carbonell, & Evans, 2017; Zhou, Yu, & Duong, 2014). These atypical patterns of frontal and temporal lobe cortical thickness were related to ASD symptom severity, complementing previous studies of smaller sample sizes demonstrating links between cortical thickness abnormalities and social and executive function impairments (Baribeau et al., 2019; Prigge et al., 2018; Wallace et al., 2015). These effects were most evident during childhood and adolescence, while in adulthood, they appeared to reverse direction in some regions and diminish in others (Bedford et al., 2020; van Rooij et al., 2018). In addition, cortical thickness in frontal and temporal areas in ASD was less asymmetrical relative to controls (Postema et al., 2019).

As alterations in grey matter may influence white matter structure (Cauda et al., 2014; Ecker et al., 2016), individuals with ASD expectedly show atypicalities in interhemispheric white matter tracts, especially in the corpus callosum. Several studies have found decreased integrity in the corpus callosum in children, adolescents, and adults with ASD (Aoki, Abe, Nippashi, & Yamasue, 2013; Bloemen et al., 2010; Di, Azeez, Li, Haque, & Biswal, 2018; Travers et al., 2012; Vogan, Morgan, Leung, et al., 2016), which was related to their level of adaptive functioning (Ameis et al., 2016), and which did not improve with age, unlike in typicallydeveloping children (Mak-Fan et al., 2013). Disruptions in the superior longitudinal fasciculus, which connects the frontal and posterior lobes, have also been observed (Aoki et al., 2013; Im et al., 2018), which also did not diminish with age (Karahanoğlu et al., 2018; Koolschijn, Caan, Teeuw, Olabarriaga, & Geurts, 2017; Lisiecka et al., 2015; but see Libero, Burge, Deshpande, Pestilli, & Kana, 2016). Reduced white matter fractional anisotropy in the corpus callosum and in other tracts has also been associated with the social communication deficits and restricted, repetitive behaviours characteristic of ASD (Ameis & Catani, 2015; Aoki et al., 2017; Fitzgerald, Gallagher, & McGrath, 2019). As with cortical thickness, white matter tracts exhibit decreased or atypical asymmetry between the two hemispheres in ASD (Carper, Treiber, DeJesus, & Müller, 2016; Fitzgerald et al., 2018).

These disparities in grey and white matter structure may negatively impact neuronal firing and communication, thereby contributing to altered neural function in ASD, which has been observed across a range of studies (for reviews, see Di Martino et al., 2009; Dickstein et al., 2013; Philip et al., 2012; Sato & Uono, 2019), including tasks of ToM and executive function, which will be detailed in the following sections. Of particular interest in recent work has been how active communication among brain areas, or functional connectivity, may differ in individuals with ASD, given their morphological differences, as functional connectivity is tightly linked with structural (white matter) connectivity (Damoiseaux & Greicius, 2009; Honey, Kötter, Breakspear, & Sporns, 2007; Straathof, Sinke, Dijkhuizen, & Otte, 2019). Alterations in white matter have been linked to reductions in functional connectivity between distant brain regions in people with ASD (Hong, Hyung, Paquola, & Bernhardt, 2019; Just, Cherkassky, Keller, Kana, & Minshew, 2007; McGrath et al., 2013). These results support contemporary theories postulating that while individuals with ASD demonstrate atypical brain activation across a variety of tasks, the clinical and cognitive profiles of ASD may be better characterized by atypical functional

connectivity – in particular, long-range underconnectivity and short-range overconnectivity (Anagnostou & Taylor, 2011; Belmonte et al., 2004; Kessler et al., 2016; Minshew & Keller, 2010; Rane et al., 2015; Vissers, Cohen, & Geurts, 2012; Wass, 2011).

#### 1.4.1 Functional connectivity in ASD

Behaviour and cognition are achieved by bringing together information from sensory inputs and one's internal goals. Functional connectivity is thought to be a means of actualizing the communication of neural information via the coordinated activity of two or more distant brain regions (Friston, 1994). While there have been a few mixed reports of the directionality of atypical functional connectivity patterns in ASD (e.g., Doyle-Thomas et al., 2015; Monk et al., 2009; Noonan, Haist, & Müller, 2009; Shih et al., 2010; see Maximo, Cadena, & Kana, 2014; Picci, Gotts, & Scherf, 2016 for reviews), studies commonly find decreased long-range connectivity between different lobes of the cortex (Castelli, Frith, Happé, & Frith, 2002; Cherkassky, Kana, Keller, & Just, 2006; Ebisch et al., 2011; Just et al., 2007; Just, Cherkassky, Keller, & Minshew, 2004; Kleinhans et al., 2008; Mostofsky et al., 2009; Sato & Uono, 2019; Yerys et al., 2017) and some evidence for increased short-range connectivity, often between subcortical and cortical structures (Di Martino et al., 2014; Mizuno, Villalobos, Davies, Dahl, & Müller, 2006; Turner, Frost, Linsenbardt, McIlroy, & Müller, 2006) in both resting-state (taskfree) and various task-based paradigms. Furthermore, connectivity within known, well-defined functional networks is decreased, while connectivity between these networks is increased (Gabrielsen et al., 2018; Lawrence, Hernandez, Bookheimer, & Dapretto, 2019; Morgan et al., 2019). Discrepancies in functional connectivity may shift over development, as children with ASD tend to exhibit increased long-range connectivity, while adolescents and adults with ASD mainly demonstrate decreased long-range connectivity (Uddin, Supekar, & Menon, 2013). These findings suggest that throughout life, modulation of neural communication is impaired in individuals with ASD, which can lead to the cognitive and behavioural difficulties experienced by this population.

Most functional connectivity studies in this literature have been conducted using functional MRI (fMRI), which measures changes in blood flow to active brain regions, known as the blood oxygenation level-dependent (BOLD) signal (Ogawa, Lee, Kay, & Tank, 1990). More direct measures of neuronal activity, electroencephalography (EEG) and magnetoencephalography

(MEG), which record the electrical currents (Caton, 1875) and magnetic fields (Cohen, 1968) generated by neuronal firing, respectively, have also been used to characterize functional connectivity patterns in ASD. Whereas fMRI is an indirect measure of brain activity via fluctuations in the BOLD signal, EEG/MEG afford a more direct, multifaceted evaluation of neural communication, as they quantify changes in neurophysiological responses, which are comprised of neural oscillations occurring at different frequencies (Buzsáki & Draguhn, 2004; Lopes da Silva, 2013; Wang, 2010), to which fMRI is blind. These frequency-specific oscillations are associated with particular neural functions (Jensen, Spaak, & Zumer, 2019) and mediate the formation of distinct functional networks (Hipp, Hawellek, Corbetta, Siegel, & Engel, 2012; Palva, Palva, & Kaila, 2005; Siegel et al., 2012).

Importantly, EEG/MEG studies show differences in functional connectivity in ASD that are frequency dependent, whereby reduced long-range functional connectivity is observed in lower frequency bands, and a mix of increased and decreased long-range connectivity is seen in higher frequency bands (Doesburg, Vidal, & Taylor, 2013; Khan et al., 2013; Murias, Webb, Greenson, & Dawson, 2007; Perez Velazquez et al., 2009; Safar et al., 2019; Shou et al., 2017; Takesaki et al., 2016; Ye, Leung, Schäfer, Taylor, & Doesburg, 2014; see O'Reilly, Lewis, & Elsabbagh, 2017 for a review). Such functional connections can be formed on the basis of, for example, correlations in the amplitude envelopes of these oscillations, synchrony in their phases, and coupling between the phase of one signal and the amplitude of another (Bastos & Schoffelen, 2016; Brookes, Woolrich, & Price, 2019; Jensen & Colgin, 2007; Tort, Komorowski, Eichenbaum, & Kopell, 2010). Although these different methods of functional connectivity all facilitate information integration in the brain, this thesis will focus on the contributions of phase synchrony.

#### 1.4.1.1 Phase synchrony

Neuronal activity is oscillatory or cyclical. These oscillations occur at a range of frequencies (Hutcheon & Yarom, 2000; Llinás, 1988), and they interact with each other in a complex manner to perform neuronal computations that give rise to cognition and behaviour (Buzsáki, 2006). Oscillations within a population of neurons synchronize and desynchronize, relative to a baseline period, in response to some event (Pfurtscheller & Lopes da Silva, 1999), and this coordination of activity gives rise to macroscale oscillatory changes that can be measured by EEG/MEG.

The notion that large neuronal ensembles synchronize and produce detectable oscillatory activity in humans arose after Hans Berger first recorded electric signals across the scalp, discovering that when an awake person closed their eyes, the brain produced rhythmic activity at 10 Hz, and when they opened their eyes, the frequency of these oscillations increased (Berger, 1929). He referred to this 10 Hz signal as the "alpha" rhythm, and the faster one as the "beta" rhythm. Other lower- and higher-frequency oscillations in the brain were later determined by other groups (Jasper & Andrews, 1938; Walter, 1936). Their discovery prompted the delineation of frequency bands or ranges in which similar oscillations would occur. These frequency bands are classically named and defined as the delta (<4 Hz), theta (4–7 Hz), alpha (8–13 Hz), beta (14–30 Hz), and gamma (>30 Hz) bands (Chatrian et al., 1974; Kane et al., 2017). Initially, these ranges were somewhat arbitrarily established, though there is now evidence from statistical classification (Lopes da Silva, 2011) and cellular work (Amzica & Lopes da Silva, 2011; Jensen et al., 2019; Steriade, Gloor, Llinás, Lopes da Silva, & Mesulam, 1990) supporting a neurobiological basis for this approximate categorization.

Coordination of frequency-specific oscillations occurs at both the local and global level. Synchronization and desynchronization within a population of neurons produces increases and decreases in focal brain activity, which is sometimes referred to as local power. Fluctuations in local, frequency band-limited power have been linked to a range of cognitive functions. Delta power increases have been observed in decision making, face perception, mental calculation, semantic processing, working memory, and inhibition tasks (Güntekin & Başar, 2016; Harmony, 2013), and it is thought that they are associated with salience detection (Knyazev, 2007) and motivation (Knyazev, 2012). Theta oscillations are involved in phase coding for spatial location (Jensen & Lisman, 2000; O'Keefe & Recce, 1993), episodic memory encoding and retrieval (Herweg, Solomon, & Kahana, 2020; Klimesch, Doppelmayr, Russegger, & Pachinger, 1996; Klimesch et al., 2001; Nyhus & Curran, 2010; Weiss & Rappelsberger, 2000), working memory (Hsieh & Ranganath, 2014; Jensen & Tesche, 2002; Raghavachari et al., 2001; Rutishauser, Ross, Mamelak, & Schuman, 2010), attention (Deiber et al., 2007; Green & McDonald, 2008; Sauseng, Hoppe, Klimesch, Gerloff, & Hummel, 2007), and error processing (Luu, Tucker, & Makeig, 2004; Mazaheri, Nieuwenhuis, van Dijk, & Jensen, 2009; van de Vijver, Ridderinkhof, & Cohen, 2011). Alpha rhythms have been most strongly linked to cortical inhibition of taskirrelevant areas (Bonnefond & Jensen, 2013; Haegens, Nacher, Luna, Romo, & Jensen, 2011;

Jensen & Mazaheri, 2010; Klimesch, Sauseng, & Hanslmayr, 2007; Worden, Foxe, Wang, & Simpson, 2000), which influences conscious awareness and attention (Foxe & Snyder, 2011; Klimesch, 2012; Mathewson, Gratton, Fabiani, Beck, & Ro, 2009; Van Diepen, Foxe, & Mazaheri, 2019). Increased alpha power has also been observed during working memory maintenance (Jensen, Gelfand, Kounios, & Lisman, 2002; Palva & Palva, 2007), though it has been hypothesized that such alpha oscillations are specifically inhibiting brain regions to support working memory maintenance (Bonnefond & Jensen, 2012; Scheeringa et al., 2009; Tuladhar et al., 2007). Beta oscillations have been implicated in movement (Baker, 2007; Jurkiewicz, Gaetz, Bostan, & Cheyne, 2006; Kilavik, Zaepffel, Brovelli, MacKay, & Riehle, 2013; Pfurtscheller, Stancák, & Neuper, 1996; Stancák & Pfurtscheller, 1996), working memory (Chen & Huang, 2016; Deiber et al., 2007; Spitzer & Haegens, 2017; Wimmer, Ramon, Pasternak, & Compte, 2016), decision making (Haegens, Nacher, Hernandez, et al., 2011; Herding, Spitzer, & Blankenburg, 2016), and reward and reinforcement learning (van de Vijver et al., 2011; Yaple et al., 2018). Gamma power is thought to index neuronal information processing (Fries, 2009; Singer, 1993) for feature binding (Desmedt & Tomberg, 1994; Engel & Singer, 2001; Singer & Gray, 1995; Tallon-Baudry & Bertrand, 1999), movement (Crone, Miglioretti, Gordon, & Lesser, 1998; Muthukumaraswamy, 2010; Nowak, Zich, & Stagg, 2018), attention (Fell, Fernández, Klaver, Elger, & Fries, 2003; Fries, Reynolds, Rorie, & Desimone, 2001; Gobbelé, Waberski, Schmitz, Sturm, & Buchner, 2002; Tiitinen, May, & Näätänen, 1997), working memory (Jensen, Kaiser, & Lachaux, 2007; Kaiser & Lutzenberger, 2003; Pesaran, Pezaris, Sahani, Mitra, & Andersen, 2002; Tallon-Baudry, Bertrand, Peronnet, & Pernier, 1998), episodic memory encoding and retrieval (Fell et al., 2001; Nyhus & Curran, 2010; Osipova et al., 2006), and consciousness (Llinás & Ribary, 2006; Llinás, Ribary, Contreras, & Pedroarena, 1998).

Neural oscillations also synchronize over long distances to transmit information between distant brain areas, thereby forming functional networks that contribute to cognition. One method by which this long-range communication occurs is through phase synchrony, wherein the oscillatory phases from disparate neuronal populations align, leading to interregional integration of information (Canolty et al., 2010; Fries, 2015; Palva et al., 2005; Varela et al., 2001; Voytek & Knight, 2015). These long-range connections are mediated more often by lower frequencies (i.e., theta, alpha, and beta) (Schnitzler & Gross, 2005; Solomon et al., 2017; von Stein & Sarnthein, 2000; Zhang, Watrous, Patel, & Jacobs, 2018), as higher gamma frequencies are more prone to

attenuation over long distances (Kopell, Ermentrout, Whittington, & Traub, 2000; Ray & Maunsell, 2015). Importantly, phase synchrony occurs independently from the amplitude or power of local oscillations (Cox, Schapiro, & Stickgold, 2018; Hipp, Engel, & Siegel, 2011; Pesaran, Nelson, & Andersen, 2008; Rosenblum, Pikovsky, & Kurths, 1996; Salinas & Sejnowski, 2001; Siegel, Donner, Oostenveld, Fries, & Engel, 2008), so the processes associated with local power changes are not necessarily carried out via phase synchrony. However, its role in cognitive functions has not been explored as in-depth as that of local power. Phase synchrony in these slower oscillations has been generally linked to interregional communication and topdown control (Buschman & Miller, 2007; Cavanagh & Frank, 2014; D'Andrea et al., 2019; Engel & Fries, 2010; Gross et al., 2004; Klimesch et al., 2007; Sadaghiani et al., 2012; Sauseng et al., 2007; von Stein, Chiang, & König, 2000). In addition, theta-band synchrony between the hippocampus and the cortex is believed to be responsible for memory encoding (Kirk & Mackay, 2003; Lega, Jacobs, & Kahana, 2012; Siapas, Lubenov, & Wilson, 2005), and both theta- (Payne & Kounios, 2009; Sarnthein, Petsche, Rappelsberger, Shaw, & von Stein, 1998; Sauseng, Griesmayr, Freunberger, & Klimesch, 2010; Sauseng et al., 2004) and alpha-band synchrony have been implicated in working memory processes, such as maintenance (Daume, Graetz, Gruber, Engel, & Friese, 2017; Haarmann & Cameron, 2005; Palva, Monto, Kulashekhar, & Palva, 2010; Palva & Palva, 2007; Sato et al., 2018).

Therefore, examining phase synchrony will be key to understanding the specific neural mechanisms underlying long-range functional connectivity differences in the ASD population. The remaining sections of this chapter will detail what we do and do not know regarding phase synchrony and functional connectivity more generally in ASD as they pertain to the cognitive functions of interest in this thesis.

#### 1.4.2 Inhibitory control network in ASD

Inhibition is thought to be regulated by a mainly right-lateralized network of frontoparietal regions (Nee, Wager, & Jonides, 2007; Simmonds, Pekar, & Mostofsky, 2008; Swick, Ashley, & Turken, 2011; Zhang, Geng, & Lee, 2017), including the inferior frontal gyrus (IFG) and adjacent insula, pre-supplementary motor area (pre-SMA), anterior cingulate cortex (ACC), superior parietal lobule (SPL), and inferior parietal lobule (IPL). Of these regions, the right IFG in particular appears to play a significant role in prepotent response inhibition (Aron, Fletcher,

Bullmore, Sahakian, & Robbins, 2003; Aron, Robbins, & Poldrack, 2014; Chambers et al., 2006; Rubia, Smith, Brammer, & Taylor, 2003), especially the posterior portion of the right IFG (Buchsbaum, Greer, Chang, & Berman, 2005; Chikazoe et al., 2009; Swann et al., 2009). In addition, connectivity between the right IFG and pre-SMA may be crucial for suppressing motor responses (Allen, Singh, Verbruggen, & Chambers, 2018; Duann, Ide, Luo, & Li, 2009).

Despite the fact that individuals with ASD show some deficit in response inhibition (Corbett et al., 2009; Geurts et al., 2004; Robinson, Goddard, Dritschel, Wisley, & Howlin, 2009; Solomon, Ozonoff, Cummings, & Carter, 2008; Uzefovsky, Allison, Smith, & Baron-Cohen, 2016; Verté et al., 2005), there has been surprisingly little neuroimaging research investigating differences in brain activation and connectivity related to this aspect of inhibitory control. One EEG study found that children with ASD showed reduced theta power in the ACC (Chan, Han, Leung, et al., 2011), which is typically involved in error and response conflict monitoring (Braver, Barch, Gray, Molfese, & Snyder, 2001; Carter et al., 1998; Carter & van Veen, 2007). Adolescents with ASD, however, demonstrate reduced activity in the IPL (Solomon et al., 2014) in addition to increased activation of the right IFG (Vara, Pang, Doyle-Thomas, et al., 2014). In adulthood, people with ASD exhibit more widespread differences in activation of this inhibitory control network compared to controls. Specifically, they show reduced activation of the right IFG/insula (Shafritz, Bregman, Ikuta, & Szeszko, 2015), ACC (Agam, Joseph, Barton, & Manoach, 2010; Kana, Keller, Minshew, & Just, 2007; Velasquez et al., 2017), and right IPL (Padmanabhan et al., 2015). Other work has demonstrated potential compensatory neural mechanisms in adults with ASD who perform well on inhibition tasks, such as increased right IFG and right fusiform gyrus activity (Duerden et al., 2013), and increased left IFG/insula activation (Schmitz et al., 2006).

In terms of functional connectivity, individuals with ASD show mainly decreased connectivity in this inhibition network across development. Children with ASD show increasingly reduced connectivity between the right IFG and bilateral pre-SMA with age (Lee et al., 2009). Another study found that adolescents with ASD had decreased connectivity between the middle frontal gyrus (MFG) and ACC, but increased connectivity between the IFG and ACC, which the authors speculated reflected a greater reliance on reactive vs. proactive cognitive control in ASD (Solomon et al., 2014). Finally, decreased functional connectivity among nodes of the inhibition network, such as the insula, ACC, and IPL, has been observed in adults with ASD (Kana et al.,

2007). Only one MEG study to date has investigated the spectral component of these connectivity differences in the inhibitory control network during an antisaccade task, where participants must direct their gaze away from a salient cue. It revealed that adults with ASD displayed decreased alpha-band connectivity between the right ACC and right frontal eye field (Kenet et al., 2012), which controls eye movements (Bruce, Goldberg, Bushnell, & Stanton, 1985; Krauzlis, 2005; Vernet, Quentin, Chanes, Mitsumasu, & Valero-Cabré, 2014). This result importantly demonstrated that the ACC may exert less influence on the frontal eye fields in ASD, as alpha oscillations have been linked to inhibition and top-down control (Haegens, Nacher, Luna, et al., 2011; Jensen & Mazaheri, 2010; Klimesch et al., 2007; Snyder, Morais, Willis, & Smith, 2015).

Taken together, atypical activation of and connectivity within the inhibition network appears to be present at all ages in the ASD population. However, there is clearly a paucity of research in this field, especially as the few functional connectivity studies described above included <20 participants in each group. Therefore, further work is needed particularly with regards to understanding the specific functional connectivity differences underlying inhibitory control in ASD, especially as inhibition over the lifespan may be influenced more by network connectivity rather than activity of inhibition-related brain regions (Tsvetanov et al., 2018). In Study 1 (Chapter 2), I explore how whole-brain functional connectivity within different frequency bands during a response inhibition task varies within a relatively large sample of 40 adults with ASD and 39 control adults.

#### 1.4.3 Working memory network in ASD

Working memory is subserved by a bilateral frontoparietal network encompassing the dorsolateral prefrontal cortex (dlPFC), IFG/insula, dorsal cingulate cortex and neighbouring ACC, IPL, and precuneus (Mencarelli et al., 2019; Owen, McMillan, Laird, & Bullmore, 2005; Rottschy et al., 2012; Yaple, Stevens, & Arsalidou, 2019). The two most prominent regions of this network are the IPL and dlPFC. The left and right IPL are thought to represent the phonological loop and visuospatial sketchpad of Baddeley's (2012) model, respectively, being involved in the maintenance of verbal and visuospatial stimulus representations (Andersen, Essick, & Siegel, 1985; Baldo & Dronkers, 2006; Finke, Bublak, & Zihl, 2006; Geier, Garver, Terwilliger, & Luna, 2009; Jonides et al., 1998; Paulesu, Frith, & Frackowiak, 1993; Tsukiura et

al., 2001). The dIPFC acts as the central executive, supporting the maintenance and manipulation of items in working memory by exercising top-down control over the IPL (Barbey, Koenigs, & Grafman, 2013; Blumenfeld & Ranganath, 2006; D'Esposito et al., 1995; D'Esposito, Postle, & Rypma, 2000; D'Esposito & Postle, 2015; Edin et al., 2009; Wager & Smith, 2003). Connectivity between the dIPFC and posterior regions, including the IPL, has been linked to the active maintenance of information in working memory (Egner & Hirsch, 2005; Feredoes, Heinen, Weiskopf, Ruff, & Driver, 2011; Friedman & Goldman-Rakic, 1994; Gazzaley, Rissman, & D'Esposito, 2004; Honey et al., 2002; Rottschy et al., 2013), which may be mediated by alpha oscillations (Daume et al., 2017; Palva et al., 2010; Sato et al., 2018; Sauseng et al., 2005). However, theta-band synchrony has also been observed in working memory tasks, potentially subserving top-down control and memory retrieval processes (Dai et al., 2017; Hoy et al., 2016; Johnson et al., 2017; Klimesch, Freunberger, Sauseng, & Gruber, 2008; Payne & Kounios, 2009; Roux & Uhlhaas, 2014; Sauseng et al., 2004, 2006).

