THINKING IN PICTURES ACCOUNT OF AUTISM: INSIGHTS FROM BEHAVIOURAL AND NEUROIMAGING RESEARCH IN ADULTS WITH AUTISTIC-LIKE TRAITS

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Bachelor of Science (Honours)

This thesis is presented for the degree of Doctor of Philosophy of the University of Western Australia
School of Psychological Science
2019
Thesis Declaration

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The research involving human data reported in this thesis was assessed and approved by The University of Western Australia Human Research Ethics Committee (approval #: RA/4/1/5236) and the Sir Charles Gairdner Group Human Research Ethics Committee (approval #: 2015-082).

Some of the work described in this thesis was funded by an Australia Research Council Discovery Project grant shared by Murray Maybery and Andrew Whitehouse (DP120102313). Funding was also provided by a University of Western Australia Postgraduate Award and School of Psychological Science for conference-related travel.

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Abstract

Individuals with an autism spectrum condition (ASC) often display an uneven cognitive profile characterised by stronger visuospatial abilities and weaker verbal abilities, relative to their neurotypical counterparts. This profile is also often observed in individuals who do not meet clinical criteria for ASC, but still display high levels of autistic traits. The aim of this thesis is to better understand the cognitive and neural mechanisms which underpin verbal and visuospatial skills in individuals with high versus low levels of autistic traits, with reference to a conceptualisation of ASC cognition known as the Thinking in Pictures (TiP) account.

Developed by Kunda and Goel (2011), the TiP account proposes that individuals with ASC and those with high levels of autistic traits show a strong cognitive bias towards using visuospatial mental representations rather than verbal representations. Accordingly, people on the autism spectrum are hypothesized to exhibit a visual style of thinking, leading to relatively superior performance on visuospatial tasks and poorer performance on verbal tasks.

In the introductory chapter of this thesis, I consider whether cognitive disparities between verbal and visuospatial skills in ASC could be underpinned by atypical cerebral lateralisation, drawing on the neuroimaging literature. Three core issues concerning the assessment of the TiP account are also raised. The first issue is that while Kunda and Goel (2011) recommend that individual thinking preferences can be further understood by administering ambiguous tasks that are solvable by either verbal or visuospatial processing strategies, there is no accepted behavioural measure that quantifies cognitive biases. Second, a cognitive bias towards visual thinking could be closely linked to an individual’s relative profile of verbal and visuospatial abilities, or be somewhat independent of that profile; an issue not addressed in the TiP account. Finally, whether cerebral activation differences in people on the autism spectrum reflect underlying differences in cortical organisation, or preferential engagement in visuospatial processing, can be clarified by incorporating assessments of language and visuospatial cerebral laterality in research on the TiP account.

These issues were in the focus of six experimental studies designed to provide rigorous empirical examination of the TiP framework. Three studies (Experiments 1, 3 and 4) prioritised development of a novel sentence verification...
task containing three statement types - verbal and visual, to assess verbal and visuospatial functions, and ambiguous statements to evaluate cognitive biases in verbal-visual thinking. All of the pilot studies involved recruitment of young adults drawn from the undergraduate student population. In the remaining three studies (Experiments 2, 5 and 6), the sentence verification task was combined with behavioural and neuroimaging methodologies to examine the TiP account in undergraduate students selected for low versus high levels of autistic traits, as measured by the Autism-Spectrum Quotient. For the low/high autistic trait comparison studies, standardised assessment measures of verbal (Wechsler Vocabulary) and visuospatial abilities (Wechsler Visual Puzzles) were administered to assess cognitive abilities as well as cognitive biases (via sentence verification). To further characterise patterns of language and visuospatial cerebral organisation, gold standard laterality tasks (word generation, visual short-term memory) were also employed in the neuroimaging studies.

The first experiment involved the development of the sentence verification task. A total of 180 verbal, visual and ambiguous candidate auditory statements were created. Twenty young adults rated the extent to which they employed visualising or verbalising strategies to solve each of the statements, depending on the dominant strategy reported across the sample. Statements were categorised as ambiguous where a subset of the sample reported use of visualising strategies, while another subset reported verbalising strategies. A final set of 30 verbal, 30 visual and 30 ambiguous statements were identified for subsequent use in the sentence verification task.