During tasks of both verbal and visuospatial working memory, individuals with ASD exhibit atypical activation of this working memory-related frontoparietal network. Children and adolescents with ASD demonstrate increased activity in the dlPFC (Urbain, Pang, & Taylor, 2015; Yeung, Lee, & Chan, 2019). On the other hand, adults with ASD have decreased activation of the dlPFC (Braden et al., 2017; Koshino et al., 2008; Luna et al., 2002) and dorsal ACC (Di Martino et al., 2009), as well as atypical lateralization of IPL activity (Koshino et al., 2005). Therefore, it seems that recruitment of the dlPFC may follow a distinctive maturational trajectory, where it is overactive in childhood and adolescence, but underactive in adulthood. However, throughout development, people with ASD do not show appropriate load-dependent activation of the dlPFC and other frontoparietal network regions (Rahko et al., 2016; Vogan, Francis, Morgan, Smith, & Taylor, 2018; Vogan, Morgan, Smith, & Taylor, 2018; Vogan, Morgan, Smith, & Taylor, 2019). One MEG study determined that this poor modulation of dlPFC activity may be restricted to the theta frequency band (Larrain-Valenzuela et al., 2017).

Reduced connectivity among frontoparietal regions and other brain areas also appears to persist from childhood into middle age (Barendse et al., 2018; Braden et al., 2017; Koshino et al., 2005, 2008; Urbain et al., 2016). In adulthood, this frontoparietal network may demonstrate atypical lateralization, as during a verbal working memory task, the bilateral dlPFC was synchronized with the left IPL in controls, but they showed stronger connectivity with the right IPL in the ASD group (Koshino et al., 2005). The frequency band(s) in which these disparities occur has only been examined by one MEG study of children with ASD, which found that they had reduced alpha-band connectivity relative to typically-developing children during recognition of stimuli in working memory (Urbain et al., 2016). Hence, the spectral differences in frontoparietal network connectivity in adults with ASD and their relationship to specific working memory processes remain to be explored, which will be crucial to understanding the particular neurophysiological basis of the working memory difficulties reported in the ASD population. Study 2 (Chapter 3) addresses this gap by examining whether adults with ASD show atypical frontoparietal network connectivity within particular frequency bands during maintenance and recognition of recently presented visual stimuli in working memory.

#### 1.4.4 ToM and FB network in ASD

Several reviews and meta-analyses have pinpointed a set of core regions involved in ToM, including FB understanding: the medial prefrontal cortex (mPFC), temporoparietal junction (TPJ), and precuneus (Bzdok et al., 2012; Molenberghs, Johnson, Henry, & Mattingley, 2016; Schurz, Radua, Aichhorn, Richlan, & Perner, 2014; Tso, Rutherford, Fang, Angstadt, & Taylor, 2018; Van Overwalle, 2009; van Veluw & Chance, 2014). The mPFC has been implicated in decoupling mental states from reality (Döhnel et al., 2012; Fletcher, Happé, et al., 1995; Frith & Frith, 2003; Jenkins & Mitchell, 2010; Schuwerk, Döhnel, et al., 2014). It is furthermore thought to help differentiate one's own mental state from others', in that the dorsal and ventral portions are associated with processing other and self mental representations, respectively (Amodio & Frith, 2006; Denny, Kober, Wager, & Ochsner, 2012; Frith & Frith, 2006; Mitchell, Banaji, & Macrae, 2005), a distinction which arises over development (Moriguchi, Ohnishi, Mori, Matsuda, & Komaki, 2007). The TPJ is involved in attributing mental states and intentions to individuals (Apperly, Samson, Chiavarino, & Humphreys, 2004; Gobbini, Koralek, Bryan, Montgomery, & Haxby, 2007; Kobayashi, Glover, & Temple, 2007; Perner, Aichhorn, Kronbichler, Staffen, & Ladurner, 2006; Saxe & Kanwisher, 2003; Schuwerk, Döhnel, et al., 2014; Van Overwalle, 2009; Zaitchik et al., 2010). Activation of the right TPJ, in particular, is believed to signify mental states that are incongruent with either one's own mental state or with reality, which takes place in FB tasks (Aichhorn, Perner, Kronbichler, Staffen, & Ladurner, 2006; Mossad et al., 2016; Quesque & Brass, 2019; Saxe & Wexler, 2005; Sommer et al., 2007; but see Döhnel et al., 2012; Lombardo, Chakrabarti, Bullmore, MRC AIMS Consortium, &

Baron-Cohen, 2011). The precuneus' role in ToM has been less explored, but some have speculated that it may be responsible for visualizing people's perspectives using mental imagery (Arora, Schurz, & Perner, 2017; Cavanna & Trimble, 2006; Schurz, Aichhorn, Martin, & Perner, 2013; Vogeley et al., 2004). An EEG study revealed that FB processing may be facilitated by broad fronto-parieto-occipital connectivity in the beta band, potentially signalling the need for greater top-down control to consider conflicting perspectives and mental states (Guan, Farrar, & Keil, 2018).

Although FB tasks are frequently used in the behavioural literature to assess ToM, very few studies have investigated the neural correlates of FB understanding in the ASD population. This work has demonstrated that although their performance on first-order FB tasks is comparable to controls, individuals with ASD show atypical activation of ToM-related brain regions during these paradigms. One MEG study found that children with ASD, compared to typicallydeveloping children, showed decreased activation of the TPJ but simultaneous increased activation of the right IFG, indicating that children with ASD may rely more on executive functions, specifically inhibition, rather than mentalizing to infer FB (Yuk et al., 2018). Similarly, one fMRI study of adults with ASD observed decreased activity in the TPJ for FB reasoning (Nijhof, Bardi, Brass, & Wiersema, 2018), although others have found increased TPJ activation (Sommer et al., 2018) or no differences in recruitment of any region of the FB/ToM network between adults with and without ASD (Dufour et al., 2013). While some fMRI work utilizing other ToM tasks has documented increased activation of the mPFC and TPJ in children (Kim et al., 2016) and adolescents with ASD (White, Frith, Rellecke, Al-Noor, & Gilbert, 2014), or no neural differences between individuals with and without ASD across development (Moessnang et al., 2020), several other studies have established that children, adolescents, and adults with ASD exhibit decreased activity in these regions (Assaf et al., 2013; Happé et al., 1996; Kana, Keller, Cherkassky, Minshew, & Just, 2009; Kana, Libero, Hu, Deshpande, & Colburn, 2014; Kana et al., 2015; Lombardo et al., 2011; O'Nions et al., 2014), which are atypically recruited for both ToM and non-ToM functions (Mason, Williams, Kana, Minshew, & Just, 2008; von dem Hagen, Stoyanova, Rowe, Baron-Cohen, & Calder, 2014). Of note, a recent EEG study of joint attention in children with ASD found decreased beta power in the right TPJ in the ASD group (Soto-Icaza, Vargas, Aboitiz, & Billeke, 2019).

To date, there have been no neuroimaging studies examining whether individuals with ASD show differential functional connectivity during FB understanding. Only three fMRI studies from one group using mental state and intention attribution tasks have reported reduced connectivity in the ToM network in children, adolescents, and adults with ASD (Kana et al., 2009, 2014, 2015). With regards to phase synchrony, one MEG experiment using a resting-state paradigm found that adolescents and adults with ASD may have reduced top-down control of the ToM network, as they showed reduced alpha-band connectivity between relevant brain regions, which was associated with greater social impairment in everyday life (Ghuman, van den Honert, Huppert, Wallace, & Martin, 2017). As these connectivity studies had <20 participants in each of the ASD and control groups, further research is needed to replicate these findings with larger samples, which provide greater statistical power. This will also help us better understand the nature of connectivity differences underlying ToM and especially FB reasoning in ASD, which may also help clarify the mixed reports of brain activation related to FB processing in adults with ASD is investigated in Study 3 (Chapter 4).

#### 1.5 Thesis rationale and hypotheses

There are large gaps in the literature regarding our understanding of how differences in brain networks contribute to the ToM and executive function difficulties experienced by adults with ASD. While existing neuroimaging work in ASD points to a general impairment in functional connectivity among brain regions involved in these higher cognitive functions, potential differences in the neural mechanisms through which these areas communicate have yet to be determined. Therefore, this thesis investigates whether phase synchrony in the theta, alpha, and beta frequency bands, which are known to mediate long-range connectivity in the brain (Hipp et al., 2012; Siegel et al., 2012; Varela et al., 2001; von Stein et al., 2000; Wang, Göschl, Friese, König, & Engel, 2019), differs between adults with and without ASD during standard tasks of executive functions and ToM. To this end, large, mostly overlapping samples of 39 control adults and 40 adults with ASD were recruited to participate in tasks of inhibition, working memory, and FB while undergoing neuroimaging.

Study 1 (Chapter 2) examines whether adults with and without ASD show different profiles of functional connectivity while exercising inhibitory control in a Go/No-go response inhibition

task. As alpha band oscillations have been linked to suppression of neural activity (Haegens, Nacher, Luna, et al., 2011; Jensen & Mazaheri, 2010; Klimesch et al., 2007), I hypothesized that adults with ASD would show decreased alpha-band connectivity between brain regions responsible for exerting inhibition, such as the right IFG, and those that may interfere with task performance compared to control adults.

Study 2 (Chapter 3) investigates how frontoparietal network connectivity may diverge in adults with ASD while maintaining and recognizing visual stimuli in working memory during an *n*-back task. Given the widely acknowledged role of alpha-band synchrony in working memory maintenance (Palva et al., 2010; Sato et al., 2018; Sauseng et al., 2005), and previous work revealing reduced alpha-band connectivity in children with ASD during working memory recognition (Urbain et al., 2015), I predicted that relative to control adults, the frontoparietal network in adults with ASD would exhibit impaired alpha-band connectivity with the rest of the brain during working memory maintenance and recognition processes.

Study 3 (Chapter 4) explores functional connectivity patterns in cortical regions of the brain in adults with and without ASD while performing a first-order FB task. I expected that adults with ASD would show atypical beta-band connectivity during FB reasoning, especially between the two major nodes of the FB/ToM network, the mPFC and TPJ, since recent work found involvement of beta-band oscillations in FB understanding (Guan et al., 2018).

In all three studies, I use MEG to record neural activity related to the cognitive functions elicited by each task. The high temporal resolution of MEG recordings not only affords a precise examination of brain networks that evolve on the order of milliseconds, but it also allows for accurate measurement of phase synchrony between brain regions in the theta, alpha, and beta frequency bands, neither of which is possible with the often-used fMRI. These advantageous facets of MEG data provide a more comprehensive picture of the neurobiology underlying ToM and executive function processes. Thus, these experiments will expand our current understanding of neural mechanisms that contribute to cognitive impairments in adults with ASD. Findings from these studies are valuable, as they can be leveraged to identify viable targets for neurostimulation interventions, as well as to examine the efficacy of behavioural therapies in modifying relevant brain activity to improve outcomes in adults with ASD.
# Chapter 2 Study 1

# 2 Alpha connectivity and inhibitory control in adults with autism spectrum disorder

Yuk, V., Dunkley, B.T., Anagnostou, E., & Taylor, M.J.

This chapter is a reformatted version of a manuscript under revision for Molecular Autism.

# 2.1 Abstract

Background: Individuals with autism spectrum disorder (ASD) often report difficulties with inhibition in everyday life. During inhibition tasks, adults with ASD show reduced brain activity and functional connectivity, suggesting impairments in inhibitory control on the neural level. Our study further investigated these differences by using magnetoencephalography (MEG) to examine the frequency band(s) in which functional connectivity underlying response inhibition occurs, as brain functions are frequency specific, and whether connectivity in certain frequency bands differs in adults with ASD.

Methods: We analyzed MEG data from 40 adults with ASD (27 males;  $26.94 \pm 6.08$  years old) and 39 control adults (27 males;  $27.29 \pm 5.94$  years old) who performed a Go/No-go task. The task involved two blocks with different proportions of No-go trials: Inhibition (25% No-go) and Vigilance (75% No-go). We compared whole-brain connectivity in the two groups during correct No-go trials in the Inhibition vs. Vigilance blocks between 0–400 ms.

Results: Despite comparable performance on the Go/No-go task, adults with ASD showed reduced connectivity compared to controls in the alpha band (8–14 Hz) in a network with a main hub in the right inferior frontal gyrus. Decreased connectivity in this network predicted more self-reported difficulties on a measure of inhibition in everyday life.

Limitations: Measures of everyday inhibitory control were not available for all participants, so this relationship between reduced network connectivity and inhibitory control abilities may not be necessarily representative of all adults with ASD or the larger ASD population. Further research with independent samples of adults with ASD, including lower functioning participants would be valuable.

Conclusions: Our findings demonstrate reduced functional brain connectivity during response inhibition in adults with ASD. As alpha-band synchrony has been linked to top-down control mechanisms, we hypothesize that the lack of alpha synchrony observed in our ASD group may reflect difficulties in suppressing task-irrelevant information, interfering with inhibition in real-life situations.

# 2.2 Introduction

The extent to which individuals with autism spectrum disorder (ASD) experience difficulties with inhibition has been investigated across a variety of tasks. While there are reports showing some preserved inhibition in this population (Adams & Jarrold, 2012; Goldberg et al., 2005; Sanderson & Allen, 2013), others appear to suggest deficits in inhibitory control in people with ASD (Corbett et al., 2009; Gioia, Isquith, Kenworthy, & Barton, 2002; Uzefovsky et al., 2016; van den Bergh et al., 2014), such as in response inhibition specifically (Demetriou et al., 2018; Geurts, van den Bergh, et al., 2014; Hill, 2004; Luna et al., 2007). Moreover, as inhibition may underlie working memory (Hasher et al., 2007) and cognitive flexibility (Diamond, 2013), impairments in inhibition can have significant downstream effects on more complex behaviours required in everyday life in individuals with ASD, such as in reciprocal conversation (Hutchison, Müller, & Iarocci, 2020).

These behavioural reports of inhibition deficits suggest differences in the functioning of the inhibitory control brain network in ASD. This network consists of several right-lateralized frontoparietal regions (Sebastian et al., 2013; Swick et al., 2011; Zhang et al., 2017), including the inferior frontal gyrus (IFG), insula, supplementary motor area (SMA), anterior cingulate cortex (ACC), and inferior and superior parietal lobules (IPL and SPL), of which the right IFG plays a prominent role (Aron et al., 2003, 2014; Chambers et al., 2006; Rubia et al., 2003). Studies using magnetoencephalography (MEG), which is sensitive to the timing of neural activity (Hari & Salmelin, 2012), have illustrated that these regions appear to be maximally active between 200-400 ms, after stimulus onset (Lin, Tseng, & Cheng, 2018; Vara, Pang, Vidal, Anagnostou, & Taylor, 2014; Vidal, Mills, Pang, & Taylor, 2012). This neural activity consists of oscillations at different frequencies, specifically in the theta (4–7 Hz), alpha (8–14 Hz), and beta bands (15–30 Hz), each of which plays a certain role in successful inhibition. For instance, greater oscillatory activity or power in the theta band has been observed selectively in trials involving response inhibition (Kirmizi-Alsan et al., 2006; Yamanaka & Yamamoto, 2010), potentially indicating the monitoring of conflicting responses (Huster, Enriquez-Geppert, Lavallee, Falkenstein, & Herrmann, 2013; Nigbur, Ivanova, & Stürmer, 2011). Increases in alpha power within brain regions are thought to reflect inhibition of a learned response or of taskirrelevant areas (de Pesters et al., 2016; Jensen & Mazaheri, 2010; Klimesch et al., 2007), while

beta oscillations are believed to signify inhibition of a motor response (Fonken et al., 2016; Picazio et al., 2014; Swann et al., 2012) and maintenance of an ongoing sensorimotor or cognitive state (Engel & Fries, 2010). However, the significance of connectivity or synchrony of these oscillations between brain regions in the context of inhibitory control has not been well investigated, though inter-areal theta, alpha, and beta synchrony appear to be related generally to top-down control and information communication and integration (Brovelli et al., 2004; Fries, 2005; Kopell et al., 2000; Palva & Palva, 2011; Sadaghiani et al., 2012; von Stein et al., 2000).

Several studies have demonstrated atypical activation and functional connectivity of this inhibition brain network in the ASD population, even when behavioural differences were not observed. Compared to controls, many individuals with ASD exhibit reduced activation of regions in this network, such as in the right IFG and insula (Shafritz et al., 2015), ACC (Agam et al., 2010; Kana et al., 2007; Velasquez et al., 2017), and right IPL (Padmanabhan et al., 2015; Vara, Pang, Doyle-Thomas, et al., 2014), as well as decreased connectivity between nodes of the inhibition network (Agam et al., 2010; Kana et al., 2007), which may be specific to the alpha band (Kenet et al., 2012), and which may worsen with age (Lee et al., 2009). Conversely, a few fMRI studies have shown increased activity in areas within and outside of the inhibition network (Duerden et al., 2013; Schmitz et al., 2006) and increased connectivity between regions within this network that differed from connectivity patterns in controls (Solomon et al., 2014), suggesting the development of alternative neural mechanisms of inhibitory control in these samples. Furthermore, some studies have found that these differences in activity and connectivity relate to task performance and ASD symptomatology (Agam et al., 2010; Shafritz et al., 2015; Solomon et al., 2014; Velasquez et al., 2017). Taken together, it appears that individuals with ASD have alterations in their recruitment of brain regions responsible for inhibitory control, which correlate with behaviour.

The present study further examines functional brain connectivity involved in inhibition in adults with ASD to better understand the relationship between these differences in brain function and the inhibitory difficulties experienced by this population. Despite considerable evidence that individuals with ASD have altered functional connectivity – often reduced connectivity (Di Martino et al., 2014; Just et al., 2012; Maximo et al., 2014; O'Reilly et al., 2017) – there has been little research investigating differences in connectivity patterns during inhibitory control in individuals with ASD. Only one study with a small N (11/group) has explored the specificity of

these differences to particular frequency bands (Kenet et al., 2012), even though oscillations at different frequencies are thought to underlie distinct inhibitory processes. Thus, we investigated whether adults with ASD, compared to controls, would show differences in functional brain connectivity during a Go/No-go response inhibition task using MEG, which is capable of accurately resolving the timing and frequency of neural activity (Hari & Salmelin, 2012). Specifically, we examined whole-brain connectivity in the theta, alpha, and beta frequency bands between 0–400 ms, post stimulus onset, as this window would capture the peak activation of the inhibitory control network and relevant oscillation frequencies described above. Based on previous work implicating alpha oscillations in inhibition (Jensen & Mazaheri, 2010; Klimesch et al., 2007; Palva & Palva, 2011) and demonstrating reduced alpha-band connectivity in adults with ASD while suppressing prepotent saccadic eye movements (Kenet et al., 2012), we hypothesized that adults with ASD would show decreased connectivity in the alpha band during response inhibition. Although this alpha-band underconnectivity may not lead to task performance differences, we predicted that its effects may be exacerbated in real-life settings and would therefore contribute to these difficulties with inhibition in everyday life.

# 2.3 Methods and materials

#### 2.3.1 Participants

We recruited 45 control adults and 54 adults with ASD between the ages of 18–40 years for this study. We screened for full-scale, two subtest IQ  $\geq$  70 (as measured by the Wechsler Abbreviated Scale of Intelligence (WASI or WASI-II; Wechsler, 1999, 2011), no premature birth, no MRI or MEG contraindications, and in the control group specifically, no history of developmental, neurological, psychiatric, or psychological disorders. All participants with ASD received a primary diagnosis of ASD from a clinical expert. After standard preprocessing of the MEG data, we excluded 14 adults with ASD due to poor task performance ( $\leq$ 50% on Go trials, or  $\leq$ 50% on No-go trials in the Vigilance condition; see the 'Go/No-go MEG task' section for a description of the Vigilance condition), poor head localization, or excessive artefacts in the MEG data, such that <40 trials (half the total possible number of trials) remained after data preprocessing. Subsequently, six control adults were excluded when matching the groups on age and sex.

In the final sample, there were 39 control adults and 40 adults with ASD. The two groups did not differ on age (t(77) = 0.26, p = 0.79), sex ( $X^2(1) = 0$ , p = 1), or IQ (t(65.28) = 1.01, p = 0.32). In the ASD group, 37 adults were scored on the Autism Diagnostic Observation Schedule, Generic or Version 2 (ADOS-G or ADOS-2; Lord et al., 2000, 2012), where higher scores denote greater ASD symptomatology. Demographic data are presented in Table 2.1. No control adults reported taking any psychotropic medication, while 21 adults with ASD stated current psychotropic medication use (Appendix A). All participants gave informed written consent. This study was approved by the Research Ethics Board at the Hospital for Sick Children.

#### Table 2.1

	<b>Control</b> ( <i>N</i> = <b>39</b> )	<b>ASD</b> ( $N = 40$ )
	Mean (SD) or Count	Mean (SD) or Count
Age	27.29 (5.94)	26.94 (6.08)
Sex	27 M, 12 F	27 M, 13 F
Handedness	33 R, 6 L	35 R, 5 L
Full-scale IQ	114.24 (11.33) Range: [92–157], <i>n</i> = 38	110.95 (16.63) Range: [72–136], <i>n</i> = 38
ADOS CSS		6.95 (2.15) Range: [2–10], <i>n</i> = 37

Demographic data

ADOS = Autism Diagnostic Observation Schedule; CSS = calibrated severity score

# 2.3.2 Experimental design

#### 2.3.2.1 Questionnaires

We asked participants to rate themselves on their executive functioning abilities using the Behavior Rating Inventory of Executive Function, Adult Version (BRIEF-A; Roth, Isquith, & Gioia, 2005). Participants were also rated on this questionnaire by an informant, or someone who knew the participant well (i.e., parent, partner, close friend, etc.). *T* scores on the Inhibit scale of the BRIEF-A were taken as measures of their everyday inhibitory control, with higher scores indicating poorer inhibition. Participants were also asked to complete the Social Responsiveness

Scale, Second Version (SRS-2; Constantino & Gruber, 2012). SRS-2 Total *t* scores were used as a measure of ASD symptom severity, wherein higher scores represent more severe ASD symptomatology.

## 2.3.2.2 Go/No-go MEG task

Participants performed a Go/No-go task in the MEG scanner (Fig. 2.1), adapted from previous work in our lab (Vara, Pang, Doyle-Thomas, et al., 2014; Vara, Pang, Vidal, et al., 2014; Vidal et al., 2012). They were asked to press a button as quickly as possible in response to Go stimuli, which were five geometric shapes that were either blue or purple, totalling ten possible stimuli. Participants were also instructed to refrain from responding to No-go stimuli, which consisted of the same Go stimuli, but with a white 'x' superimposed on the centre of the shape. On each trial, the stimuli appeared in the middle of a grey box measuring 5x5 cm, centred on a black background. Between trials, a black fixation cross appeared in the centre of the grey box.

To maintain a rapid response rate, we adapted the stimulus and interstimulus interval (ISI) durations to participants' performance, as done previously (e.g., Vara, Pang, Vidal, et al., 2014). Stimulus duration ranged between 300-700 ms, while ISI duration ranged between 650-1300 ms, plus a random jitter of  $\pm 200$  ms; at the beginning of the task, stimulus and ISI durations were at maximum. Durations were increased or decreased within these ranges to maintain an overall accuracy of about 80% in No-go trials and 95% in Go trials. A more detailed description of the protocol for adjusting these durations can be found in Appendix B.

The task was run in two counterbalanced blocks: Inhibition and Vigilance. In the Inhibition condition, 75% of trials were Go and 25% were No-go, to ensure the establishment of a prepotent response that would have to be inhibited during the No-go trials. In the Vigilance condition, 25% of trials were Go and 75% were No-go, so very little inhibitory control was required for No-go trials. The Vigilance condition was run as a control for the Inhibition condition; while much of the existing literature has compared No-go trials to Go trials, the Go trials contain a strong motor response not present in No-go trials, so we instead contrasted No-go trials from a highly demanding situation (i.e., Inhibition) to those in a less demanding situation (i.e., Vigilance).

Participants were familiarized with both blocks of the task before the MEG session. In the MEG scanner, the stimuli were back-projected onto a screen that was 80 cm away from the dewar and presented using *Presentation 18.1* (Neurobehavioral Systems Inc.,

https://www.neurobs.com/presentation). Each of the blocks ended when participants successfully completed 80 correct No-go trials or until 10 minutes had passed; the protocol was the same across all participants. There were no significant group differences in the total number of trials completed (Appendix C) in either the Inhibition (t(76.38) = 1.44, p = 0.16) or Vigilance conditions (t(76.56) = 0.37, p = 0.71).



**Figure 2.1** – The Go/No-go task. Participants were instructed to press a button as quickly as possible upon seeing the Go stimuli (solid blue or purple shapes) and inhibit this response for No-go stimuli (solid blue or purple shapes with a white 'x' in the middle). No-go trials are highlighted in this figure with a coloured border. Stimuli were presented for a duration ranging from 300–700 ms, and ISIs lasted from 650–1300 ms, with a jitter of ±200 ms. Stimulus presentation and ISI length were adapted to participants' performance. Participants completed two blocks of this task: Inhibition (75% Go and 25% No-go trials) and Vigilance (25% Go and 75% No-go trials).

# 2.3.2.3 MEG data acquisition

Participants' MEG data were acquired while lying supine in a 151-channel CTF MEG system (Coquitlam, British Columbia, Canada) inside a magnetically shielded room. Head position was

monitored in real time using fiducial coils located on the nasion and the left and right preauricular points. Data were sampled at 600 Hz, and a third-order spatial gradient and an antialiasing low-pass filter of 150 Hz were applied.

## 2.3.2.4 MRI data acquisition

Participants' MRI data were acquired in a 3.0 T MRI scanner (MAGNETOM, Siemens AG, Erlangen, Germany) using a 12-channel head coil. Radio-opaque markers were placed at the MEG fiducial points, allowing for later MEG-MRI co-registration. T1-weighted MRI scans were obtained with the 3D SAG MPRAGE sequence (GRAPPA = 2, TR/TE/FA = 2300 ms/2.96 ms/9°, FOV = 192x240x256 mm, voxel size = 1.0 mm isotropic).

## 2.3.3 Statistical analysis

#### 2.3.3.1 Behavioural data

We examined the effects of group (control vs. ASD), rater (self vs. informant) and IQ, as well as the interaction between group and rater, on Inhibit scale scores of the BRIEF-A. We also investigated the effects of group (control vs. ASD), condition (Inhibition vs. Vigilance), age, and IQ, in addition to the interaction between group and condition, on participants' accuracy on our Go/No-go task. D-prime (d') was used as a measure of accuracy or ability to distinguish between Go and No-go stimuli. It was calculated by taking the difference between the *z*-transformed hit rate and the *z*-transformed false alarm rate: d' = z(hit rate) - z(false alarm rate). Correct No-go trials were considered as hits, while incorrect Go trials were deemed as false alarms. All behavioural data were analyzed using linear mixed effects models, as implemented by the nlme package, in R 3.5.0 (R Core Team, https://www.r-project.org/). Significant results are reported at p < 0.05.

# 2.3.3.2 MEG data

We analyzed the MEG data using FieldTrip (Oostenveld, Fries, Maris, & Schoffelen, 2011) in MATLAB 2017b (The MathWorks, www.mathworks.com/products/matlab/). Trials were epoched from -1500 to 2000 ms, relative to the onset of the No-go stimulus. Data were filtered offline between 1–150 Hz using a fourth-order Butterworth bandpass filter. A notch filter was also applied to remove line noise and its harmonic (60 and 120 Hz). Eyeblink and heartbeat artefacts were manually identified and removed from the data using independent component

analysis. Trials containing signals exceeding 2000 fT or head motion exceeding 5 mm from the median head position were deemed artefactual and removed. Only correct trials were analysed.

To generate the forward model, each participant's MRI data were co-registered to their MEG data using the fiducials, then used to calculate a subject-specific head model based on the single-shell method (Nolte, 2003). Source activity was estimated at the centre of mass of the 90 AAL atlas regions (Tzourio-Mazoyer et al., 2002) using a linearly constrained minimum variance beamformer (Van Veen, Van Drongelen, Yuchtman, & Suzuki, 1997) with 5% regularization and centre-of-head bias correction via the neural activity index. A common spatial filter was created using the covariance matrix computed over all trials, through which the entire continuous dataset (after artefact removal) was then projected. This dataset was then epoched as described above.

We took the weighted phase lag index (wPLI; Vinck, Oostenveld, Van Wingerden, Battaglia, & Pennartz, 2011) as a measure of phase synchrony between each pairwise connection (excluding those to and from Heschl's gyrus and olfactory cortex, as the primary auditory and olfactory areas are irrelevant to this task). wPLI values were calculated over trials using the cross-spectral density matrix, which was computed for signals from -500 to 1000 ms within each frequency band of interest (theta: 4–7 Hz; alpha: 8–14 Hz; beta: 15–30 Hz) using wavelets with a width of seven cycles. Pairwise wPLI values were transformed into *z* scores using the values in the baseline window (-500 to 0 ms), then averaged over our time window of interest, 0–400 ms. Connectivity matrices containing these normalized wPLI values were then subjected to statistical analysis to examine within- and between-group differences in network connectivity.

We used the Network-Based Statistic toolbox (Zalesky, Fornito, & Bullmore, 2010) to identify broadly distributed networks in theta, alpha, and beta that were specifically recruited for inhibitory control, relative to our control condition. We performed planned comparison *t* tests to detect networks that showed increased connectivity in the Inhibition vs. Vigilance condition in each group (Control, Inhibition > Vigilance; ASD, Inhibition > Vigilance), as well as between groups (ASD < Control, Inhibition > Vigilance; ASD > Control, Inhibition > Vigilance). To determine these networks, the *t* tests were applied at each pairwise connection and thresholded at values exceeding *t* = 2.641 (equivalent to *p* < 0.005). The largest network of contiguous suprathreshold connections was then subjected to permutation testing (5000 permutations), whereby an empirical null distribution of maximal network size was established by shuffling group labels. A family-wise error (FWE) corrected *p* value was calculated, signifying the probability of finding a network of equivalent or greater size, given the number of permutations, if the null hypothesis were true. Significant networks are reported at  $p_{FWE} < 0.05$  and visualized using BrainNet Viewer (Xia, Wang, & He, 2013).

## 2.3.3.3 Brain-behaviour relations

We explored the relations between any networks showing significant group differences and participants' everyday inhibitory control, ASD symptom severity, and task performance. Specifically, we tested whether mean network connectivity values in these networks would predict any of these measures, and whether group status moderated this effect. Self-rated scores on the Inhibit scale of the BRIEF-A were used as an estimate of inhibitory control. SRS-2 self-rated Total scores were taken as an indication of severity of ASD symptoms. Task performance was determined using d' scores. Analyses were performed in R 3.5.0 (R Core Team, https://www.r-project.org/). Significant results are reported at p < 0.05.

# 2.4 Results

# 2.4.1 BRIEF-A ratings

While adults with ASD were rated by both themselves and their informants overall on the BRIEF-A as having more difficulties with inhibition compared to controls, this main effect of group across both self and informant ratings was only trending toward significance (F(1,39) = 3.95, p = 0.054, d = 0.25). However, scores did significantly differ between raters (F(1,40) = 7.17, p = 0.011, d = 0.13), such that participants reported having more inhibitory control problems than their informants did (Fig. 2.2). Both self and informant ratings on the BRIEF-A are described in Table 2.2.



**Figure 2.2** – *T* scores on the Inhibit scale of the BRIEF-A. Only the difference in raters' scores was statistically significantly different (F(1,40) = 7.17, p = 0.011, d = 0.13). There was a small, but nonsignificant difference between groups (F(1,39) = 3.95, p = 0.054, d = 0.25).

\* p < 0.05

#### Table 2.2

Questionnaire self and informant ratings

	<b>Control</b> ( <i>N</i> = <b>39</b> )	ASD (N = 40)	
-	Mean (SD)	Mean (SD)	
BRIEF-A Inhibit Scale t Score			
Self	49.47 (8.74) Range = [37–65], <i>n</i> = 17	53.63 (8.19) Range = [37–71], <i>n</i> = 27	
Informant	45.47 (5.43) Range = [39–57], <i>n</i> = 17	51.30 (11.39) Range = [39–76], <i>n</i> = 27	
SRS-2 Total t Score			
Self	48.63 (9.00) Range = [36–72], <i>n</i> = 16	66.71 (9.69) Range = [51–90], <i>n</i> = 28	
Informant	43.94 (6.79) Range = [36–59], <i>n</i> = 16	64.82 (10.93) Range = [48–86], <i>n</i> = 28	

BRIEF-A = Behavior Rating Inventory of Executive Function, Adult Version; SRS-2 = Social Responsiveness Scale, Second Version

# 2.4.2 Task performance

Adults with and without ASD performed equally well on the Go/No-go task (F(1,72) = 0.044, p = 0.84, d = 0.002), measured by d'. Both groups showed decreased accuracy during the Inhibition condition compared to the Vigilance condition (F(1,74) = 197.81, p < 0.0001, d = 1.02; Fig. 2.3). Measures of task performance are detailed in Table 2.3, and trial numbers in each condition are detailed in Appendix C.



**Figure 2.3** – Accuracy on the Go/No-go task. There was a main effect of condition, where accuracy was poorer in the Inhibition than the Vigilance condition (F(1,74) = 197.81, p < 0.0001, d = 1.02).

\*\*\* *p* < 0.001

#### Table 2.3

Performance on the Go/No-go task

	<b>Control</b> ( <i>N</i> = <b>39</b> )	ASD (N = 40)
	Mean (SD)	Mean (SD)
Inhibition		
Accuracy (d')	3.41 (0.60)	3.43 (0.76)
Hit rate (%)	82.72 (7.37)	83.31 (3.43)
False alarm rate (%)	1.39 (1.91)	1.70 (3.21)
Median RT of Go trials (ms)	298.72 (37.77)	321.79 (42.54)
Vigilance		
Accuracy (d')	4.41 (0.24)	4.38 (0.29)
Hit rate (%)	99.44 (1.04)	99.18 (1.26)
False alarm rate (%)	0.58 (1.38)	0.29 (1.02)
Median RT of Go trials (ms)	379.83 (54.79)	393.00 (66.54)

RT = response time

## 2.4.3 Neuroimaging

## 2.4.3.1 Within-group results

Control adults displayed greater functional connectivity in the Inhibition than the Vigilance condition in the theta, alpha, and beta frequency bands between 0–400 ms (Fig. 2.4A). In the theta band, a broadly distributed network with a main hub (i.e., having a high number or degree of connections) in the right IFG was recruited ( $p_{FWE} < 0.001$ ). A network in the alpha band with hubs in the left thalamus, left ventromedial prefrontal cortex (vmPFC), and right SPL, and which involved the right IFG, was also engaged ( $p_{FWE} = 0.004$ ). A right-lateralized network in the beta band was additionally recruited ( $p_{FWE} = 0.037$ ), with the right middle frontal gyrus (MFG), fusiform gyrus, and putamen showing the greatest degree.

Adults with ASD only showed greater connectivity for the Inhibition versus Vigilance condition in a network in the theta band ( $p_{\text{FWE}} < 0.001$ ; Fig. 2.4B). Regions that had high degrees were the



**Figure 2.4** – Networks of increased connectivity in (**A**) control adults and (**B**) adults with ASD for correct No-go trials in the Inhibition compared to the Vigilance condition between 0–400 ms, post stimulus onset. (**A**) Control adults showed significantly increased network connectivity in the theta ( $p_{\text{FWE}} < 0.001$ ), alpha ( $p_{\text{FWE}} = 0.004$ ), and beta ( $p_{\text{FWE}} = 0.037$ ) bands, while (**B**) adults with ASD only demonstrated greater network connectivity in the theta band ( $p_{\text{FWE}} < 0.001$ ). Note that nodes are scaled by relative degree, or number of connections.

# 2.4.3.2 Between-group results

Adults with ASD demonstrated decreased connectivity, compared to controls, in a network in the alpha band between 0–400 ms for the Inhibition condition relative to the Vigilance condition (Fig. 2.5;  $p_{FWE} = 0.038$ ), such that mean connectivity in this network in the Inhibition condition was lower in adults with ASD than controls. The node with the highest degree in this network was the right IFG, which showed decreased connectivity with the left superior temporal gyrus (STG), fusiform gyrus, thalamus, and hippocampus. The two groups did not differ significantly in terms of connectivity in either direction in the theta or beta band (all  $p_{SFWE} > 0.05$ ).



**Figure 2.5** – Network of regions showing connectivity differences between the ASD and control groups, occurring between 0–400 ms, post No-go stimulus onset in the Inhibition condition over the Vigilance condition. Adults with ASD had significantly ( $p_{FWE} = 0.038$ ) decreased alpha-band connectivity compared to controls. Note that nodes are scaled by relative degree, or number of connections.

# 2.4.4 Brain-behaviour relations

Mean network connectivity values during the Inhibition condition in the alpha-band network showing significantly decreased connectivity in the ASD group negatively predicted self-rated scores on the Inhibit scale of the BRIEF-A (b = -5.09, B = -0.33, p = 0.042; Fig. 2.6). That is, greater connectivity in this network during response inhibition was associated with lower ratings on the Inhibit scale, or fewer self-reported issues with inhibitory control. There was no moderating effect of group on this relationship (b = -3.84, B = 0.25, p = 0.121). Neither mean connectivity in this network nor its interaction with group were significantly predictive of selfrated Total scores on the SRS-2 or task performance (all ps > 0.05).



**Figure 2.6** – Relationship between mean network connectivity values (z scores) in the alpha band in the Inhibition condition of the Go/No-go task and BRIEF-A self-reported t scores on the

Inhibit scale. Mean alpha-band network connectivity inversely predicted BRIEF-A Inhibit scale scores (b = -5.09, B = -0.33, p = 0.042), such that participants who had greater connectivity in this network when inhibiting a prepotent response reported fewer problems with inhibition in everyday life. Mean network connectivity values were derived from the network in which adults with ASD demonstrated decreased connectivity compared to controls between 0–400 ms, post-stimulus onset, for the Inhibition greater than Vigilance condition in the alpha band. Solid lines represent the regression line for each group, while the dashed line signifies the regression line for the sample as a whole.

# 2.5 Discussion

The current study revealed that while adults with ASD exhibited no behavioural differences in an experimental Go/No-go task, there was a tendency for them to report experiencing difficulties with inhibition in everyday life on the BRIEF-A. Although behavioural performance on the Go/No-go task did not differentiate inhibitory control in each group, and the disparity in real-life inhibition between adults with and without ASD was small, patterns of brain connectivity related to inhibition in adults with ASD remained distinct from those without ASD.

At the group level, control adults activated networks in the theta, alpha, and beta bands, whose hubs mainly resided in the midline and right hemisphere, whereas adults with ASD only recruited a somewhat left-lateralized network in the theta band. Major nodes of the theta-band network in the ASD group comprised left homologues of brain regions implicated in inhibition, such as the IFG and IPL. Given that individuals with ASD have demonstrated atypical lateralization of language (Escalante-Mead, Minshew, & Sweeney, 2003; Lindell & Hudry, 2013) and motor (Floris et al., 2016; Floris & Howells, 2018) networks, it may not be surprising that they also show a more left-lateralized configuration of inhibitory control networks. Furthermore, a recent review of studies using MEG and EEG to examine functional brain connectivity in the ASD population (O'Reilly et al., 2017) observed generally greater left lateralization of brain networks, which the authors believed indicated decreased integration of information between brain regions due to impairments in long-range connectivity typically found in the right hemisphere. Therefore, the left lateralization of the hubs of the theta-band network in our sample of adults with ASD may reflect a failure in communication between brain regions in the right hemisphere involved in inhibition, leading to atypical organization of homologous regions in the left hemisphere for inhibitory processes.

A similar narrative of impaired right hemisphere connectivity emerged when we compared the two groups directly: in the alpha band, adults with ASD showed decreased connectivity in a network with its main hub in the right IFG. In particular, the right IFG was less synchronized with other brain regions in the midline and left hemisphere, such as the thalamus, STG, and fusiform gyrus. As control adults demonstrated increased connectivity between these areas in the alpha band, whereas adults with ASD showed no differences in functional connectivity between the Inhibition and Vigilance conditions, this finding implies that in the ASD group, the right IFG fails to communicate effectively with these regions, as inter-areal alpha-band connectivity has been linked to top-down processing and coordination of distant brain regions (Sadaghiani et al., 2012; von Stein et al., 2000). Our results complement those of Kenet and colleagues (2012), who also observed decreased alpha-band connectivity between brain regions involved in an antisaccade task, which they suggested implied that top-down mechanisms were impaired in adults with ASD. Although it is still unclear whether alpha-band synchrony is involved in recruiting task-relevant areas or suppressing task-irrelevant areas (Palva & Palva, 2011), as the right IFG has consistently been shown to be involved in response inhibition (Aron et al., 2014; Cai, Ryali, Chen, Li, & Menon, 2014; Dodds, Morein-Zamir, & Robbins, 2011; Levy & Wagner, 2011), and as the other regions in this network have not been reliably associated with inhibitory control, it is likely that this deficit in alpha-band synchrony may indicate difficulty in constraining task-irrelevant activity. Considering that greater connectivity in this alpha-band network during the Inhibition condition was correlated with reports of better inhibitory control on the BRIEF-A, we propose that this decreased capability for inhibiting extraneous information impedes efficient top-down processing, ultimately leading to problems with inhibition in everyday life. Since participants completed our Go/No-go task in a very controlled and quiet environment, there were few distractors hindering task performance, but the degree of interference experienced in real-world situations from one's surroundings is much greater, hence the dissociation between the behavioural results on our Go/No-go task and those on the BRIEF-A. This hypothesis is in line with research suggesting that individuals with ASD also experience difficulties with interference control (Adams & Jarrold, 2012; Geurts, van den Bergh, et al., 2014; Sanderson & Allen, 2013), and that the right IFG is also involved in selecting appropriate strategies to achieve complex task goals (Dippel & Beste, 2015; Robinson et al., 2015), such as those encountered in everyday life.

#### 2.5.1 Limitations

As we were unable to obtain BRIEF-A and/or SRS-2 scores for all participants due to attrition, our findings involving either of these measurements do not necessarily characterize our entire sample. In addition, the difference between adults with and without ASD in scores on the Inhibit scale of the BRIEF-A was only significant at a trend level. Though this result may have been partly due to the informants reporting fewer inhibition difficulties in our sample compared to participants' own ratings, this small difference in inhibition skills may indicate that our sample of adults with ASD had relatively preserved inhibitory control, so our findings may not extend to the larger ASD population, especially those who experience more difficulties with inhibition. Furthermore, many of our reported effect sizes were in the small to medium range, which warrants future replication of our results in an independent group of adults with ASD.

## 2.5.2 Conclusions

Overall, our study demonstrates that adults with ASD show atypical recruitment of brain networks during inhibitory control due to deficits in connectivity of right hemisphere regions typically involved in inhibition. We suggest that the lack of alpha-band connectivity observed in our ASD group, compared to our control group, implies reduced inhibition of task-irrelevant information by the right IFG. Since there was likely limited interference from extraneous stimuli in the Go/No-go task, the effects of this difficulty may be minimal during task performance. However, in complex, cognitively-demanding real-life situations, this decreased ability to suppress distractors may be more apparent and therefore interfere with their ability to exert inhibitory control, as seen in the association between lower alpha-band synchrony during prepotent response inhibition and poorer self-reported inhibition in everyday life. Future work should investigate whether adults with ASD also show atypical brain connectivity during tasks involving interference control, as impairments in this aspect of inhibitory control may account more precisely for the difficulties with inhibition that adults with ASD typically experience.

# Chapter 3 Study 2

# 3 Frontoparietal network connectivity during an *n*-back task in adults with autism spectrum disorder

Yuk, V., Urbain, C, Anagnostou, E., & Taylor, M.J.

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# 3.1 Abstract

Background: Working memory deficits have been demonstrated in individuals with autism spectrum disorder (ASD) and may emerge through atypical functional activity and connectivity of the frontoparietal network, which exerts top-down control necessary for successful working memory. Little is known regarding the specific spectral properties of the frontoparietal network during working memory processes in ASD, even though certain frequencies of synchrony between brain regions have been linked to specific neural mechanisms.

Methods: We analyzed magnetoencephalographic data from 39 control adults (26 males; 27.15  $\pm$  5.91 years old) and 40 adults with ASD (26 males; 27.17  $\pm$  6.27 years old) during the 1-back load of an *n*-back task, and from a subset of this sample during the 2-back condition. We performed seed-based connectivity analyses using regions of the frontoparietal network. Interregional synchrony in theta, alpha, and beta bands was assessed with the phase difference derivative and compared between groups during periods of working memory maintenance and recognition.

Results: During maintenance of newly presented vs. repeated stimuli, the two groups did not differ significantly in theta, alpha, or beta phase synchrony for either condition. Adults with ASD showed alpha-band synchrony in a network containing the right dorsolateral prefrontal cortex, bilateral inferior parietal lobules (IPL), and precuneus in both 1- and 2-back tasks, whereas controls demonstrated alpha-band synchrony in a sparser set of regions, including the left insula and IPL, in only the 1-back task. During recognition of repeated vs. newly presented stimuli, adults with ASD exhibited decreased theta-band connectivity compared to controls in a network with hubs in the right inferior frontal gyrus and left IPL in the 1-back condition. While there were no group differences in connectivity in the 2-back condition, adults with ASD showed no frontoparietal network recruitment during recognition, while controls activated networks in the theta and beta bands.

Conclusions: Our findings suggest that since adults with ASD performed well on the *n*-back task, their appropriate, but effortful recruitment of alpha-band mechanisms in the frontoparietal network to maintain items in working memory may compensate for atypical modulation of this network in the theta band to recognize previously presented items in working memory.

# 3.2 Introduction

Adults with autism spectrum disorder (ASD) demonstrate difficulties with a variety of executive functions (Demetriou et al., 2018; Hill, 2004; Pellicano, 2012; Wallace et al., 2016), one of which is working memory, or the ability to hold and manipulate information in mind (Baddeley, 2012; D'Esposito, 2007). As working memory is linked to other executive functions (Friedman & Miyake, 2017) which together influence cognitive capabilities, such as intelligence and academic achievement (Alloway & Alloway, 2010; Conway, Kane, & Engle, 2003; Gathercole, Pickering, Knight, & Stegmann, 2004; Wilhelm, Hildebrandt, & Oberauer, 2013), understanding the nuances and the extent of working memory impairments in ASD is a crucial first step in improving cognitive outcomes in this population. The current literature points to a more severe deficit in ASD in visual, especially visuospatial, aspects of working memory, rather than in verbal working memory (Chien et al., 2015; Habib et al., 2019; Tse et al., 2019; Wang et al., 2017; Williams et al., 2005). Despite this apparent domain-specific impairment in working memory task performance, neuroimaging work has shown that individuals with ASD exhibit atypical neural activity and connectivity across both visual and verbal working memory tasks (Braden et al., 2017; Koshino et al., 2005; Silk et al., 2006; Urbain et al., 2016; Vogan et al., 2018).

Several functional neuroimaging studies of working memory have demonstrated activation of a frontoparietal network (Mencarelli et al., 2019; Owen et al., 2005; Rottschy et al., 2012; Yaple et al., 2019) consisting mainly of the dorsolateral prefrontal cortex (dlPFC), which includes the superior and middle frontal gyri (SFG and MFG), and of the inferior parietal lobule (IPL). The frontoparietal network is thought to exercise cognitive control to adapt to rapidly changing goals and demands (Corbetta & Shulman, 2002; Dosenbach et al., 2007; Fair et al., 2007; Harding, Harrison, Breakspear, Pantelis, & Yücel, 2016; Marek & Dosenbach, 2018), such as those encountered in working memory tasks. In particular, the dlPFC and IPL of this network have been implicated in working memory maintenance (Becke, Müller, Vellage, Schoenfeld, & Hopf, 2015; Courtney, Petit, Haxby, & Ungerleider, 1998; Curtis & D'Esposito, 2003; Gazzaley et al., 2004; Jonides et al., 1998; Petrides, 2005; Ragland et al., 2002), which entails the temporary storage of information in working memory. Updating or manipulation of this information also involves the dlPFC (Barbey et al., 2013; D'Esposito, Postle, Ballard, & Lease, 1999; Nyberg &

Eriksson, 2015; Postle et al., 2006; Ragland et al., 2002), as does recognition that a present stimulus has been previously presented (D'Esposito et al., 2000; Ranganath, Johnson, & D'Esposito, 2003; Rowe, Toni, Josephs, Frackowiak, & Passingham, 2000; Veltman, Rombouts, & Dolan, 2003), a function which encompasses access to or selection of relevant stimulus representations in working memory. Much of the working memory literature in ASD has utilized paradigms tapping maintenance and recognition processes; during such tasks, individuals with ASD show differential activation of this frontoparietal network across development, exhibiting increased activity in the dIPFC during childhood (Urbain et al., 2015; Yeung et al., 2019), but the opposite in adulthood (Koshino et al., 2005; Luna et al., 2002). Moreover, they show poor modulation of these frontoparietal regions with increasing cognitive load (Rahko et al., 2016; Vogan et al., 2018, 2019).

More recent work has examined not only the activation of regions in the frontoparietal network, but also how they communicate or synchronize with each other and with other brain areas. These connections are thought to be fundamental for exerting top-down control on other areas and networks for successful task performance (Cocchi, Zalesky, Fornito, & Mattingley, 2013; Cohen & D'Esposito, 2016; Cole et al., 2013; Dixon et al., 2018; Fair et al., 2007; Finc et al., 2017; Marek & Dosenbach, 2018; Spreng, Stevens, Chamberlain, Gilmore, & Schacter, 2010). In the ASD population, studies generally demonstrate that areas in the frontoparietal network are less coupled with each other and with other regions of the brain (Braden et al., 2017; Koshino et al., 2005, 2008). This reduced functional connectivity suggests impairments in integrating information among brain areas during working memory maintenance and recognition, which may contribute to ASD symptomatology (Barendse et al., 2018; Urbain et al., 2016). These findings echo the current literature on connectivity in ASD, which posits that individuals with ASD show decreased long-range functional connectivity and altered local connectivity across a range of contexts (Belmonte et al., 2004; Di Martino et al., 2014; Geschwind & Levitt, 2007; Kana, Libero, & Moore, 2011; Kessler et al., 2016; O'Reilly et al., 2017), suggesting that a deficit in neural communication may account for the cognitive difficulties observed in the ASD population.

Although neural long-range synchrony, especially in the theta and alpha frequency bands, has been linked to working memory maintenance and recognition processes (Dai et al., 2017; Johnson et al., 2017; Klimesch, Freunberger, & Sauseng, 2010; Muthukrishnan, Soni, & Sharma,

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2020; Palva et al., 2010; Roux & Uhlhaas, 2014; Sarnthein et al., 1998), the specific frequency band(s) in which these connectivity differences occur in individuals with ASD have been less explored. To our knowledge, only one study has demonstrated reduced alpha-band connectivity in children with ASD during a working memory task, reflecting inefficient processing during working memory recognition of repeated stimuli that was associated with severity of their ASD symptoms (Urbain et al., 2016). Frequency-specific differences in working memory-related connectivity in adults with ASD and their relation to behaviour have yet to be examined, even though working memory abilities can impact adaptive behaviours in adulthood in ASD (Nyrenius & Billstedt, 2020; Wallace et al., 2016).

Thus, the present study investigated whether adults with ASD demonstrate connectivity differences when engaging working memory processes, and if they are frequency-dependent. Adults with and without ASD performed an *n*-back task, a classic paradigm in which participants view a series of stimuli and are asked to recall whether the current stimulus was also presented n trials earlier (Kirchner, 1958). We measured and compared connectivity between the control and ASD groups during maintenance and recognition of novel visual stimuli for both 1-back and 2back versions of the task. Due to their involvement in working memory mechanisms (Daume et al., 2017; Johnson et al., 2017; Palva et al., 2010; Roux & Uhlhaas, 2014; Salazar, Dotson, Bressler, & Gray, 2012) as well as long-range interregional communication (Bressler & Richter, 2015; Kopell et al., 2000; von Stein et al., 2000), we specifically contrasted phase synchrony in the theta, alpha, and beta frequency bands. We also focused on connections among frontoparietal network regions and the rest of the brain, given its known role in working memory (Johnson et al., 2019; Mencarelli et al., 2019; Murray, Jaramillo, & Wang, 2017; Owen et al., 2005), and since prior work has demonstrated deficits in this network in ASD (Barendse et al., 2018; Koshino et al., 2005; Urbain et al., 2015). As individuals with ASD show deficits in tasks involving working memory maintenance (Wang et al., 2017) and reduced connectivity during working memory recognition (Urbain et al., 2016), we predicted that adults with ASD would demonstrate decreased interregional connectivity during both maintenance and recognition of novel stimuli. We further hypothesized that these differences would appear in the alpha band, in line with our previous findings in children with ASD (Urbain et al., 2016), and given its link with working memory processes, especially maintenance (Crespo-Garcia et al., 2013; Palva et al., 2010; Sato et al., 2018; Sauseng et al., 2005).

# 3.3 Methods and materials

#### 3.3.1 Participants

We recruited 92 adults aged 18–40 years, inclusive, for this study, approved by the Research Ethics Board at the Hospital for Sick Children. Individuals were included if they were not born prematurely, had no MRI or MEG contraindications, and demonstrated an IQ  $\geq$  70, measured using the full-scale, two-subtest version of the Wechsler Abbreviated Scale of Intelligence (WASI or WASI-II; Wechsler, 1999, 2011). Control adults were additionally screened for any developmental, neurological, or psychological disorders. Adults with ASD had a primary diagnosis of ASD by an experienced clinician, which was confirmed by the Autism Diagnostic Observation Schedule (ADOS-G or ADOS-2; Lord et al., 2000, 2012). All participants gave informed written consent before taking part in the study.

Participants were excluded if they performed poorly on the task (i.e.,  $\leq$ 50% accuracy on 1-back task or  $\geq$ 50% false alarm rate), had a low number of correct trials (<40 in each condition) after accounting for artefacts, or poor data quality (e.g., poor head localization in the MEG). We then matched participants in the ASD group with those in the control group on age (within two years) and sex, and subsequently excluded any control participants who could not be matched. As participants tended to perform better on the 1-back than the 2-back version of the task, and as we evaluated the 1- and 2-back data separately, the final samples for these two analyses differed; the sample for the 2-back analysis was a subset of that for the 1-back analysis. For the 1-back task, 39 control adults (26 males; 27.15 ± 5.91 years old) and 40 adults with ASD (26 males; 27.17 ± 6.27 years old) met all inclusion and exclusion criteria. In this sample, 23 adults with ASD reported current use of psychotropic medication (Appendix A). For the 2-back task, 29 control adults (19 males; 26.40 ± 5.79 years old) and 30 adults with ASD (19 males; 26.36 ± 6.26 years old) were included in the analyses, of which 21 adults with ASD were taking medication. Neither sample differed significantly in age, sex, or IQ, and mean calibrated severity scores on the ADOS for both ASD samples were around 7 (Table 3.1).

#### Table 3.1

Demograph	ics for	1-back and	2-back	samples
				~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~

	Control	ASD		
	Mean (SD) or Count	Mean (SD) or Count	<i>t</i> or <i>X</i> <sup>2</sup>	р
1-back	N = 39	N = 40		
Age	27.15 (5.91)	27.17 (6.27)	0.02	0.99
Sex	26 M, 13 F	26 M, 14 F	2.43x10 <sup>-31</sup>	1
IQ	114.34 (11.36)	111.79 (14.37)	0.86	0.39
ADOS CSS		6.89 (2.25)		
2-back	<i>N</i> = 29	N = 30		
Age	26.40 (5.79)	26.36 (6.26)	0.03	0.98
Sex	19 M, 10 F	19 M, 11 F	6.01x10 <sup>-31</sup>	1
IQ	115.45 (11.98)	113.48 (13.04)	0.60	0.55
ADOS CSS		7.00 (2.09)		

ADOS = Autism Diagnostic Observation Schedule; CSS = calibrated severity score

# 3.3.2 Experimental design

## 3.3.2.1 Questionnaires

To obtain a standardized measure of working memory, we asked participants and their informants (e.g., partner or parent) to complete the Behavior Rating Inventory of Executive Function, Adult Version (BRIEF-A; Roth, Isquith, & Gioia, 2005). This questionnaire assesses difficulties with a variety of executive functions that an individual may experience in everyday life. It provides *t* scores reflecting the degree of impairment on a particular executive function scale, as well as composite scores. We used *t* scores on the Working Memory scale of the BRIEF-A, with higher scores denoting more severe deficits in working memory. Participants also filled out the Social Responsiveness Scale, Second Edition (SRS-2; Constantino & Gruber, 2012). The Total *t* score was taken to gauge ASD symptom severity.

## 3.3.2.2 *N*-back MEG task

Participants performed a visual *n*-back task with two loads, 1- and 2-back (Fig. 3.1A), to elicit working memory processes. This task was used in our previous work examining differences in brain activation and functional connectivity between children with and without ASD (Urbain et al., 2015; Urbain et al., 2016). Our task protocol was similar; stimuli consisted of novel colourful abstract images presented serially for 200 ms each on a black background. During the interstimulus interval, participants saw a white fixation cross for a random duration between 1050–1300 ms. Participants pressed a button if the most recently presented stimulus matched that shown *n* trials previously.

The two loads of the *n*-back task were run in separate blocks. The l-back load scenario consisted of 285 trials: 190 unique images were presented, and 95 of these were shown again on the subsequent trial. The 2-back load segment of the task contained 330 trials: 220 distinct images were shown, of which 110 were repeated two trials later. Stimuli in the 1- and 2-back loads did not overlap. We refer to trials in which stimuli are presented for the first time as 'New', and those in which they are shown again as 'Repeat'.

All participants first practiced both blocks of the task and were given feedback outside of the MEG scanner to ensure they understood the task requirements. Individuals viewed the task on a rear projection screen 80 cm away from the MEG dewar. *Presentation 18.1* software (Neurobehavioral Systems Inc., https://www.neurobs.com/presentation) was used to display the task, as well as record participant responses.



**Figure 3.1** – The *n*-back task. (A) Participants' performance on two loads of this task — 1-back (top row) and 2-back (bottom row) — were tested in separate blocks. They were instructed to press a button as quickly as possible when they recognized that a stimulus had been repeated one or two trials earlier. Images were presented for 200 ms, and the interstimulus interval varied between 1050–1300 ms. (B) A schematic of the time windows used to analyze working memory maintenance and recognition processes, with the 1-back load as an example.

# 3.3.2.3 Neuroimaging data acquisition

A 151-channel CTF MEG system (Coquitlam, British Columbia, Canada) recorded MEG data at a 600 Hz sampling rate from participants during the task. Adults lay supine with their head in the MEG dewar. Head position was tracked continuously through three fiducial coils on the nasion and left and right pre-auricular points. To reduce noise in the data, an anti-aliasing low-pass filter at 150 Hz and a third order spatial gradient were applied.

A 12-channel head coil in a 3T MRI scanner (MAGNETOM, Siemens AG, Erlangen, Germany) recorded T1-weighted MRI data from participants. A sagittal 3D MPRAGE sequence (TR/TE = 2300/2.96 ms, FA = 9°, FOV = 192x240x256 mm, voxel size = 1.0 mm isotropic) was utilized. Participants were scanned with radio-opaque markers at the MEG fiducial points to allow for coregistration of functional MEG data with structural MRI data.

# 3.3.3 Statistical analysis

## 3.3.3.1 Behavioural data

Working memory capability in everyday life was compared between adults with and without ASD in the 1- and 2-back samples by examining whether there were group (control vs. ASD) or rater (self vs. informant) effects, as well as an interaction between the two, on the Working Memory scale of the BRIEF-A. Performance on the *n*-back task was contrasted between groups by assessing the effect of group (control vs. ASD) on accuracy and median response time (RT) for the 1- and 2-back loads independently. Accuracy was assessed using d-prime (d'), which was computed by subtracting the *z*-transformed false alarm rate from the *z*-transformed hit rate: d' = z(hit rate) - z(false alarm rate). Hits were correct Repeat trials, and false alarms were incorrect New trials.

We used linear mixed effects models to investigate the effects on BRIEF-A data and *t* tests for the task performance measures. Analyses were carried out separately for the 1-back and 2-back samples in R 3.5.0 (R Core Team, https://www.r-project.org/). Significant results are reported for p < 0.05.

#### 3.3.3.2 MEG data

MEG data preprocessing and analyses were done using the FieldTrip toolbox (Oostenveld et al., 2011) in MATLAB 2017b (The MathWorks, www.mathworks.com/products/matlab/). Data were epoched from -1500–2000 ms, relative to stimulus onset. Signals were then filtered from 1–150 Hz with a fourth-order Butterworth bandpass filter, with 60 and 120 Hz notch filters. Artefacts from physiological sources (e.g., eyes and heart) were detected and removed with independent component analysis. Trials in which the signal was >2000 fT or head movement was >5 mm were excluded. Of the remaining trials, only correct New and Repeat trials were used for further analyses.

Forward models based on the single-shell method (Nolte, 2003) were created from each participant's T1-weighted MRI data. Inverse models were constructed using the forward model and constrained to the centroids of the 90 regions of the Automated Anatomic Labeling (AAL) atlas (Tzourio-Mazoyer et al., 2002). Activity at each centroid was taken to represent that respective AAL region. Time series at these sources were estimated using a linearly constrained minimum variance beamformer (Van Veen et al., 1997). The covariance matrix was computed on the MEG signal from -400–800 ms, to which 5% regularization was applied. The neural activity index was calculated to ensure attenuation of centre-of-head noise biases.

As our task involved strong visual and motor responses, we performed seed-based analyses to focus on connectivity between core regions of the working memory frontoparietal network and the rest of the brain to assess phase synchrony directly related to working memory maintenance and recognition of novel visual stimuli. Therefore, we examined the connections among six bilateral regions of interest (ROIs) from the AAL atlas, as well as their links to the other AAL regions (except Heschl's gyrus and olfactory cortex, as their roles in audition and olfaction are not involved in our task). Our ROIs were chosen based on meta-analyses of *n*-back studies (Mencarelli et al., 2019; Owen et al., 2005; Yaple et al., 2019). They consisted of the superior frontal gyri (SFG; [-19, 35, 42] and [20, 31, 44]), medial superior frontal gyri (mSFG; [-6, 49, 31] and [8, 51, 30]), middle frontal gyri (MFG; [-34, 33, 35] and [37, 33, 34]), inferior frontal gyri (IFG; [-47, 30, 14] and [49, 30, 14]), insulae ([-36, 7, 3] and [38, 6, 2]), and inferior parietal lobules (IPL; [-44, -46, 47] and [45, -46, 50]).

Connectivity between each pair of sources was quantified using the phase difference derivative (PDD; Breakspear, Williams, & Stam, 2004). Source-estimated data were filtered into our frequency bands of interest with Hamming-windowed FIR bandpass filters at the following passbands: 4–7 Hz (theta), 8–14 Hz (alpha), and 15–30 Hz (beta). The lower and upper stopband frequencies for each filter were at 0.6 and 1.9 times the lower and upper frequency cutoffs of each passband, respectively. To reduce detection of spurious connections due to signal leakage, filtered data were subsequently orthogonalized. The instantaneous phase for each source timeseries in each frequency band was obtained with the Hilbert transform. PDD values were calculated at each timepoint from -400–800 ms using the method outlined by Tewarie and colleagues (2019).

Interregional neural communication during maintenance and recognition of novel visual stimuli was determined by considering phase synchrony values in two time windows: 400–800 ms, after the onset of a New stimulus, and 0–400 ms, following the presentation of a Repeat stimulus, respectively (Fig. 3.1B). These windows were established based on average median RTs in both groups, which ranged from ~425–525 ms, across both loads (see Results section). Regarding recognition, we examined a window from 0-400 ms, post-Repeat stimulus onset and just before the lower end of the average median RT, as it would encompass processing related to successful recognition during correct Repeat trials. We compared phase synchrony in this window to that in a similar window of 0-400 ms, post-New stimulus onset (Repeat > New, 0-400 ms, poststimulus onset), as New trials act as a control condition that involves the first occurrence of the stimulus. To investigate maintenance, we evaluated a window from 400–800 ms, post-New stimulus onset, to prevent capturing any perceptual, encoding, and/or identification functions that may occur during early visual processing. Furthermore, we chose this interval to avoid overlap with our recognition analysis and the baseline window. We contrasted connectivity in this time window in New trials with connectivity in an equivalent window of 400-800 ms, post-Repeat stimulus onset in Repeat trials (New > Repeat, 400–800 ms, post-stimulus onset). Mean connectivity at all pairwise connections for each participant and each condition in these comparisons was obtained by standardizing PDD values in these windows by the baseline period, -400-0 ms, then averaging the resultant z scores over the entire time window of interest.

Statistical comparisons of within-group connectivity during maintenance and recognition were conducted as described above for both adults with and without ASD. We then tested for statistically significant group differences in each of these scenarios (e.g., Control vs. ASD, New > Repeat for maintenance; Control vs. ASD, Repeat > New for recognition). All within- and between-group comparisons were performed for the 1- and 2-back samples separately. For both types of contrasts, we performed cluster-based permutation testing, as implemented in the Network-Based Statistic toolbox (Zalesky et al., 2010), to find networks demonstrating significant differences between conditions and groups. Essentially, the Network-Based Statistic approach begins by performing t tests at each connection and applying a threshold, which we chose to be t = 2.641 (1-back) or t = 2.665 (2-back), which are equivalent to p < 0.005 in their respective samples. The robustness of the largest contiguous network formed from the suprathreshold connections was assessed with permutation testing. A null distribution of maximal network size was obtained by rearranging group labels over 5000 permutations. This procedure allowed for the calculation of a family-wise error-corrected p value ( $p_{\text{FWE}}$ ) of the observed network. Networks were considered significant at  $p_{\text{FWE}} < 0.05$ . We used BrainNet Viewer (Xia et al., 2013) and code provided by Koelewijn and colleagues (2019) to visualize these networks.

#### 3.3.3.3 Brain-behaviour relations

We explored whether mean network connectivity in any of our group comparisons was associated with working memory abilities as measured by the BRIEF-A, task performance (accuracy and median RT), and with ASD symptom severity. Thus, for any networks that differed significantly between groups, we performed regressions of each the BRIEF-A Working Memory scale scores, d', median RT, and SRS-2 Total scores on mean PDD values in those networks. We report any significant main effects of mean connectivity and/or its interaction with group for p < 0.05.

# 3.4 Results

## 3.4.1 Behaviour

On the Working Memory subscale of the BRIEF-A, adults with ASD demonstrated significantly more working memory difficulties than controls (Fig. 3.2 and Table 3.2) in both the 1-back

(F(1,43) = 25.56, p < 0.0001, d = 0.65) and 2-back (F(1,38) = 22.18, p < 0.0001, d = 0.64) samples. Adults with ASD, compared to their informants, generally rated themselves higher on the Working Memory scale (1-back: F(1,43) = 19.38, p = 0.0001, d = 0.34; 2-back: F(1,38) = 14.06, p = 0.0006, d = 0.32), indicating a greater number of difficulties with working memory.



**Figure 3.2** – T scores on the Working Memory scale of the BRIEF-A for the 1-back (left panel) and 2-back (right panel) samples. There were significant main effects of both group and rater on Working Memory scores.

\*\*\* p < 0.001

#### Table 3.2

	Control	
	Mean (SD)	Mean (SD)
1-back	<i>N</i> = 39	N = 40
Self	50.28 (8.95) Range = [39–69], <i>n</i> = 18	64.07 (11.24) Range = [46–86], <i>n</i> = 27
Informant	43.50 (3.63) Range = [39–52], <i>n</i> = 18	56.70 (12.85) Range = [39–90], <i>n</i> = 27
2-back	N = 29	<i>N</i> = 30
Self	50.35 (9.22) Range = [39–69], <i>n</i> = 17	63.04 (10.76) Range = [46–83], <i>n</i> = 23
Informant	43.59 (3.73) Range = [39–52], <i>n</i> = 17	56.87 (13.05) Range = [39–90], <i>n</i> = 23

Self and informant ratings on the BRIEF-A Working Memory scale (t scores)

BRIEF-A = Behavior Rating Inventory of Executive Function, Adult Version

On the *n*-back task, there were no group differences in accuracy (1-back: t(76.93) = 0.77, p = 0.44, d = 0.17; 2-back: t(55.30) = 0.51, p = 0.61, d = 0.13) in the 1- or 2-back loads (Fig. 3.3A). The two groups also had similar median RTs in the 1-back load (t(76.97) = 1.51, p = 0.13, d = 0.34), but their differences in median RT during the 2-back load approached significance (t(54.71) = 1.93, p = 0.058, d = 0.50), such that adults with ASD had slightly longer median RTs than controls (Fig. 3.3B). A summary of accuracy and median RT values on the *n*-back task are reported in Table 3.3 and trial numbers are listed in Appendix D.



**Figure 3.3** – Accuracy (A) and median RT (B) on the two loads of the *n*-back task: 1-back (left panel) and 2-back (right panel). Adults with ASD showed a trend of having longer median RTs than control adults on the 2-back task (p = 0.058). Analyses of all other task performance measures did not reveal any significant group differences.

#### Table 3.3

Performance on the n-back task

	Control	ASD
	Mean (SD)	Mean (SD)
1-back	N = 39	<i>N</i> = 40
Accuracy (d')	4.13 (0.78)	3.99 (0.77)
Hit rate (%)	93.62 (8.41)	93.11 (8.25)
False alarm rate (%)	1.45 (1.94)	1.91 (2.07)
Median RT (ms)	424.44 (80.63)	452.52 (84.49)
2-back	N = 29	<i>N</i> = 30
Accuracy (d')	2.38 (0.48)	2.45 (0.60)
Hit rate (%)	66.39 (11.55)	68.67 (13.96)
False alarm rate (%)	3.40 (2.34)	4.31 (4.19)
Median RT (ms)	479.63 (99.52)	526.00 (83.77)

RT = response time

# 3.4.2 Neuroimaging

#### 3.4.2.1 Maintenance

For the 1-back task, during the maintenance window, both control adults ( $p_{FWE} = 0.048$ ) and adults with ASD ( $p_{FWE} = 0.001$ ) recruited aspects of the frontoparietal network selectively in the alpha band; neither group showed any significant connectivity during New compared to Repeat trials in either the theta or beta bands (all  $p_{SFWE} > 0.05$ ). In the control group, the network hub with the most (four) connections was the left IPL, which mainly communicated with other left hemisphere regions, such as the left insula (Fig 3.4A). The right IPL and IFG were also involved in this network, though they were each only connected to two other regions. In the ASD group, both the right SFG and MFG were the main hubs with five connections each, linking the right dIPFC with the right IPL and with several left posterior regions, including the left IPL and precuneus (Fig. 3.4B). In this network, the right IFG also showed synchrony with the right IPL and precuneus.
For the 2-back load, adults with ASD continued to show increased alpha-band connectivity during New versus Repeat trials ( $p_{FWE} = 0.002$ ) in a right dlPFC-left posterior network linking the right SFG hub with the left IPL and precuneus (Fig. 3.4B). The ASD group again did not display any changes in theta- or beta-band connectivity throughout this period, and the control group did not exhibit greater engagement of any networks in any frequency band for New compared to Repeat trials for this load (all  $p_{SFWE} > 0.05$ ). There were no significant group differences in the maintenance interval for either load.



**Figure 3.4** – Networks showing increased connectivity during maintenance of novel visual stimuli (New versus Repeat trials, 400–800 ms, post-stimulus onset) during the 1-back (left) and 2-back (right) loads. Node size is scaled by number of connections. (A) Control adults showed recruitment of a network in the alpha band in the 1-back load ( $p_{FWE} = 0.048$ ), but not in the 2-back load. (B) Adults with ASD displayed greater connectivity in a network in the alpha band similar between the 1-back ( $p_{FWE} = 0.001$ ) and 2-back ( $p_{FWE} = 0.002$ ) samples.

#### 3.4.2.2 Recognition

Recognition processes in the 1-back load were associated with a trend ( $p_{FWE} = 0.056$ ) increase in theta-band network connectivity in control adults for Repeat relative to New trials. This network was sparse, consisting mainly of a few connections (two each) among the left MFG, right IFG, bilateral IPL, and precuneus (Fig. 3.5). Control adults did not demonstrate any differential connectivity for Repeat versus New trials in either the alpha or beta bands, nor did adults with ASD in any frequency band (all  $p_{SFWE} > 0.05$ ). When comparing the two groups, adults with ASD exhibited significantly decreased theta-band connectivity compared to control adults ( $p_{FWE} = 0.046$ ) in a network of regions in which the right IFG and left IPL were major hubs (Fig. 3.6).

Within-group analyses for the 2-back load during recognition revealed organization of networks in the theta ( $p_{FWE} = 0.0084$ ) and beta ( $p_{FWE} = 0.015$ ) bands in the control group (Fig. 3.5B), but not in the alpha band ( $p_{FWE} = 1$ ). The theta-band network primarily involved coordination between the mSFG and temporal regions, for example the right fusiform gyrus. The beta-band network displayed a different topography, with the right IFG having the highest (five) number of connections, followed by the right MFG and left insula (three each). Although adults with ASD in this sample also did not show any differential connectivity for this analysis in any frequency band (all  $p_{S_{FWE}} > 0.05$ ), no significant group differences were found for the 2-back load.



**Figure 3.5** – Networks showing increased connectivity during recognition of repeated visual stimuli (Repeat versus New trials, 0–400 ms, post-stimulus onset) for the 1-back (left) and 2-back (right) loads in the control group. Node size is scaled by number of connections. In the 1-back load, control adults recruited a theta-band network, but it was only significant at a trend



level ( $p_{\text{FWE}} = 0.056$ ). In the 2-back load, they exhibited greater connectivity in networks in the theta ( $p_{\text{FWE}} = 0.0084$ ) and beta ( $p_{\text{FWE}} = 0.015$ ) bands. Adults with ASD did not show differential

connectivity during recognition (all  $p_{\text{SFWE}} > 0.05$ ).

**Figure 3.6** – Theta-band connectivity in adults with ASD compared to controls during recognition of novel visual stimuli (Repeat versus New trials, 0–400 ms, post-stimulus onset) in the 1-back load. (A) Adults with ASD showed significantly reduced ( $p_{\text{FWE}} = 0.046$ ) theta-band

connectivity in a network with hubs in the right IFG and left IPL. Node size is scaled by number of connections. (B) Mean connectivity in this network between -400–800 ms in the control (top) and ASD (bottom) groups. Connectivity values are given as z scores. (C) Network connectivity represented as a circle plot. Nodes are colour-coded in the following manner, from top to bottom: medial frontal structures (red), frontal areas (orange), parietal regions (turquoise), temporal areas (blue), medial parietal structures (dark blue), occipital areas (purple).

#### 3.4.2.3 Brain-behaviour relations

Mean connectivity in the theta-band network that differed between groups was not associated with any of our behavioural or clinical measures, nor was its interaction with group (all ps > 0.05).

### 3.5 Discussion

Our study illustrates the complex distinctions in working memory processing between adults with and without ASD on both the behavioural and neural level. In our sample, adults with ASD performed equally as well as control adults on our visual *n*-back task, although there was a tendency for adults with ASD to have longer RTs in the 2-back block. This pattern was also observed by Lever and colleagues (2015), who similarly demonstrated that despite being as accurate as controls on an *n*-back task, adults with ASD took significantly longer to respond. Slower RTs may be indicative of slower processing speed, which has also been reported in ASD (Haigh, Walsh, Mazefsky, Minshew, & Eack, 2018; Hedvall et al., 2013; Luna et al., 2007; Mayes & Calhoun, 2007; Oliveras-Rentas, Kenworthy, Roberson, Martin, & Wallace, 2012; Travers et al., 2014; but see Cardillo, Lanfranchi, & Mammarella, 2019; Wallace, Anderson, & Happé, 2009). While it may not affect performance on simple experimental working memory tasks, this trend toward longer responses or processing could have more noticeable effects in complex, everyday behaviours. Since deficits in both processing speed and working memory have been found in individuals with ASD (Braaten et al., 2020; Fried et al., 2016; Mayes & Calhoun, 2008; Nyrenius & Billstedt, 2020; Tse et al., 2019), further work is needed to clarify the link between processing speed and working memory abilities in ASD, especially as our ASD group reported more severe working memory difficulties on the BRIEF-A. Our neuroimaging analyses examined the underlying neural differences in the frontoparietal network responsible for maintenance and recognition of novel visual stimuli that may contribute to these impairments.

#### 3.5.1 Maintenance

During maintenance of novel visual stimuli, we observed that while adults with and without ASD did not differ significantly from each other, they exhibited distinct topologies and sizes of the networks they recruited. During the 1-back task, the alpha-band network recruited by controls was fairly left-lateralized, as the left IPL and left insula showed the most connections. The IPL is an integral part of the frontoparietal network involved in *n*-back tasks (Mencarelli et al., 2019; Owen et al., 2005; Yaple et al., 2019), and it may serve to maintain stimulus information in working memory (Becke et al., 2015; Gazzaley et al., 2004; Jonides et al., 1998; Paulesu et al., 1993; Ragland et al., 2002; Tsukiura et al., 2001), as well as shift attention to specific items in working memory (Berryhill, 2012; Nee et al., 2013). Although the IPL is more commonly associated with spatial working memory (e.g., Alain, Shen, Yu, & Grady, 2010; Andersen et al., 1985; Courtney, Ungerleider, Keil, & Haxby, 1996; Passaro et al., 2013; Rottschy et al., 2013; Thomas et al., 1999), there is evidence that it similarly participates in object or image identity working memory (Duggirala, Saharan, Raghunathan, & Mandal, 2016; Finke et al., 2006; Mencarelli et al., 2019; Olson & Berryhill, 2009; Owen et al., 2005). The insula has also been associated with object working memory capacity (Konstantinou, Constantinidou, & Kanai, 2017), but its principal function is in recruiting the frontoparietal network when attentional and executive resources are needed (Eckert et al., 2009; Menon & Uddin, 2010; Sridharan, Levitin, & Menon, 2008) through its functional connections with the dlPFC (Cauda et al., 2012; Uddin, Kinnison, Pessoa, & Anderson, 2014).

In comparison, adults with ASD demonstrated greater alpha-band interregional synchrony for New versus Repeat trials during the 1- and 2-back loads. The networks recruited in both loads were similar; they had a right frontal-to-left parietal configuration and included the right dlPFC, bilateral IPLs, and precuneus. The dlPFC is a key region in working memory processing, employing top-down control to maintain, monitor or update, and manipulate task-relevant information in mind (Barbey et al., 2013; D'Esposito & Postle, 2015; O'Reilly, Braver, & Cohen, 1999; Petrides, 2005; Wager & Smith, 2003), by focusing attention to target stimulus representations in the IPL (Curtis & D'Esposito, 2003; Edin et al., 2009; Feredoes et al., 2011; Murray et al., 2017). The precuneus mediates several higher-order cognitive functions (Cavanna & Trimble, 2006; Margulies et al., 2009; Zhang & Li, 2012), and given its connections with the IPL, it is likely involved in visuospatial processing (Leichnetz, 2001; Mahayana, Tcheang, Chen, Juan, & Muggleton, 2014; Selemon & Goldman-Rakic, 1988) and visual recall (Fletcher, Frith, et al., 1995; Suchan et al., 2002; Sugiura, Shah, Zilles, & Fink, 2005) in this task. The particular involvement of the precuneus in the ASD group may reflect greater mental engagement, as our previous work showed that children with ASD activated the precuneus more with heavier cognitive load (Urbain et al., 2015). While we did not detect any significant group differences, the recruitment of additional working memory regions — the dlPFC and precuneus — in the ASD group compared to controls, as well as of several other brain regions, may reflect effortful maintenance processes in ASD adults.

The particular arrangement of this right frontal, left posterior network not only mirrors previous work finding atypical functional lateralization in ASD during a working memory task (Koshino et al., 2005), but also suggests that maintenance of novel visual information is challenging for adults with ASD. In control adults, increasing task load has been associated with bilateral activation of the IPL (Nyberg, Dahlin, Stigsdotter Neely, & Bäckman, 2009; Robitaille, Grimault, & Jolicœur, 2009) and dlPFC (Linden et al., 2003; Rottschy et al., 2012; Vogan, Morgan, Powell, Smith, & Taylor, 2016), with a few demonstrating stronger effects in right dlPFC (Gould, Brown, Owen, Ffytche, & Howard, 2003; Höller-Wallscheid, Thier, Pomper, & Lindner, 2017; Rypma, Prabhakaran, Desmond, Glover, & Gabrieli, 1999). Greater dlPFC-IPL (frontoparietal) connectivity has also been linked to higher task load (Heinzel, Lorenz, Duong, Rapp, & Deserno, 2017; Palva et al., 2010). Therefore, the strong involvement of the right dlPFC and its connection to the left IPL in the ASD group in both the 1- and 2-back loads indicates that holding visual stimuli in mind is mentally taxing for adults with ASD. In both groups, however, brain regions synchronized selectively in the alpha band, which has been implicated in working memory maintenance (Jensen et al., 2002; Palva et al., 2010; Sauseng et al., 2005; Wianda & Ross, 2019). Thus, our findings demonstrate that adults with ASD utilize appropriate neural mechanisms to successfully maintain novel visual stimuli in working memory, but it may be effortful for them.

#### 3.5.2 Recognition

During recognition of repeated visual stimuli, adults with ASD exhibited no differential connectivity between Repeat and New trials for either the 1- or 2-back load. Hence, when contrasted with the control group, they showed significantly decreased theta-band synchrony

compared to controls during the 1-back load in a network with hubs in the right IFG and left IPL. The ventrolateral PFC, which includes the IFG, is thought to work with the IPL for active retrieval of information (Petrides, 2005). Specifically, the right IFG plays a major role in inhibition (Aron et al., 2014; Forstmann et al., 2008; Rubia et al., 2003; Vara, Pang, Vidal, et al., 2014; Vidal et al., 2012) and potentially preventing proactive interference during working memory (Anderson et al., 2004; Bomyea, Taylor, Spadoni, & Simmons, 2018; Emch, von Bastian, & Koch, 2019; Nee et al., 2013), whereas the IPL, in addition to storing stimulus representations, may be responsible for working memory retrieval (Olson & Berryhill, 2009). Since the selection of relevant information in working memory during recognition may not only involve enhancement of target stimulus representations, but also suppression of irrelevant ones, and given evidence that individuals with ASD experience deficits in interference control (Adams & Jarrold, 2012; Christ et al., 2011; Geurts, van den Bergh, et al., 2014; but see Lever et al., 2017; Ozonoff & Strayer, 1997), the reduced involvement of the IFG and IPL during recognition may reflect a potential breakdown in regulating interference from other stimuli in working memory. This possible deficit in inhibiting task-irrelevant stimuli is further corroborated by the fact that these differences occurred in the theta band, as interregional theta-band connectivity is thought to mediate long-range neural communication, top-down control, and integration of distant regions (Cavanagh & Frank, 2014; Sauseng et al., 2010, 2006; von Stein et al., 2000), especially during retrieval (Sauseng et al., 2004).

A similar effect was not found when contrasting the two groups in the 2-back task, which may be attributable to the slightly smaller sample size and therefore less power due to a greater variation in response in this condition. Importantly, the control group showed recruitment of theta-band networks for both loads (and additionally a beta-band network in the 2-back load), whereas the ASD group showed no greater connectivity in either load for Repeat compared to New trials. As the pattern of within-group results is similar across loads, a comparable but subthreshold trend may exist in the 2-back condition.

Taking into account that decreased connectivity has been observed in fMRI in ASD during other *n*-back tasks (Barendse et al., 2018; Braden et al., 2017; Koshino et al., 2005), our findings in the 1-back condition substantiate reports of long-range underconnectivity in ASD (Di Martino et al., 2014; Just et al., 2012; O'Reilly et al., 2017; Picci et al., 2016; Vissers et al., 2012). In contrast to our previous work (Urbain et al., 2016), we found that these differences occurred in the theta

band rather than the alpha band during recognition of repeated visual stimuli. However, there are some key distinctions between these two studies. First, the present work observed that connectivity in the frontoparietal network was only significantly reduced in the ASD relative to control group in the theta band during the 1-back condition, while we previously reported decreased alpha-band synchrony in a frontotemporal network in individuals with ASD during the 2-back condition (Urbain et al., 2016). Therefore, it is unclear from our prior work whether frontoparietal network connectivity also differed between individuals with and without ASD in the 2-back condition in either the theta or alpha bands, and whether frontotemporal network connectivity was affected in the current study. Second, our earlier study assessed children with ASD, whereas here we included only adults with ASD; thus, part of this discrepancy may be attributable to maturational processes. As both theta and alpha bands have been associated with working memory functions (Daume et al., 2017; Jensen et al., 2002; Klimesch et al., 2008; Palva et al., 2010; Popov et al., 2018; Roux & Uhlhaas, 2014; Sauseng et al., 2004; Schack, Klimesch, & Sauseng, 2005), it may be that connectivity related to recognition strengthens in the alpha band but weakens in the theta band over development in ASD. While global network efficiency in the theta and alpha bands increases with age (Hunt et al., 2019), these longitudinal changes in frequency-specific, long-range neural connectivity have not been characterized in ASD, neither has the frontoparietal network or any other networks related to working memory explicitly. Future work into the developmental trajectory of the spectral component of the frontoparietal network and its relation to working memory in ASD will be necessary to clarify these distinct findings in children and adults with ASD.

Another important consideration is that mean connectivity in the theta-band network that differed between groups in the 1-back load was not correlated with our behavioural measures. However, as our analyses probed very specific working memory mechanisms, it may be challenging to relate these fine neural differences to overall task performance and more complex behaviours drawing on working memory abilities in everyday life. Therefore, it will be valuable for prospective work to evaluate whether these findings persist in more ecologically valid tasks of working memory.

#### 3.5.3 Conclusion

Our neuroimaging study revealed unique aspects of working memory maintenance and recognition processes in adults with ASD. We demonstrated that while adults with ASD appropriately employ alpha-band oscillatory mechanisms to facilitate maintenance of novel visual stimuli in working memory, the distinct topology and extent of the recruited networks suggest that these functions are effortful for individuals with ASD. The strong engagement of maintenance processes may offset the observed atypicalities in theta-band connectivity in the ASD group during recognition of previously presented visual stimuli, at least in the 1-back task. Given the spatial and spectral specificity of our findings, we propose that alpha-band connectivity between the dIPFC and IPL in the frontoparietal network enhances the neural representations of target stimuli during maintenance, thereby countering potentially stronger interference effects that occur during recognition due to reduced theta-band synchrony of the IFG and IPL with other regions of the brain. We are the only study to date to use MEG to detail these maintenance and recognition processes and their spectral properties in the frontoparietal network in ASD. Thus, additional work is needed to independently validate our findings and interpretations in other investigations of working memory functions.

## Chapter 4 Study 3

# 4 Altered connectivity during a false-belief task in adults with autism spectrum disorder

Yuk, V., Anagnostou, E., & Taylor, M.J.

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### 4.1 Abstract

Background: Deficits in social communication are one of the main features of autism spectrum disorder (ASD). Adults with ASD show atypical brain activity during false-belief understanding, an aspect of social communication involving the ability to infer that an individual can have an incorrect belief about a situation. Our study is the first to investigate whether adults with ASD exhibit differences in frequency-specific functional connectivity patterns during false-belief reasoning.

Methods: We used magnetoencephalography to contrast functional connectivity underlying false-belief understanding between 40 adults with ASD and 39 control adults. We examined whole-brain phase synchrony measures during a false-belief task in three frequency bands: theta (4–7 Hz), alpha (8–14 Hz), and beta (15–30 Hz).

Results: Adults with ASD demonstrated reduced theta-band connectivity compared with control adults between several right-lateralized and midline regions, such as the medial prefrontal cortex, right temporoparietal junction, right inferior frontal gyrus, and right superior temporal gyrus. During false-belief trials, they also recruited a network in the beta band that included primary visual regions, such as the bilateral inferior occipital gyri, and the left anterior temporarietal junction.

Conclusions: Reduced theta-band synchrony between areas associated with mentalizing, inhibition, and visual processing implies some difficulty in communication among these functions in ASD. This impairment in top-down control in the theta band may be counterbalanced by their engagement of a beta-band network, as both the left anterior temporoparietal junction and beta-band oscillations are associated with attentional processes. Thus, adults with ASD demonstrate alternative neural mechanisms for successful false-belief reasoning.

#### 4.2 Introduction

One of the main characteristics of autism spectrum disorder (ASD) is an impairment in social communication (American Psychiatric Association, 2013). An important element of effective social communication is having theory of mind (ToM), or the ability to attribute mental states (e.g., thoughts, beliefs, etc.) to oneself and others (Premack & Woodruff, 1978). Numerous studies have reported deficits in individuals with ASD on a variety of ToM tasks (Baron-Cohen, 2001; Yirmiya, Erel, Shaked, & Solomonica-Levi, 1998), such as social perception (Mathersul et al., 2013) and intention and mental state inference (Baron-Cohen, Jolliffe, Mortimore, & Robertson, 1997; Jolliffe & Baron-Cohen, 1999; Moran et al., 2011; Murray et al., 2017). Performance on these tasks appear to be linked to ASD severity and social functioning (Bishop-Fitzpatrick et al., 2017; Hoogenhout & Malcolm-Smith, 2017).

This link between ToM and ASD began with work by Baron-Cohen and colleagues (1985), who tested an aspect of ToM known as false-belief (FB) understanding in children with ASD. At around four years of age, typically-developing children begin to realize that an individual can possess FB (Wimmer & Perner, 1983), whereby their belief of a situation may differ from the child's own perspective or from reality, such as in instances where an object's location is moved without one's knowledge. Baron-Cohen and colleagues (1985) determined that children with ASD of the same or higher mental age as typical four-year-olds often fail to make this inference, suggesting that ToM is impaired in ASD, and that this outcome is not necessarily attributable to other cognitive deficits. Independent studies have since confirmed that children with ASD perform worse on FB tasks than typically-developing children (Begeer et al., 2012; Burnside, Wright, & Poulin-Dubois, 2017; Colle, Baron-Cohen, & Hill, 2007; Kimhi, Shoam-Kugelmas, Agam Ben-Artzi, Ben-Moshe, & Bauminger-Zviely, 2014; Senju et al., 2010). However, older children with ASD who have advanced cognitive capabilities and adults with ASD demonstrate first-order FB understanding, in that an individual can have a FB of a situation, as well as second-order FB comprehension, whereby an individual has a FB about another's belief (Baron-Cohen, 2001; Bowler, 1992; Happé, 1995; Kimhi, 2014; Rasga et al., 2017; Scheeren et al., 2013).

While adults with ASD are generally able to ascribe FB to others, they may be less accurate compared to controls (Bradford et al., 2018), show deficits in making inferences using this

knowledge (Rosenthal et al., 2019), and exhibit difficulties with more complex ToM tasks (Baron-Cohen et al., 1997; Golan, Baron-Cohen, Hill, & Golan, 2006; Mathersul et al., 2013; Roeyers & Demurie, 2010; Spek et al., 2010). Moreover, neuroimaging research has revealed atypical neural processes underlying even first-order FB attribution in ASD. One meta-analysis (Schurz et al., 2014) found that during FB tasks, typical adults activate the precuneus, bilateral temporoparietal junctions (TPJs), insula, and medial prefrontal cortex (mPFC). While one study found no differences in brain activity between adults with and without ASD during FB processing (Dufour et al., 2013), recent work has revealed neural distinctions in adults with ASD on other first-order FB tasks both within and outside of this network of FB-related brain regions. One group showed that adults with ASD had increased activation of the bilateral frontal poles, left TPJ, and left superior temporal gyrus (STG) when inferring true belief (TB) or FB (Sommer et al., 2018). Conversely, Nijhof and colleagues (2018) demonstrated that adults with ASD had decreased activity in the right TPJ and temporal pole when viewing situations involving FB versus TB.

No studies yet have investigated whether this atypical brain activity during FB understanding is accompanied by different patterns of functional brain connectivity, despite a growing literature suggesting that individuals with ASD have altered functional connectivity (Di Martino et al., 2014; Hong, Vos de Wael, et al., 2019; O'Reilly et al., 2017; Rane et al., 2015). Only a few studies of other ToM domains, namely mental state and intention attribution, have demonstrated that individuals with ASD show reduced connectivity among brain regions involved in ToM (Kana et al., 2009; von dem Hagen et al., 2014). Moreover, whereas current neuroimaging work has established that oscillations in distant brain regions synchronize and form distinct networks at different frequency bands (Cox et al., 2018; De Domenico, 2017; Hipp et al., 2012; Thompson & Fransson, 2015) to perform specific functions (Klimesch, 2018; Palva & Palva, 2012; Wang et al., 2019), little is known regarding the spectral component of FB understanding in ASD. Evidence from one EEG study of children with ASD revealing decreased beta power in the right TPJ during a joint attention (ToM) task (Soto-Icaza et al., 2019), and from work in typical adults implicating connectivity in the beta band for selective processing of FBs (Guan et al., 2018), points to potential ToM-related differences in beta synchrony in ASD. However, an explicit characterization of frequency-specific interregional connectivity in the ASD population during FB understanding is still needed.

This study therefore contrasted patterns of whole-brain functional connectivity in adults with and without ASD during a FB task. We used magnetoencephalography (MEG) to characterize these networks, as MEG provides precise temporal, spatial, and spectral information of brain activity (Baillet, 2017; Hari & Salmelin, 2012). Our analyses focused on connectivity between 0–400 ms, post-stimulus onset, as our previous work has indicated that during this time window, adults elicit activation of FB-related brain regions (Mossad et al., 2016), and children with ASD show atypical activity in the TPJ and right inferior frontal gyrus (IFG; Yuk et al., 2018). We specifically examined connectivity, or interregional synchrony, of theta, alpha, and beta oscillations, as these frequency bands facilitate communication between distant brain areas (Bressler & Richter, 2015; Kopell et al., 2000; von Stein et al., 2000). We predicted that adults with ASD would show decreased connectivity in the beta band during FB understanding relative to control adults, and that differences in network connectivity would be associated with behavioural measures of FB and more general ToM abilities, as well as severity of ASD symptoms.

## 4.3 Methods and materials

#### 4.3.1 Participants

One hundred adults between 18–40 years old (55 ASD, 45 controls) were recruited for our study approved by the Hospital for Sick Children Research Ethics Board. All participants gave informed written consent. Inclusion criteria comprised having a full-scale, two-subtest IQ  $\geq$  70 on the Wechsler Abbreviated Scale of Intelligence (WASI or WASI-II; Wechsler, 1999, 2011), no premature birth, and no MRI or MEG contraindications. Control adults had no history of developmental, neurological, or psychological disorders. Adults with ASD had a primary diagnosis of ASD from an experienced clinician, supported by the Autism Diagnostic Observation Schedule (ADOS-G or ADOS-2; Lord et al., 2000, 2012). Participants were excluded from all analyses if they performed at  $\leq$ 50% accuracy on our FB task (11 ASD) or had poor data quality due to head motion artefacts or inadequate head localization (4 ASD). Six controls were excluded to match the ASD group's male-to-female ratio.

Our final sample comprised 39 control adults and 40 adults with ASD. There were no group differences in age, sex, full-scale (two-subtest) IQ, or verbal IQ. Current psychotropic

medication use was reported in 22 adults with ASD (Appendix A). Demographic data and statistics are available in Table 4.1.

#### Table 4.1

Demographic data

	<b>Control</b> ( <i>N</i> = <b>39</b> )	ASD (N = 40)		
	Mean (SD) or Count	Mean (SD) or Count	$t$ or $X^2$	p
Age	26.97 (5.30)	26.94 (5.45)	0.03	0.98
Sex	26 M, 13 F	26 M, 14 F	2.43x10 <sup>-31</sup>	1
Handedness	34 R, 5 L	34 R, 6 L		
Full-scale IQ	115.79 (10.49)	114.41 (14.85)	0.48	0.64
Verbal IQ	115.61 (9.93)	110.82 (17.11)	1.19	0.24
ADOS CSS		6.89 (2.17)		

ADOS = Autism Diagnostic Observation Schedule; CSS = calibrated severity score

#### 4.3.2 Experimental design

#### 4.3.2.1 Assessments

Participants completed the social inference segments (Minimal and Enriched; see Fig. 4.2 for a brief description) of The Awareness of Social Inference Test (TASIT; McDonald, Flanagan, Rollins, & Kinch, 2003). Participants watched short clips of social interactions portraying sincere, sarcastic, or deceitful conversations. For each video, participants were asked four questions regarding what the actors were doing, saying (or trying to say), thinking, and feeling. We used accuracy on the Thinking questions as a measure of first-order ToM (Mathersul et al., 2013), which most closely relates to the aspect of ToM probed by our MEG task.

Participants rated themselves on the Social Responsiveness Scale, Second Version (SRS-2; Constantino & Gruber, 2012), which provides an assessment of overall ASD symptom severity. The SRS-2 also includes subscales gauging an individual's difficulties with social communicative and restricted, repetitive behaviours. We took scores on the Social Cognition scale as a measure of impairment in social cognition. Informants also rated participants' behaviour on the SRS-2. In both cases, *t* scores were used in our analyses, with higher scores indicating greater severity.

#### 4.3.2.2 False-belief MEG task

Participants performed a FB task (Dennis et al., 2012) adapted for MEG (Fig. 4.1). This task has been described previously in developmental studies (Mossad, Smith, Pang, & Taylor, 2017; Yuk et al., 2018). Briefly, adults responded whether a character, Jill, had a TB or FB about a ball's location. Each trial began with a picture in which Jill would see where another character, Jack, intended to place a ball, either in a red or blue hat. In a subsequent picture, Jack would drop the ball into either the intended hat (Unswitched) or the other hat (Switched). Jill would either see him place the ball (Witnessed) or leave beforehand (Unwitnessed). Thus, only after presentation of the second image could participants conclude that in the Unwitnessed-Switched condition, Jill had a FB, whereas in all other scenarios, she had a TB.

The first image of each trial was presented for 500 ms. The second image then replaced the first, and participants indicated with a button box whether Jill thinks the ball is in the left or right hat using their corresponding hand. The second picture was displayed for 3500 ms or until the participant responded. Participants immediately received feedback in the form of a red 'x' for incorrect responses or a green checkmark for correct responses. Feedback was shown for a duration ranging from 900–1100 ms.

All participants were familiarized with the task during a practice session before the MEG scan. The task was displayed using *Presentation 18.1* (Neurobehavioral Systems Inc., https://www.neurobs.com/presentation) and back-projected onto a screen positioned 80 cm from the MEG dewar. The task ended after participants correctly answered at least 100 trials in each condition, or after 20 minutes had passed.



**Figure 4.1** – An example trial of the FB task. Each trial began with an image depicting Jill witnessing Jack holding a ball over one of two hats (top row). Then, one of four images was presented in which Jack either drops the ball into the same hat he held it over or switches the location, and in which Jill either witnesses this event or does not (middle row). These images corresponded to one of four conditions: Witnessed-Unswitched, Witnessed-Switched, Unwitnessed-Unswitched, and Unwitnessed-Switched. Correct performance in the first three conditions represented an understanding of TB, while the latter condition represented awareness of FB. Participants were asked to respond where Jill thinks the ball is located after the onset of this second image, using their left hand to indicate the hat on the left, and their right hand for the hat on the right. Participants were given feedback in the form of a green checkmark or a red 'x' (bottom row). The first image was presented for 500 ms, the second for 3500 ms (or until the participant responded), and the feedback for a random duration between 900–1100 ms. We compared performance and brain connectivity in the FB condition, Unwitnessed-Switched, to one of the TB conditions, Witnessed-Switched.

#### 4.3.2.3 Neuroimaging data acquisition

MEG data were recorded and sampled at 600 Hz while participants lay supine in a 151-channel CTF MEG system (Coquitlam, British Columbia, Canada). Continuous head localization was achieved via three fiducial coils at the nasion and left and right pre-auricular points. Noise was attenuated using an anti-aliasing low-pass filter at 150 Hz and a third-order spatial gradient.

Anatomical T1-weighted MRI data were acquired sagittally using a 12-channel head coil in a Siemens 3T scanner (Erlangen, Germany) with the 3D MPRAGE sequence (TR/TE = 2300/2.96 ms, FA = 9°, FOV = 192x240x256 mm, voxel size = 1.0 mm isotropic). To enable accurate corregistration of MEG and MRI data, participants were scanned with radio-opaque markers indicating the location of the MEG fiducial points.

#### 4.3.3 Statistical analysis

#### 4.3.3.1 Assessment and behavioural data

To compare ToM abilities and broader social cognitive skills, we tested for group differences (control vs. ASD) on the Thinking questions of the TASIT and the Social Cognition scale of the SRS-2, as well as the effects of condition (Minimal vs. Enriched) of the TASIT and rater (self vs. informant) of the SRS-2. Accuracy and median response time (RT) on the FB task were contrasted between groups. We focused our analyses on the Unwitnessed-Switched and Witnessed-Switched conditions, as our group has done previously (Mossad et al., 2016; Yuk et al., 2018). Since successful performance on the Unwitnessed-Switched and Witnessed-Switched and TB, respectively, they are henceforth referred to as the FB and TB conditions. Thus, we investigated the effects of group (control vs. ASD) and condition (FB vs. TB) on accuracy and median RT on the FB task.

We used linear mixed effects models in all our analyses of assessment and behavioural data. We also correlated accuracy on the FB task separately with performance on each block of Thinking questions of the TASIT and the Social Cognition scale of the SRS-2 to assess the validity of our FB task. All tests were performed in R 3.5.0 (R Core Team, https://www.r-project.org/), and we report results significant at p < 0.05.

#### 4.3.3.2 MEG data

The FieldTrip toolbox (Oostenveld et al., 2011) was used to preprocess and analyse all MEG data. Only correct trials were analysed. Trial epochs spanned -1500–2500 ms, relative to the onset of the second image. Data were filtered by a fourth-order Butterworth bandpass filter of 1–150 Hz and notch filters at 60 and 120 Hz. Physiological artefacts (e.g., eyeblinks and heartbeats) in the data were attenuated using independent component analysis. Trials were considered as artefactual and excluded from further analysis if they contained signals >2000 fT or head motion >5 mm.

Forward models were generated based on individuals' T1-weighted MRIs using the single-shell method (Nolte, 2003). The inverse model was calculated using a linearly constrained minimum variance beamformer (Van Veen et al., 1997). The neural activity index was used to correct for centre-of-head biases. Covariance was calculated based on activity in the time window of interest and corresponding baseline period, -400–400 ms, over all trials, and 5% regularization was applied. Estimates of activity over time were generated at the centroids of 112 regions: 74 cortical regions derived from the Automated Anatomic Labeling atlas (Tzourio-Mazoyer et al., 2002) and 38 regions of interest (ROIs) from the Power atlas (Power et al., 2011). These ROIs provided better spatial resolution of the ToM network, namely the mPFC, TPJ, and precuneus, as previous work demonstrated distinct cognitive processes associated with subdivisions of these areas (Amodio & Frith, 2006; Bzdok et al., 2013; Krall et al., 2015; Mars et al., 2012; Schurz, Tholen, Perner, Mars, & Sallet, 2017). All ROIs were ≥5 mm apart (see Appendix E for details of these 112 regions). ROIs were nonlinearly warped from template to subject space prior to timeseries estimation.

The phase difference derivative (PDD; Breakspear et al., 2004) was calculated as described by Tewarie and colleagues (2019) for all pairwise connections, giving a measure of the stability of interregional phase synchrony. Timeseries data were first filtered into our frequency bands of interest (theta: 4-7 Hz; alpha: 8-14 Hz; beta: 15-30 Hz). Orthogonalization was applied to reduce signal leakage. The instantaneous phase of each timepoint was computed using the Hilbert transform. PDD values were calculated across trials within each condition for each timepoint between -400–400 ms. Values in our time window of interest, 0-400 ms, were converted to *z* scores based on values in the baseline period, -400–0 ms, and subsequently

averaged, yielding values representing mean phase synchrony in this time window for each connection and participant.

We tested for within- and between-group connectivity differences in the theta, alpha, and beta bands using the Network-Based Statistic toolbox (Zalesky et al., 2010). We examined networks recruited more for FB than TB within each group (Control, FB > TB; ASD, FB > TB), and whether these networks showed group differences. *T* tests were conducted at each connection, and resulting *t* statistics were thresholded at values exceeding t = 2.826 (approximately equivalent to p < 0.003, a moderate threshold for this task, based on our previous work (Yuk et al., 2018)). Permutation testing was performed on suprathreshold connections forming the largest network. Group labels were shuffled, and an empirical null distribution of maximal network size was computed over 5000 permutations. A family-wise error-corrected *p* value ( $p_{FWE}$ ) was thus obtained for each network. We report networks significant at  $p_{FWE} < 0.05$ . Network visualizations were generated using BrainNet Viewer (Xia et al., 2013) and code from Koelewijn and colleagues (2019).

#### 4.3.3.3 Brain-behaviour relations

We performed exploratory analyses to investigate whether mean connectivity in networks significantly different between groups was related to ToM abilities, level of social cognition, task performance, and ASD symptom severity. Specifically, we tested whether mean connectivity in these networks predicted TASIT Thinking scores, self-rated SRS-2 Social Cognition scores, FB task accuracy, and self-rated SRS-2 Total scores, respectively. We also examined whether the effect of mean network connectivity was moderated by group status for each assessment.

### 4.4 Results

#### 4.4.1 Assessments and task performance

Adults with ASD performed more poorly on the Thinking questions on the TASIT (F(1,52) = 16.61, p = 0.0002) than controls (Fig. 4.2). They were also rated on the SRS-2 as having more difficulties with social cognition than control adults (F(1,44) = 57.31, p < 0.0001; Fig. 4.3). There was no main effect of condition of the TASIT or rater for the SRS-2, nor was there an interaction with group for either measure (ps > 0.05). Scores on the TASIT and SRS-2 are presented in Appendix F.



**Figure 4.2** – Accuracy on the Thinking questions of the Minimal and Enriched segments of the TASIT. In both cases, participants watched videos of social interactions and inferred what a character was thinking, but in the Enriched condition, participants were shown a scene revealing the reality of a situation or a character's actual belief. There was a main effect of group (F(1,52) = 16.61, p = 0.0002), such that adults with ASD were less accurate on these questions than control adults. The violin plots illustrate the range and probability density of the data, and the black horizontal lines indicate the median value.

\*\*\* *p* < 0.001



**Figure 4.3** – *T* scores on the Social Cognition scale of the SRS-2. Ratings on the SRS-2 were completed by the participants themselves, as well as by an informant who knew the participant well. There was a main effect of group (F(1,44) = 57.31, p < 0.0001), demonstrating that adults with ASD were rated as having more problems with social cognition than control adults. For a description of how data are presented in the violin plots, see Figure 4.2.

\*\*\* *p* < 0.001

There were no group differences in accuracy (F(1,77) = 2.76, p = 0.10) or median RT (F(1,77) = 0.87, p = 0.35) on the FB task. Both adults with and without ASD performed more poorly (F(1,77) = 61.98, p < 0.0001) and were slower (F(1,77) = 93.54, p < 0.0001) in the FB than the TB condition (Fig. 4.4 and Table 4.2), as their accuracy was at ceiling in the TB condition. Accuracy on the FB task was negatively correlated with the SRS-2 Social Cognition scale (r = -0.35, p = 0.017), such that individuals who performed better on the FB task reported fewer difficulties with social cognition on the SRS-2. FB task performance was not related to Thinking question accuracy in the Minimal (r = 0.20,  $p_{corr} = 0.28$ ) condition and only marginally correlated with that in the Enriched (r = 0.28,  $p_{corr} = 0.077$ ) condition of the TASIT, after correcting for multiple comparisons using the Bonferroni method.



**Figure 4.4** – Accuracy (**A**) and median RT (**B**) on the FB task. There was a main effect of condition for both accuracy (F(1,77) = 61.98, p < 0.0001) and median RT (F(1,77) = 93.54, p < 0.0001), where participants were less accurate and slower on the FB trials compared with the TB trials, but no effect of group. Please refer to Figure 4.2 for an explanation of how data are depicted in violin plots.

\*\*\* p < 0.001

#### Table 4.2

Performance on the FB task

	<b>Control</b> ( <i>N</i> = <b>39</b> )	<b>ASD</b> $(N = 40)$	
	Mean (SD)	Mean (SD)	
Accuracy (%)			
FB	89.77 (8.05)	86.40 (10.63)	
ТВ	95.79 (4.22)	94.52 (4.65)	
Number of Correct Trials			
FB	99.13 (4.71)	98.13 (5.83)	
ТВ	99.05 (3.71)	97.83 (5.45)	
Median RT (ms)			
FB	783.23 (203.18) Range: [472.5–1379.17]	841.67 (223.92) Range: [480–1533.33]	
TB	689.38 (179.76) Range: [441.67–1348.33]	710.10 (169.09) Range: [363.33–1159.17]	

FB = false belief; TB = true belief

#### 4.4.2 Neuroimaging

#### 4.4.2.1 Within-group

Control adults showed increased theta-band connectivity between 0–400 ms in the FB condition compared with the TB condition ( $p_{FWE} = 0.031$ ) in a diffuse, whole-brain network (Fig. 4.5A). Hubs with the greatest number of connections in this network included the right superior occipital gyrus, left fusiform gyrus, right STG, left inferior temporal gyrus, and dorsal mPFC. This network also involved several nodes located in the right TPJ, precuneus, and ventral mPFC. They did not display any significant connectivity in the alpha ( $p_{FWE} = 0.835$ ) or beta ( $p_{FWE} = 0.624$ ) bands.

Conversely, adults with ASD exhibited greater beta-band connectivity in this window for FB more than TB processing ( $p_{FWE} = 0.039$ ) in a more left-lateralized network (Fig. 4.5B). This network's hubs were in the parietal and occipital lobes, specifically the left TPJ, bilateral inferior

occipital gyri, and right superior occipital gyrus. The ASD group did not show any connectivity differences between conditions in the theta ( $p_{FWE} = 0.913$ ) or alpha ( $p_{FWE} = 0.910$ ) bands.



**Figure 4.5** – Within-group comparisons of network connectivity between 0–400 ms in the FB versus TB condition of the FB task. Node size represents its relative degree, or number of connections. (**A**) In control adults, a widespread network was recruited in the theta band specifically for FB understanding ( $p_{FWE} = 0.031$ ). Hubs of this network were the left inferior temporal gyrus (ITG), left fusiform gyrus, right superior occipital gyrus (SOG), right STG, and dorsal mPFC. Other FB-relevant nodes in this network included the right TPJ, precuneus, and ventral mPFC. (**B**) In adults with ASD, a left-lateralized network anchored in posterior regions of the brain, specifically the bilateral inferior occipital gyri (IOG) and right SOG, demonstrated greater beta synchrony ( $p_{FWE} = 0.039$ ) for FB processing. The left TPJ was also a major hub of this network.

#### 4.4.2.2 Between-group

Adults with ASD showed decreased connectivity, relative to controls, between 0–400 ms, in a mainly right-lateralized theta-band network for FB compared with TB trials ( $p_{FWE} = 0.010$ ; Fig. 4.6A, 4.6C). The main hubs were the right IFG, STG, TPJ, and the dorsal and ventral mPFC.

Multiple nodes of the precuneus were also recruited in this network. Mean connectivity analyses revealed that control adults showed greater synchrony in this network for FB compared with TB trials, whereas adults with ASD tended to exhibit increased connectivity in this network during the TB condition, relative to the FB condition (Fig. 4.6B). However, when we contrasted TB with FB within the ASD group, we did not find any significant difference ( $p_{FWE} = 0.14$ ). There were no group differences in the alpha or beta bands in either direction ( $p_{FWE} > 0.05$ ).



**Figure 4.6** – Between-group comparison of network connectivity during the 0–400 ms window of the FB relative to TB trials of the FB task. (**A**) Adults with ASD demonstrated significantly reduced theta-band synchrony in a right-lateralized network compared with control adults ( $p_{FWE} =$ 0.010). Node size represents its relative degree, or number of connections. (**B**) The control group had greater mean connectivity in this network for FB versus TB processing, while the ASD group showed the opposite effect, where this network was recruited more for TB than FB understanding, although this latter effect was not significant ( $p_{FWE} = 0.14$ ). (**C**) Results in (**A**) represented as a circle plot. Nodes are grouped in the following manner, from top to bottom: medial frontal structures (red), frontal areas (orange), regions around the central sulcus (green), parietal areas (turquoise), temporal areas (blue), medial parietal structures (dark blue), occipital areas (purple).

#### 4.4.3 Brain-behaviour relations

We found no significant relations between mean connectivity values in the theta-band network that was differentially recruited by the two groups and any behavioural measures, nor was there a significant interaction between mean network connectivity and group status in predicting these outcomes (ps > 0.05).

## 4.5 Discussion

Our study confirmed previous literature indicating that while adults with ASD successfully demonstrate FB understanding in experimental tasks, they still exhibit deficits in general social cognitive abilities, shown by their scores on the TASIT and SRS-2. Despite this proficiency with the FB task, the brain networks they recruited differed from controls both spatially and spectrally.

Unlike controls, the ASD group showed no interregional synchrony in the theta band for processing FB. This lack of communication in the theta band was statistically different between groups, such that adults with ASD showed significantly less theta-band connectivity in a network of mainly right hemisphere regions during FB reasoning compared with controls. This network included several brain areas implicated in FB processing, such as the precuneus, mPFC, and right TPJ, the latter being responsible for mentalizing or making mental state representations (Aichhorn et al., 2009; Bardi, Desmet, Nijhof, Wiersema, & Brass, 2017; Bowman, Kovelman, Hu, & Wellman, 2015; Filmer, Fox, & Dux, 2019; Naughtin et al., 2017; Perner et al., 2006; Saxe & Wexler, 2005), and which has shown atypical activation in adults with ASD in other FB and ToM tasks (Lombardo et al., 2011; Murdaugh, Nadendla, & Kana, 2014; Nijhof et al., 2018;

Pantelis, Byrge, Tyszka, Adolphs, & Kennedy, 2015). One major hub of this network was the right IFG, which is linked to inhibiting or suppressing one's own knowledge to correctly infer another individual's belief (Hartwright, Hansen, & Apperly, 2016; Samson, Apperly, Kathirgamanathan, & Humphreys, 2005; Schurz & Tholen, 2016; van der Meer, Groenewold, Nolen, Pijnenborg, & Aleman, 2011). The right STG also showed decreased connectivity with several other brain regions in the ASD group. While right STG volume is altered in ASD (Boddaert et al., 2004; Jou, Minshew, Keshavan, Vitale, & Hardan, 2010), and activity in the posterior division is associated with social cognitive processes (Gobbini et al., 2007; Moessnang et al., 2017; Patel, Sestieri, & Corbetta, 2019; Puce & Perrett, 2003; van Veluw & Chance, 2014; Vander Wyk, Hudac, Carter, Sobel, & Pelphrey, 2009; Vistoli, Brunet-Gouet, Baup-Bobin, Hardy-Bayle, & Passerieux, 2011; Zaitchik et al., 2010), we found recruitment of the anterior STG, which is implicated in visuospatial processing (Committeri et al., 2007; Ellison, Schindler, Pattison, & Milner, 2004; Himmelbach, Erb, & Karnath, 2006; Shah-Basak, Chen, Caulfield, Medina, & Hamilton, 2018), visual working memory maintenance (Park et al., 2011), and some ToM tasks involving movement or spatial relationships (Abraham, Werning, Rakoczy, von Cramon, & Schubotz, 2008; Grosbras, Beaton, & Eickhoff, 2012; Han et al., 2013; Herrington, Nymberg, & Schultz, 2011).

Given that theta-band synchrony reflects interregional communication and top-down control (Siegel et al., 2012; von Stein et al., 2000; von Stein & Sarnthein, 2000; Wang et al., 2019), decreased connectivity between these disparate right hemisphere regions in adults with ASD suggests difficulty in linking their corresponding neural functions, namely mentalizing, inhibition, and visuospatial processing and memory. This finding extends earlier studies reporting decreased functional connectivity in adults with ASD during ToM tasks (Cole, Barraclough, & Andrews, 2019; Kana et al., 2009, 2014; Libero et al., 2014), which was also proposed to reflect impaired functional coordination. Furthermore, the area of the right TPJ involved in this network is situated between the anterior and posterior portions of the TPJ (Krall et al., 2015), which are associated with attention reorienting and ToM, respectively (Cabeza, Ciaramelli, & Moscovitch, 2012; Mars et al., 2012), but with some overlap (Krall et al., 2016; Schuwerk, Schurz, Müller, Rupprecht, & Sommer, 2017). Given its location and connections to the right IFG and mPFC, this right TPJ node may be engaged in both processes, and reduced synchrony with these areas may indicate some disconnect between executive and social cognitive

functions. This interpretation may explain why there were no significant relations between mean connectivity of this theta-band network and any of our ToM or social cognition measures; this network may be linked to broader difficulties with integration of mental state information with inhibitory and visuospatial processes rather than mentalizing itself. Prospective work elucidating the distinct contributions of brain areas implicated in mentalizing and executive functions, especially inhibition, to performance on ToM tasks in ASD will be essential in validating this hypothesis.

Adults with ASD also demonstrated greater connectivity in a beta-band network for FB compared with TB processing. This network was fairly left-lateralized, with many connections occurring between the bilateral visual cortices and left frontal and parietal regions, most notably the left TPJ. This left-lateralized beta-band connectivity in our ASD group contrasts with the more right-lateralized theta-band connectivity in our controls, echoing previous MEG work illustrating more leftward network configurations in ASD (Chan, Han, Sze, et al., 2011; Fiebelkorn, Foxe, McCourt, Dumas, & Molholm, 2013; Hiraishi et al., 2015; Melillo & Leisman, 2009; Murias et al., 2007). This tendency to left lateralization may be due to impaired connectivity with the right hemisphere, leading to more localized rather than integrative, global processing (O'Reilly et al., 2017). Recruitment of the left TPJ rather than its homologue extends recent studies showing increased left (Sommer et al., 2018) but decreased right (Nijhof et al., 2018) TPJ activity in adults with ASD during FB tasks, indicating atypical lateralization of FB function. As the left TPJ in this network was quite anterior, it may be more involved in visual attention reorienting, having a similar subdivision of function as the right TPJ (Krall et al., 2015), and consistent with other hubs of this network being in the visual cortex. In addition, beta-band connectivity has been implicated in top-down control during attention tasks (Buschman & Miller, 2007; Fries, 2015; Gross et al., 2004; Lee, Whittington, & Kopell, 2013), implying that this network is associated more with visual attention than ToM in the ASD group, perhaps compensating for deficits in top-down control due to lack of engagement of theta-band connectivity.

Interestingly, a recent EEG study found that typical adults showed greater beta power and connectivity during FB relative to TB understanding (Guan et al., 2018), pointing to a role of beta oscillations in FB reasoning. However, in our study, adults with ASD, but not controls, showed this effect in beta-band synchrony. Explanations for this discrepancy are that they

investigated connectivity between only one parietal-occipital EEG sensor and all other sensors in the alpha and beta bands, whereas we also examined connectivity in the theta band, and our analyses were performed for all possible pairwise connections. Yet, it is evident from our withingroup analyses that this beta-band network facilitates FB reasoning in adults with ASD. The extent to which beta-band oscillations in ASD reflect the attentional or mentalizing aspects of FB understanding could be elaborated by future studies, but given the significant involvement of the anterior left TPJ and the established link between beta-band synchrony and attention, we propose that functional connectivity in the beta band in adults with ASD underlies the visual attentional processes necessary for successful FB reasoning.

This study revealed key differences in neural processing of FB in adults with and without ASD. We uniquely showed that during a FB task, adults with ASD had decreased theta-band functional connectivity compared with controls among regions implicated in inferring mental states, inhibitory control, and visuospatial processing and memory, perhaps indicating difficulty in integrating these cognitive functions. They also exhibited increased beta-band synchrony during FB relative to TB processing, which may coordinate the visual attentional resources required for FB understanding. This arrangement could signify a reliance on intact visual abilities to complete the task (de Jonge et al., 2007; O'Riordan, 2004), as suggested in other studies of complex cognitive processing in ASD (Sahyoun, Belliveau, Soulières, Schwartz, & Mody, 2010). Thus, adults with ASD showed atypical top-down control when reasoning about FB. As our sample included only adults who performed above chance on the FB task, our findings might not necessarily extend to the wider ASD population. In fact, these discrepancies may be increased in adults with ASD with more severe FB impairments, emphasizing the need to include individuals with a broad range of ToM capabilities in future studies. Furthermore, as the present study focused on functional connectivity related to FB processing, we can only speculate about the involvement of executive functions and their influence on other ToM subdomains. There are demonstrated links between behavioural measures of executive functions and ToM in ASD (Hamilton et al., 2016; Kouklari et al., 2019; Miranda, Berenguer, Roselló, Baixauli, & Colomer, 2017; Ozonoff et al., 1991; Pellicano, 2010), and between executive brain regions and FB processing in controls (Hartwright, Apperly, & Hansen, 2012; Saxe, Schulz, & Jiang, 2006; van der Meer et al., 2011), but not in ASD. Thus, future neuroimaging work examining the interplay

between these cognitive processes will be crucial to our understanding of how they interact on the neural level to support FB reasoning in adults with ASD.

## Chapter 5 General Discussion

## 5 Summary and conclusions

The three studies of this thesis explored potential differences between adults with and without ASD in the frequency-specific networks responsible for higher cognitive functions that are directly relevant to the symptomatology of ASD. They add to our current understanding of connectivity impairments in ASD by elaborating on the precise neural mechanisms and processes that are affected in inhibition, working memory, and ToM/FB understanding.

## 5.1 Key findings

#### 5.1.1 Reduced suppression of inhibition-irrelevant brain areas in ASD

Study 1 (Chapter 2) assessed the differences in functional connectivity between adults with and without ASD during a Go/No-go response inhibition task. Adults with ASD had reduced alphaband connectivity between the right IFG, a core region for inhibition (Aron et al., 2014; Forstmann et al., 2008; Levy & Wagner, 2011; Rubia et al., 2003; Vidal et al., 2012), and non-inhibition areas, such as the STG, fusiform gyrus, and lingual gyrus. Alpha-band connectivity within this network of brain regions was inversely correlated with self-reported ratings on the Inhibit scale of the BRIEF-A, where higher scores indicate more difficulties with inhibition in everyday life. Thus, decreased alpha-band network connectivity was related to more impaired inhibitory control. These findings imply that not only are alpha oscillations involved in inhibition of local brain activity (de Pesters et al., 2016; Jensen & Mazaheri, 2010; Klimesch et al., 2007; Palva & Palva, 2011), but also that interregional phase synchrony in the alpha band plays a role in inhibitory control. Considering the brain areas implicated in these results, reduced alpha-band connectivity among these regions may reflect that adults with ASD are less able to suppress task-irrelevant brain activity, which can then interfere with successful inhibition in everyday life.

Given that previous work only examined connectivity in ASD among areas implicated in inhibitory control (Kana et al., 2007; Lee et al., 2009; Solomon et al., 2014), this study was the first to reveal that adults with ASD not only have difficulty in coordinating task-relevant brain areas, but also in restraining task-irrelevant regions to exert inhibitory control. Furthermore, given that the only other MEG study of inhibition in adults with ASD also found decreased alpha-band synchrony in the ASD group (Kenet et al., 2012), the specificity of this study's findings to the alpha band supports the role of both power and phase synchrony in the alpha band for cortical inhibition.

## 5.1.2 Frontoparietal network synchrony mediating working memory recognition, not maintenance, is impaired in ASD

Study 2 (Chapter 3) investigated whether adults with and without ASD show differential engagement of the frontoparietal network and its links to other brain regions during working memory maintenance and recognition in a visual *n*-back task. During the maintenance period, both groups elicited networks in the alpha band, which is known to be involved in working memory maintenance (Crespo-Garcia et al., 2013; Jensen et al., 2002; Klimesch et al., 2008; Palva et al., 2010; Sato et al., 2018), in the 1-back condition, whereas only the ASD group recruited a similar alpha-band network in the 2-back condition. In both cases, the alpha-band network employed by adults with ASD consisted of many more brain areas, both those within and outside of the frontoparietal network, than seen in control adults. As the maintenance period was only examined for correct trials, this stronger recruitment of the frontoparietal network, as well as other brain areas peripheral to this classic working memory network, suggests more effortful maintenance processes in adults with ASD.

Conversely, during the recognition period, control adults recruited a network in the theta band in the 1-back condition and networks in the theta and beta bands in the 2-back condition, whereas adults with ASD did not show any increased network recruitment for either condition. Therefore, when comparing the two groups, adults with ASD showed relatively decreased phase synchrony in the theta band in a network involving the right IFG and left IPL, the latter of which is responsible for storing and maintaining stimulus representations in working memory (Gazzaley et al., 2004; Jonides et al., 1998; Ragland et al., 2002). Given the regions involved and the theta band's role in exerting top-down control (Cavanagh & Frank, 2014; Johnson et al., 2017; Roux & Uhlhaas, 2014; Sauseng et al., 2010), this group difference during recognition implies a potential difficulty in inhibiting stimulus representations in working memory that are no longer relevant and which would interfere with stimulus recognition.

As adults with ASD performed equally as well as controls on the 1-back condition, it may be that greater recruitment of the frontoparietal network during maintenance is needed to strengthen

relevant stimulus representations to overcome difficulties in suppressing irrelevant stimulus representations during recognition. Despite their mastery of the *n*-back task, adults with ASD reported having difficulties with working memory in everyday life. It may be that the cognitive demands imposed on adults with ASD in everyday life may overburden their maintenance processes and exacerbate impaired neural communication during recognition processes, thereby leading to their subjective experience of working memory deficits.

The distinctive connectivity results for the maintenance and recognition periods in this study add specificity to the known connectivity impairments related to working memory in people with ASD (Barendse et al., 2018; Braden et al., 2017; Koshino et al., 2005; Urbain et al., 2016). Due to the broad temporal resolution of fMRI (Glover, 2011; Kim, Richter, & Uğurbil, 1997), much of the current neuroimaging literature in this field does not distinguish between the different components of working memory processing, making it unclear whether deficits in connectivity pertain to a certain aspect of working memory or are more extensive. The use of MEG, which measures neural activity with millisecond precision (Hämäläinen et al., 1993; Hari & Salmelin, 2012), allowed this study to determine that the source of differences in connectivity between adults with and without ASD during a working memory task may lie in recognition more than in maintenance processes. This work also builds on a prior MEG study which found decreased alpha-band connectivity during recognition in children with ASD performing a similar task (Urbain et al., 2016). Taken together, these findings suggest that reduced phase synchrony related to recognition processes is present in both childhood and adulthood in ASD, potentially affecting working memory abilities throughout life.

## 5.1.3 Decreased communication between inhibition and FB-related brain regions in ASD

Study 3 (Chapter 4) contrasted whole-brain connectivity between adults with and without ASD during a FB ToM task. Adults with ASD were found to have decreased theta-band connectivity in a network involving several brain regions implicated in ToM. Importantly, two of the major hubs of this network were the right TPJ and IFG, the former of which is a key region for attributing and processing mental states (Aichhorn et al., 2009; Bardi et al., 2017; Bowman et al., 2015; Filmer et al., 2019; Mossad et al., 2016; Saxe & Wexler, 2005). Thus, these findings suggest that adults with ASD may have difficulty inhibiting their own beliefs when evaluating the beliefs of others, especially when they do not align with their own perspective. While these

differences in theta-band connectivity did not impact task performance, they could potentially influence mentalizing processes in everyday life, as adults with ASD demonstrated more difficulty with inferring the thoughts of others when viewing naturalistic social interactions, and they reported having more issues with social cognition in everyday life than control adults.

This work is the first to determine that adults with ASD show reduced phase synchrony during FB processing, complementing previous literature showing decreased connectivity in adults with ASD during other ToM tasks (Kana et al., 2009, 2014). Thus, it appears that adults with ASD may have fundamental differences in the core ToM network that lead to reduced connectivity during tasks of various ToM domains. Moreover, this study found weaker theta-band phase synchrony not only within the ToM network, but also in its connections to other brain regions, indicating a more widespread difficulty in integrating ToM with other functions.

## 5.2 General implications

## 5.2.1 Long-range underconnectivity impacts higher cognitive functions in ASD

Across the three studies, adults with ASD displayed reduced long-range functional connectivity compared to control adults when engaging in higher cognitive functions. Specifically, they exhibited decreased theta- and alpha-band phase synchrony between distant brain areas involved in inhibiting a prepotent response, recognizing a previously presented visual stimulus, and inferring FB in another's mental state. Both theta and alpha oscillations are speculated to facilitate communication and top-down control between brain regions (Cavanagh & Frank, 2014; Palva & Palva, 2011; Sauseng et al., 2006; von Stein & Sarnthein, 2000). Given that alpha oscillations have been strongly implicated in cortical inhibition (de Pesters et al., 2016; Jensen & Mazaheri, 2010; Klimesch et al., 2007; Palva & Palva, 2011), the specificity of our finding of reduced alpha-band connectivity in adults with ASD to the inhibition task suggests that atypical alpha-band synchrony in ASD may particularly reflect impairments in the inhibitory processes involved in top-down control. On the other hand, as long-range theta-band synchrony has been linked to general top-down control mechanisms (Cavanagh & Frank, 2014; Sauseng et al., 2006; von Stein et al., 2000; Voytek et al., 2015), and since the networks showing differences between the ASD and control groups during the working memory and FB tasks comprised both taskrelevant and task-irrelevant brain regions, reduced theta-band connectivity in ASD may indicate

difficulties in recruiting task-relevant and inhibiting task-irrelevant brain areas, both of which are necessary functions for effective top-down control.

More broadly, this common finding of reduced long-range phase synchrony in all three tasks indicates some overall discoordination of activity across the brain during complex cognitive processing. Although graph theoretical properties of the networks differentially recruited by adults with and without ASD were not examined in this thesis, reduced connectivity among brain areas comprising task-specific networks (i.e., the frontoparietal working memory network and the ToM network) suggests poor functional network segregation, which is a measure of the formation of specialized networks for certain cognitive functions (Rubinov & Sporns, 2010). Additionally, decreased connectivity between these particular brain regions and others important for successful task performance, such as the right IFG, implies poor functional network integration, or the degree to which brain areas from distinct networks communicate (Rubinov & Sporns, 2010). Whereas fMRI studies have reported patterns of decreased segregation and increased integration in brain networks in ASD (Henry, Dichter, & Gates, 2018; Itahashi et al., 2014; Reiter et al., 2019; Rudie et al., 2013), EEG/MEG studies have determined that individuals with ASD display reductions in both network segregation and integration (Barttfeld et al., 2011; Boersma et al., 2013; Pollonini et al., 2010) in specific frequency bands (Kitzbichler et al., 2015; Ye et al., 2014). As these previous investigations all used resting-state paradigms, the present work suggests that brain networks in adults with ASD also exhibit decreased segregation and integration during tasks of inhibition, working memory, and FB, indicating inefficient neural processing and organization. Although these differences in connectivity were not associated with task performance, adults with ASD reported difficulties with inhibition, working memory, and social cognition in everyday life. In the case of inhibitory control, lower alpha-band synchrony was associated with more self-reported problems with inhibition, demonstrating that reduced interregional connectivity may be related to deficits in real-world functions.

These findings are in line with mounting evidence in the literature showing long-range underconnectivity in a variety of contexts in people with ASD (Anagnostou & Taylor, 2011; Belmonte et al., 2004; Castelli et al., 2002; Di Martino et al., 2014; Geschwind & Levitt, 2007; Just et al., 2004; Keown et al., 2017; Kleinhans et al., 2008; Mostofsky et al., 2009; O'Reilly et al., 2017; Sato & Uono, 2019; Vissers et al., 2012). It is worth nothing that the majority of connectivity studies in ASD have been conducted using fMRI, which measures neural activity
indirectly through the BOLD signal, and which fluctuates at frequencies <0.2 Hz (Logothetis, 2003), as opposed to MEG, which directly measures neural activity, and which is sensitive to a wide range of oscillations from around 0.1–600 Hz (Hari & Salmelin, 2012). Although there is some overlap between networks derived from fMRI data and networks in lower frequency bands obtained from EEG/MEG recordings (Brookes et al., 2011; de Pasquale et al., 2010; Hall, Robson, Morris, & Brookes, 2014), the exact relationship between fMRI and EEG/MEG varies by region, by connection, and by frequency band (Hipp & Siegel, 2015; Kujala et al., 2014; Lankinen et al., 2018; Liljeström, Stevenson, Kujala, & Salmelin, 2015). Therefore, these findings complement the current fMRI connectivity literature by critically specifying the spatial and spectral components of networks that adults with and without ASD recruit when engaging in higher cognitive functions. Furthermore, as much of this existing literature is based on restingstate data, this work furthers the theory of altered connectivity in ASD by demonstrating that reduced long-range functional connectivity occurs across several cognitive domains, as well as during rest, in adults with ASD. The pervasiveness of this pattern of reduced connectivity implies a broad, underlying issue in ASD affecting communication among brain areas. One likely explanation may lie in white matter structure, which is the physical means by which neural information is transmitted. Several studies have established that decreases in white matter in interhemispheric and long-range tracts occur in individuals with ASD from childhood to adulthood (Ameis et al., 2016; Aoki et al., 2013; Bloemen et al., 2010; Fitzgerald et al., 2019; Karahanoğlu et al., 2018; Mak-Fan et al., 2013; Travers et al., 2012; Vogan, Morgan, Leung, et al., 2016). Recent work has revealed that alterations in white matter structure are related to decreased functional resting-state connectivity (Hong, Hyung, et al., 2019; Rudie et al., 2013). Moreover, two studies separately investigating executive functions and ToM both found decreased white matter and reduced connectivity in adults with ASD (Just et al., 2007; Kana et al., 2014). Therefore, atypical white matter structure throughout development in ASD may be at the heart of this deficit in long-range connectivity, thereby hampering the normal maturation of social cognition and executive functions in ASD.

## 5.2.2 The role of inhibition in working memory and false belief neural processing in ASD

In both the working memory and FB studies of this thesis, adults with ASD demonstrated reduced theta-band synchrony relative to controls in networks where the right IFG was one of the

principal hubs. Since the right IFG plays a major role in inhibition (Aron et al., 2014; Forstmann et al., 2008; Levy & Wagner, 2011; Rubia et al., 2003; Vidal et al., 2012), its significant involvement in both tasks implies that inhibition contributes critically to working memory and FB processes. Furthermore, given that theta-band synchrony facilitates top-down control (Cavanagh & Frank, 2014; Sauseng et al., 2006; Siegel et al., 2012; von Stein et al., 2000), the right IFG may be a key player in modulating recruitment of brain areas responsible for working memory and FB understanding. Reduced theta-band connectivity between the right IFG and regions of the working memory and ToM networks may therefore result in poor coordination of these areas and subsequent deficits in these two cognitive functions in ASD.

The idea that working memory and FB understanding may depend on inhibition is certainly neither new nor novel. To accurately recognize whether a certain stimulus has been previously presented, one needs to suppress other, irrelevant stimulus representations that may compete for attention in working memory. In the case of FB reasoning, one must inhibit his/her own perspective and beliefs to correctly infer that another person has a FB. Numerous studies have associated inhibitory control with working memory (Bjorklund & Harnishfeger, 1990; Hasher et al., 2007; Kane, Bleckley, Conway, & Engle, 2001; Miyake et al., 2000; Schneider, Barth, Getzmann, & Wascher, 2017; Verté, Geurts, Roeyers, Oosterlaan, & Sergeant, 2006; Zanto & Gazzaley, 2009) and FB reasoning or social cognition (Apperly et al., 2009; Carlson et al., 2002; Green, Brown, Yap, Scheffer, & Wilson, 2020; Kouklari et al., 2019; Leung, Vogan, Powell, Anagnostou, & Taylor, 2016; Mutter et al., 2006; Pellicano, 2007; Zimmerman, Ownsworth, O'Donovan, Roberts, & Gullo, 2016) in both controls and people with ASD. fMRI work has also found that the right IFG is recruited in tasks of working memory (Kumar et al., 2016; McNab et al., 2008; Nee et al., 2013) and FB (Hartwright et al., 2012; Rothmayr et al., 2011; Saxe et al., 2006; van der Meer et al., 2011) in controls. Interestingly, one fMRI working memory study found increased right IFG activation in adults with ASD compared to control adults (Koshino et al., 2005). Greater right IFG activity in children with ASD was also observed during a FB task (Yuk et al., 2018), although this group difference may dampen by adulthood (Sommer et al., 2018). Nevertheless, it is evident that inhibitory control mediated by the right IFG is engaged in working memory and FB understanding in ASD. Considering that the first study of this thesis found decreased connectivity involving the right IFG in adults with ASD during response inhibition, such deficits in inhibition-related connectivity may well carry over to neural processes subserving working memory and FB reasoning, as well as other cognitive processes that rely on inhibition. This hypothesis is in line with a behavioural theory of inhibition that posits that inhibitory control plays a fundamental role in a wide variety of cognitive functions (Hasher, 2007; Lustig, Hasher, & Tonev, 2001; Lustig, Hasher, & Zacks, 2007). Hence, it will be crucial for future neuroimaging work to consider the influence of the right IFG and inhibitory control on higher cognitive functions in ASD.

## 5.3 Limitations and future directions

In all three studies, most participants were fairly independent and had normal IQ scores. However, it is known that people with ASD exhibit a wide variety of abilities (Charman et al., 2011; Georgiades, Szatmari, & Boyle, 2013; Geschwind, 2009; Happé, Ronald, & Plomin, 2006; Lai, Lombardo, Chakrabarti, & Baron-Cohen, 2013; Masi, DeMayo, Glozier, & Guastella, 2017; Wing, 1975), ranging from individuals who have comorbid intellectual disability and require substantial support in adulthood to those who have exceptional intellectual and cognitive capabilities. Moreover, as the samples in each study were drawn from a larger cohort of participants who performed all three tasks, there was a great deal of correspondence in the study samples (although they did not completely overlap, as some participants were excluded from particular studies due to poor data quality, low accuracy, etc.). In total, 60 adults were included in all three studies, of which 32 were controls and 28 were adults with ASD. This thesis did not restrict analyses to these 60 participants to maximize statistical power in the individual studies, but the large overlap between these samples restricts the generalizability of this thesis' implications. For example, these 28 adults with ASD may have deficits in inhibition that influence their working memory and ToM capabilities, but there may also exist adults with ASD who have intact inhibition, but impaired working memory and ToM, that are not wellrepresented in these studies. Therefore, this thesis does not address the diversity of individuals with ASD, and its findings likely pertain to only a fraction of the ASD population. In addition, questionnaire and assessment data were not available for all participants due to attrition, so the behavioural results do not necessarily represent the full samples in these studies. While this thesis provides considerable insight into how reduced connectivity may underlie cognition in higher-functioning adults with ASD, to better understand the heterogeneous profiles of executive functions and ToM in this population, it would be necessary for future studies to assess a large number of adults with ASD with a wide range of cognitive abilities. It would be interesting then

to investigate whether there are subtypes of adults with ASD that are characterized by diverse patterns of connectivity related to executive functions and ToM that may differ in unique ways from control adults, as has been done with structural and resting-state fMRI data (Chen et al., 2019; Dean et al., 2017; Easson, Fatima, & McIntosh, 2019; Hong, Valk, Di Martino, Milham, & Bernhardt, 2018; Hong et al., 2020; Tang et al., 2020). For example, during the FB task, a group of adults with ASD who have more severe deficits in executive functions may exhibit more pronounced deficits in connectivity between the right IFG and the ToM network, whereas another group of adults with ASD who are more impaired in social cognition may simply show decreased phase synchrony among ToM-related brain regions. Distinguishing between such subtypes is crucial not only for understanding the complex neurobiology underlying ASD, but also for determining effective interventions for people with ASD with diverse abilities.

It is also important to acknowledge that the overall implications of this work are not necessarily ASD-specific, as differences in executive functions and ToM, as well as brain connectivity, have also been observed in other psychiatric conditions, such as attention-deficit/hyperactivity disorder (Berenguer et al., 2018; Biederman et al., 2004; Bora & Pantelis, 2016; Castellanos & Aoki, 2016; Castellanos, Sonuga-Barke, Milham, & Tannock, 2006; Corbett et al., 2009; Fair et al., 2013; Konrad & Eickhoff, 2010; Michelini et al., 2019; Roberts, Martel, & Nigg, 2017; Sjöwall, Roth, Lindqvist, & Thorell, 2013; Uekermann et al., 2010) and schizophrenia (Brune, 2005; Couture et al., 2010; Damaraju et al., 2014; Frith, 1992; Hutton et al., 1998; Lawrie et al., 2002; Lugnegård, Unenge Hallerbäck, Hjärthag, & Gillberg, 2013; Lynall et al., 2010; Orellana & Slachevsky, 2013; Pilowsky, Yirmiya, Arbelle, & Mozes, 2000; Sharma & Antonova, 2003; Sprong, Schothorst, Vos, Hox, & Van Engeland, 2007; Tin et al., 2018). In fact, even healthy older adults demonstrate increased interference during working memory (Gazzaley, Cooney, Rissman, & D'Esposito, 2005; Lustig, May, & Hasher, 2001), reduced ToM ability (Bernstein, Thornton, & Sommerville, 2011; Bottiroli, Cavallini, Ceccato, Vecchi, & Lecce, 2016; Cavallini, Lecce, Bottiroli, Palladino, & Pagnin, 2013; Fischer, O'Rourke, & Loken Thornton, 2017) associated with inhibitory control (Moran, 2013; Rakoczy, Harder-Kasten, & Sturm, 2012; Wang & Su, 2013), and generally lower functional connectivity (Betzel et al., 2014; Campbell, Grady, Ng, & Hasher, 2012; Damoiseaux et al., 2008; Ferreira et al., 2016; Geerligs, Renken, Saliasi, Maurits, & Lorist, 2015; Grady, 2012; Madden et al., 2010; Onoda, Ishihara, & Yamaguchi, 2012; Varangis, Habeck, Razlighi, & Stern, 2019; Zonneveld et al., 2019) relative to younger

adults. Individuals with ASD also exhibit shared behavioural and neural characteristics with other neurodevelopmental disorders, especially attention-deficit/hyperactivity disorder and obsessive-compulsive disorder (Ameis et al., 2016; Baribeau et al., 2019; Carlisi et al., 2017; Carter Leno et al., 2018; Kushki et al., 2019; Park et al., 2018; Vaidya et al., 2020; Waddington et al., 2018), suggesting that similar patterns of atypical behaviour and brain structure and function observed in these groups may have common transdiagnostic etiologies. It is therefore possible that these findings reflect functional connectivity differences that occur generally in individuals with deficits in inhibition, working memory, and ToM, and it will be vital for future work to identify shared and distinct profiles of brain connectivity related to higher cognitive functions among different populations.

This thesis did not explore the contributions of medication or biological sex on cognitive function and related brain connectivity. As half of the participants with ASD in each of the three studies reported taking psychotropic medication, and since such medications can possibly alter functional connectivity in ASD (Linke, Olson, Gao, Fishman, & Müller, 2017), the results of these studies may not fully describe the innate pattern or extent of connectivity differences in adults with ASD. However, given the broad range of types and doses of medication used by participants in these samples, analyses accounting for this aspect could not be conducted. In addition, as many individuals with ASD take psychotropic medication regularly (Aman, Lam, & Collier-Crespin, 2003; Buck et al., 2014; Esbensen, Greenberg, Seltzer, & Aman, 2009; Mandell et al., 2008), the inclusion of participants using medication in these studies may in fact lead to findings that are more representative of the everyday experiences of people with ASD. Biological sex is also an important consideration in studies of individuals with ASD, as men and women with ASD show differences in behaviour and brain structure and function (Alaerts, Swinnen, & Wenderoth, 2016; Beacher et al., 2012; Greenberg, Warrier, Allison, & Baron-Cohen, 2018; Henry et al., 2018; Jung et al., 2015; Lai et al., 2011; Lai, Lombardo, Suckling, et al., 2013; Zeestraten et al., 2017), particularly in the contexts of social cognition and executive functions (Baron-Cohen et al., 2015; Bölte, Duketis, Poustka, & Holtmann, 2011; Holt et al., 2014; Hull, Mandy, & Petrides, 2017; Kiep & Spek, 2017; Kirkovski, Enticott, Hughes, Rossell, & Fitzgerald, 2016; Lai et al., 2012; White et al., 2017), compared to one another and relative to controls. As only ~10 participants with ASD in each study of this thesis were female, robust analyses of the effect of sex could not be performed. Thus, sex differences in frequency-specific

phase synchrony related to executive functions and ToM in ASD remain to be explored, and such work will be key to understanding the precise patterns of functional connectivity underlying higher cognitive functions in ASD.

The potentially confounding effect of head motion on functional connectivity is also a significant consideration in this work. A seminal fMRI study (Van Dijk, Sabuncu, & Buckner, 2012) demonstrated that failing to correct for increased head motion, which is more frequently observed in individuals with ASD than controls, can spuriously lead to a pattern of decreased long-range and increased short-range connectivity, which is also often reported in the ASD population. In all three studies of this thesis, the detrimental effect of head motion was mitigated by excluding trials with >5mm of head motion from the initial head position. As a result, for most data in these studies, the control and ASD groups were matched on head motion; adults with ASD only showed significantly greater head motion in the Inhibition condition in Study 1 (Appendix G). While this difference may impact the findings of this study, it is important to acknowledge that head motion may influence MEG data in a different manner than fMRI data. One study contrasted patterns of network connectivity before and after regression of head motion in MEG resting-state data (Messaritaki et al., 2017). They observed that head motion led to spuriously increased signal in visual and sensorimotor networks, while it had minimal effect on default mode, frontoparietal, and frontal networks. In addition, head motion had a greater influence on higher frequency bands in comparison to lower ones. Since the alpha-band network that differed between the two groups in Study 1 consisted mainly of frontotemporal connections, and alpha is a lower frequency band, it is unlikely that the increase in head motion in adults with ASD in this task drove this result. However, it is still critical to account for any differences in head motion in these data, and it will therefore be vital for future work to confirm this study's findings.

Another limitation to consider is the fact that the experimental tasks used in these studies tap very specific cognitive processes in a highly controlled setting. Such tasks often correlate poorly with the behaviours that they are meant to capture (Chaytor & Schmitter-Edgecombe, 2003; Kenworthy et al., 2008; Sbordone, 2008), bringing into question the extent to which task performance and the associated decreases in phase synchrony exemplify the actual cognitive and neural profiles of people with ASD. For instance, although accuracy on the experimental FB task was related to ratings of everyday social cognition on the SRS-2, mean network connectivity in

adults with and without ASD during the FB task did not predict these social cognition scores. Therefore, performance on the FB task may have only been associated with a particular aspect of social cognition. One might expect that differences in functional connectivity between individuals with and without ASD may be more disparate in more naturalistic settings, as such environments often involve processing more complex stimuli and place greater demands on cognitive control, which is impaired in ASD (Dichter & Belger, 2008; Hill, 2004; Mackie & Fan, 2016; Russell, 1997; Solomon et al., 2008). Thus, using ecologically valid tasks could allow one to examine the full extent of potential connectivity differences in ASD, which would be highly informative for designing clinical interventions. One promising naturalistic ToM paradigm would be hyperscanning, where two or more individuals are scanned simultaneously while they interact (Montague et al., 2002). The degree of coherence in brain activity between the interacting individuals is thought to indicate mutual engagement or coordination in a shared experience (Czeszumski et al., 2020; Hari, Henriksson, Malinen, & Parkkonen, 2015; Hasson, Ghazanfar, Galantucci, Garrod, & Keysers, 2012; Redcay & Schilbach, 2019; Stephens, Silbert, & Hasson, 2010), which inherently involves ToM. Hence, hyperscanning would enable the investigation of ToM in the context of social communication and interaction, domains in which people with ASD demonstrate impairments (American Psychiatric Association, 2013; Lord et al., 2020). This protocol is also well suited to studying ToM in ASD since it does not necessarily presuppose a certain level of cognitive functioning to engage in the task, thereby allowing for the assessment of a wide variety of individuals with ASD.

Furthermore, this thesis focused on one specific aspect of functional brain connectivity, namely phase synchrony within the theta, alpha, and beta frequency bands. As there are many avenues by which the brain communicates, these results shed light on only one method of neural interaction. For example, phase synchrony measures the degree to which two oscillatory signals synchronize, whereas phase-amplitude coupling evaluates how the phase of oscillatory activity in one region is linked to the oscillatory amplitude in another region (Jensen & Colgin, 2007; Tort et al., 2010). Examining the various methods of functional connectivity therefore would allow for a more comprehensive picture of how the brain orchestrates activity to give rise to behaviour, as well as how these mechanisms may differ in ASD. Phase-amplitude coupling in particular would be well-suited to investigating how the right IFG interacts with the working memory and ToM networks. If the right IFG is responsible for exerting top-down control during working

memory and ToM processes, as speculated in this thesis, it may modulate local power in certain brain areas, like the IPL and TPJ. Not only would this research help clarify the exact influence of inhibition on working memory and ToM, but it may also be valuable for identifying whether the right IFG would be an effective target for brain stimulation interventions to improve outcomes in ASD.

Finally, all three studies of this thesis measured phase synchrony averaged over a specific time period, yet it is believed that during cognitive processing, the brain switches between several different states, which are characterized by unique network configurations (Allen et al., 2014; Brookes et al., 2018; Hutchison et al., 2013; Vidaurre et al., 2018). Analyses of this dynamic functional connectivity show that it is a more reliable method of identifying activated brain networks (Dimitriadis, Routley, Linden, & Singh, 2018). Studies of dynamic functional connectivity during resting-state fMRI paradigms have found that individuals with ASD have greater variability in functional connectivity over time (Chen, Nomi, Uddin, Duan, & Chen, 2017; Falahpour et al., 2016), and that some of the recruited networks showed differences between people with and without ASD (Mash et al., 2019). Therefore, it would be valuable for future work to explore whether individuals with ASD exhibit increased variability in dynamic functional connectivity during tasks of higher cognitive functions, as it may be more informative of the specific functional network differences that give rise to the cognitive difficulties in ASD.

## 5.4 Concluding remarks

This thesis demonstrates that adults with ASD generally show decreased functional connectivity relative to control adults when engaging higher cognitive functions, specifically inhibition, working memory, and FB understanding. In the case of inhibition, adults with ASD exhibited reduced alpha-band phase synchrony between the right IFG and other brain regions not typically involved in inhibition, indicating a potential deficit in suppression of task-irrelevant brain activity, especially as connectivity among these areas was correlated with levels of inhibitory control in everyday life. During tasks of working memory and FB reasoning, decreased theta-band synchrony was observed in adults with ASD between key brain regions implicated in their respective cognitive domains and the right IFG, suggesting diminished top-down control of these areas. These findings not only support the theory that ASD may be partly characterized by long-range underconnectivity and thus poorer communication between distant brain regions, but they

also highlight the impact that deficits in inhibition may have on other cognitive functions in ASD. Therefore, it is imperative that future ASD research takes into account the interplay between different cognitive processes to more fully understand the specific neural mechanisms that contribute to the cognitive difficulties experienced by the ASD population.

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## Appendices

Appendix A. Participant medication information across all three studies.

In all three studies, no control participants stated taking any psychotropic medication.

In Study 1, 21 participants with ASD reported current use of psychotropic medication. This medication included Abilify (aripiprazole), Adderall (amphetamine), Ativan (lorazepam), Celexa (citalopram), Cipralex (escitalopram), clonazepam, Concerta (methylphenidate), Cymbalta (duloxetine), Imovane (zopiclone), loxapine, pregabalin, Pristiq (desvenlafaxine), Prozac (fluoxetine), Seroquel (quetiapine), trazadone, Trintellix (vortioxetine), Wellbutrin (bupropion), and Zoloft (sertraline).

In Study 2, 23 participants with ASD reported current use of psychotropic medication. This medication included Abilify (aripiprazole), Ativan (lorazepam), Celexa (citalopram), Cipralex (escitalopram), clomipramine, clonazepam, Concerta (methylphenidate), Cymbalta (duloxetine), Effexor (venlafaxine), Imovane (zopiclone), loxapine, lurasidone, mirtazapine, pregabalin, Pristiq (desvenlafaxine), Prozac (fluoxetine), quetiapine fumarate, Seroquel (quetiapine), trazadone, Trintellix (vortioxetine), Wellbutrin (bupropion), and Zoloft (sertraline).

In Study 3, 22 participants with ASD reported current use of psychotropic medication. This medication included Abilify (aripiprazole), Adderall (amphetamine), Ativan (lorazepam), Celexa (citalopram), Cipralex (escitalopram), clomipramine, clonazepam, Concerta (methylphenidate), Cymbalta (duloxetine), Effexor (venlafaxine), Imovane (zopiclone), lurasidone, mirtazapine, pregabalin, Pristiq (desvenlafaxine), Prozac (fluoxetine), quetiapine fumarate, Seroquel (quetiapine), trazadone, Trintellix (vortioxetine), Wellbutrin (bupropion), and Zoloft (sertraline).

Appendix B. Description of stimulus and ISI duration adaptation for the Go/No-go task.

Stimulus duration would speed up by one frame (i.e., 16.67 ms on a computer with a 60 Hz refresh rate) if response time was less than the stimulus duration for at least four of the last five Go trials and the participant correctly did not respond on any of the last five No-go trials. It would also decrease by one extra frame if the participant had an overall No-go accuracy of  $\geq$ 80%. Stimulus duration would slow down by one frame if response time was greater than the stimulus duration for three of the last five Go trials, or if the participant responded to two or more of the last five No-go trials and they had an overall No-go accuracy of <80%. ISI duration would speed up by one frame if participants refrained from responding on at least four of the last five No-go trials, overall No-go accuracy was  $\geq$ 80%, and overall Go accuracy was  $\geq$ 95%. It would slow down by two frames if overall Go accuracy was <80%. If both the latter two occurred, then the ISI would be increased by an additional four frames.

	<b>Control</b> ( <i>N</i> = <b>39</b> )	<b>ASD</b> ( $N = 40$ )
	Mean (SD)	Mean (SD)
Inhibition		
Hits	79.03 (2.95)	77.60 (6.23)
Misses	17.05 (7.99)	15.95 (8.21)
False alarms	4.00 (5.33)	4.63 (8.02)
Correct rejections	281.82 (24.44)	273.83 (24.52)
Total number of trials	381.90 (31.60)	372.00 (29.62)
Vigilance		
Hits	79.97 (0.16)	80.00 (0.00)
Misses	0.46 (0.85)	0.68 (1.05)
False alarms	0.15 (0.37)	0.08 (0.27)
Correct rejections	26.49 (1.99)	26.13 (2.14)
Total number of trials	107.08 (2.30)	106.88 (2.54)

Appendix C. Average trial numbers for the Go/No-go task.

	<b>Control</b> ( <i>N</i> = <b>39</b> )	<b>ASD</b> ( $N = 40$ )	
	Mean (SD)	Mean (SD)	
1-back			
Hits	88.00 (7.90)	87.53 (7.76)	
Misses	6.00 (7.90)	6.48 (7.76)	
False alarms	2.77 (3.70)	3.65 (3.95)	
Correct rejections	188.23 (3.70)	187.35 (3.95)	
2-back			
Hits	72.34 (12.61)	74.53 (15.08)	
Misses	36.62 (12.57)	34.03 (15.23)	
False alarms	7.52 (5.17)	9.50 (9.26)	
Correct rejections	213.52 (5.20)	210.70 (9.60)	

Appendix D. Average trial numbers for the *n*-back task.

Region	X	У	Z
Left Precentral Gyrus	-40	-6	51
Right Precentral Gyrus	40	-8	52
Left Superior Frontal Gyrus	-19	35	42
Right Superior Frontal Gyrus	20	31	44
Left Superior Orbital Frontal Gyrus	-18	47	-13
Right Superior Orbital Frontal Gyrus	17	48	-14
Left Middle Frontal Gyrus	-34	33	35
Right Middle Frontal Gyrus	37	33	34
Left Middle Orbital Frontal Gyrus	-32	50	-10
Right Middle Orbital Frontal Gyrus	32	53	-11
Left Inferior Frontal Gyrus, Pars Opercularis	-49	13	19
Right Inferior Frontal Gyrus, Pars Opercularis	49	15	21
Left Inferior Frontal Gyrus, Pars Triangularis	-47	30	14
Right Inferior Frontal Gyrus, Pars Triangularis	49	30	14
Left Inferior Frontal Gyrus, Pars Orbitalis	-37	31	-12
Right Inferior Frontal Gyrus, Pars Orbitalis	40	32	-12
Left Rolandic Operculum	-48	-8	14
Right Rolandic Operculum	52	-6	15
Left Supplementary Motor Area	-6	5	61
Right Supplementary Motor Area	8	0	62
Left Dorsomedial Prefrontal Cortex			
Left Superior Medial Frontal Gyrus	-6	49	31
Left Superior Medial Frontal Gyrus	-8	48	23
Left Superior Medial Frontal Gyrus	-10	39	52
Left Superior Medial Frontal Gyrus	-2	38	36
Left Superior Medial Frontal Gyrus	-3	26	44
Right Dorsomedial Prefrontal Cortex			
Right Superior Medial Frontal Gyrus	8	51	30
Right Superior Medial Frontal Gyrus	6	64	22
Right Superior Medial Frontal Gyrus	13	55	38
Right Superior Medial Frontal Gyrus	6	54	16
Right Superior Medial Frontal Gyrus	9	54	3
Right Superior Medial Frontal Gyrus	13	30	59
Left Ventromedial Prefrontal Cortex			
Left Medial Orbital Frontal Gyrus	-6	54	-7
Left Medial Orbital Frontal Gyrus	-3	44	-9
Left Gyrus Rectus	-6	37	-18

**Appendix E.** Region labels and corresponding MNI coordinates used for source estimation in the FB task.

Right Ventromedial Prefrontal Cortex			
Right Medial Orbital Frontal Gyrus	7	52	-7
Right Medial Orbital Frontal Gyrus	6	67	-4
Right Medial Orbital Frontal Gyrus	8	42	-5
Right Gyrus Rectus	7	36	-18
Left Insula	-36	7	3
Right Insula	38	6	2
Left Anterior Cingulate Cortex	-5	35	14
Right Anterior Cingulate Cortex	7	37	16
Left Middle Cingulate Cortex	-6	-15	42
Right Middle Cingulate Cortex	7	-9	40
Left Posterior Cingulate Cortex	-6	-43	25
Right Posterior Cingulate Cortex	6	-42	22
Left Parahippocampal Gyrus	-22	-16	-21
Right Parahippocampal Gyrus	24	-15	-20
Left Calcarine Sulcus	-8	-79	6
Right Calcarine Sulcus	15	-73	9
Left Cuneus	-7	-80	27
Right Cuneus	13	-79	28
Left Lingual Gyrus	-16	-68	-5
Right Lingual Gyrus	15	-67	-4
Left Superior Occipital Gyrus	-18	-84	28
Right Superior Occipital Gyrus	23	-81	31
Left Middle Occipital Gyrus	-33	-81	16
Right Middle Occipital Gyrus	36	-80	19
Left Inferior Occipital Gyrus	-37	-78	-8
Right Inferior Occipital Gyrus	37	-82	-8
Left Fusiform Gyrus	-32	-40	-20
Right Fusiform Gyrus	33	-39	-20
Left Postcentral Gyrus	-43	-23	49
Right Postcentral Gyrus	40	-25	53
Left Superior Parietal Lobule	-24	-60	59
Right Superior Parietal Lobule	25	-59	62
Left Inferior Parietal Lobule	-44	-46	47
Right Inferior Parietal Lobule	45	-46	50
Left Temporoparietal Junction			
Left Supramarginal Gyrus	-57	-34	30
Left Supramarginal Gyrus	-53	-22	23
Left Supramarginal Gyrus	-54	-23	43
Left Supramarginal Gyrus	-50	-34	26
Left Angular Gyrus	-45	-61	36
Left Angular Gyrus	-42	-55	45

Left Angular Gyrus	-39	-75	44
Right Temporoparietal Junction			
Right Supramarginal Gyrus	57	-32	34
Right Supramarginal Gyrus	59	-17	29
Right Supramarginal Gyrus	54	-28	34
Right Supramarginal Gyrus	49	-42	45
Right Supramarginal Gyrus	55	-45	37
Right Angular Gyrus	45	-60	39
Right Angular Gyrus	47	-50	29
Right Angular Gyrus	33	-53	44
Right Angular Gyrus	52	-59	36
Right Angular Gyrus	37	-65	40
Left Precuneus			
Left Precuneus	-8	-56	48
Left Precuneus	-13	-40	1
Left Precuneus	-3	-49	13
Left Precuneus	-7	-52	61
Left Precuneus	-7	-55	27
Left Precuneus	-11	-56	16
Left Precuneus	-7	-71	42
Right Precuneus			
Right Precuneus	9	-56	44
Right Precuneus	10	-46	73
Right Precuneus	4	-48	51
Right Precuneus	11	-54	17
Right Precuneus	6	-59	35
Right Precuneus	10	-62	61
Right Precuneus	15	-63	26
Right Precuneus	11	-66	42
Left Paracentral Lobule	-9	-25	70
Left Paracentral Lobule	6	-32	68
Left Superior Temporal Gyrus	-54	-21	7
Right Superior Temporal Gyrus	57	-22	7
Left Superior Temporal Pole	-41	15	-20
Right Superior Temporal Pole	47	15	-17
Left Middle Temporal Gyrus	-57	-34	-2
Right Middle Temporal Gyrus	56	-37	-1
Left Middle Temporal Pole	-37	15	-34
Right Middle Temporal Pole	43	15	-32
Left Inferior Temporal Gyrus	-51	-28	-23
Right Inferior Temporal Gyrus	53	-31	-22

Region labels highlighted in grey were associated with several different node coordinates, denoted in the rows below each label. The original gyral labels are presented to the left of each coordinate, in italics.

	$\overline{\text{Control} (N = 39)}$	$\mathbf{ASD} \ (N = 40)$
	Mean (SD)	Mean (SD)
TASIT Thinking Accuracy (%)		
Minimal	88.17 (12.01) Range = [53.33–100], <i>n</i> = 31	78.26 (13.96) Range = [40.00–93.33], <i>n</i> = 23
Enriched	90.12 (5.54) Range = [81.25–100], <i>n</i> = 31	80.98 (9.51) Range = [56.25–93.75], <i>n</i> = 23
SRS-2 Social Cognition t Score		
Self	45.68 (6.16) Range = [37-55], <i>n</i> = 19	64.04 (10.22) Range = [48-86], <i>n</i> = 27
Informant	44.84 (6.90) Range = [37-62], <i>n</i> = 19	62.04 (11.89) Range = [42-84], <i>n</i> = 27

Appendix F. Assessment data for the TASIT and SRS-2.

SRS-2 = Social Responsiveness Scale, Second Version; TASIT = The Awareness of Social Inference Test

	<b>Control</b> ( <i>N</i> = <b>39</b> )	ASD (N = 40)
	Mean (SD)	Mean (SD)
Study 1		
Inhibition*	2.32 (1.19)	2.92 (1.44)
Vigilance	1.72 (1.25)	1.99 (1.17)
Study 2		
1-back	2.30 (1.08)	2.59 (1.33)
2-back	2.74 (1.47)	2.62 (1.31)
Study 3	3.24 (1.23)	3.47 (1.46)

Appendix G. Head motion data for all three studies.

Note that head motion is not broken down by condition for Study 3, as all conditions were run in one block, whereas in Study 1 and 2, participants performed the different conditions of the task in separate blocks. Also note that for Study 2, the sample size in the 2-back condition is a subset of that in the 1-back condition, such that there were 29 control adults and 30 adults with ASD.

\* *p* < 0.05