The second experiment examined the extent to which sentence verification performance in individuals with low and high autistic traits was contingent on verbal and visuospatial processing strategies. Using dual-task methods, articulatory suppression and spatial tapping were employed to interfere with verbal and visuospatial processing, respectively. It was predicted that if the high autistic trait sample rely predominantly on visuospatial processing strategies to support comprehension, verification performance should be more adversely affected during spatial tapping, or less affected by articulatory suppression, relative to their low autistic trait counterparts. Contrary to TiP predictions, similar patterns of dual-task articulatory suppression and spatial tapping interference were observed among the low and high autistic trait groups, across the verbal, visual and ambiguous
statements. Furthermore, while participants with high levels of autistic traits
displayed superior visuospatial abilities to those with low autistic traits, dual-task
results on the ambiguous statements provided limited support for a visual thinking
bias in the high autistic trait sample.

The third and fourth experiments used functional Transcranial Doppler
(fTCD) imaging to explore how the two cerebral hemispheres function to subserve
language and visuospatial processing during sentence verification performance, in
young adults not selected for particular levels of autistic traits. The approach in
Experiments 3 and 4 commonly involved identifying the cerebral hemisphere
specialised for language (assessed on the word generation task) and visuospatial
functions (assessed on the visual short-term memory task) in each participant, before
examining the profile of language and visuospatial activity on the sentence
verification task.

The fTCD results from Experiments 3 and 4 failed to sufficiently distinguish
the verbal, visual and ambiguous statements on relative language and visuospatial
processing demands. In Experiment 3, most of the unselected sample were found to
show dominant activation in their language hemisphere across all three sets of
statements. Changing the verification task from an auditory (Experiment 3) to a
reading (Experiment 4) presentation modality did not influence the pattern of results,
with the three statement types overlapping on degree of language activation.
However, using high spatial resolution functional Magnetic Resonance Imaging
(fMRI) in Experiment 6, the verbal, visual and ambiguous statements were
distinguished in cerebral activation across regions within the language and
visuospatial network, consistent with self-report strategy results (in Experiment 1).
Thus, the work in this thesis contributes to the design of a new reading sentence
verification task, which can facilitate assessment of language and visuospatial
cerebral functions.

The final two experiments utilised the reading sentence verification task, and
focused on examining the TiP account in individuals with low and high levels of
autistic traits using fTCD (Experiment 5) and fMRI (Experiment 6). Similar to the
previous neuroimaging studies (Experiments 3 and 4), in Experiments 5 and 6, gold
standard tasks were administered to establish the pattern of cerebral lateralisation for
the low and high autistic trait samples, before comparing group differences in
language and visuospatial activation on the verification task. On a group level, the
high autistic trait sample exhibited differences in right hemisphere cortical responses on the visual short-term memory (Experiment 5) and word generation (Experiment 6) laterality tasks, relative to the low autistic trait sample. However, there were no significant differences in the rates of typical cerebral lateralisation (i.e. left hemisphere language and right hemisphere visuospatial functions) or atypical lateralisation (e.g. reversed language and visuospatial organisation) among the low and high autistic trait groups. Although participants with high levels of autistic traits exhibited relative strengths in visuospatial abilities and weaker verbal abilities, their cognitive profiles were not associated with atypical cerebral lateralisation. Furthermore, with the exception of the right dorsomedial prefrontal region, the low and high autistic trait groups generally showed overlapping responses across core regions in the language and visuospatial networks during the sentence verification task. Focal differences in right hemisphere dorsomedial prefrontal activity likely reflect subtle differences in visuospatial/executive function strategies between the low and high autistic trait samples, but were not indicative of visual thinking biases in the high autistic trait group.

The findings from this thesis add to the TiP account by showing that a discrepant cognitive profile of stronger visuospatial abilities and weaker verbal abilities in individuals with high levels of autistic traits does not confer a cognitive bias towards visual thinking. Additionally, such disparities between verbal and visuospatial abilities in individuals with high autistic trait levels do not seem to stem from atypical development of cerebral lateralisation. Overall, the results from this thesis provide new insights into the TiP framework and have theoretical and practical implications for neuroimaging research involving individuals with ASC.
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Acknowledgements

Seven years is a long time. Writing this acknowledgment section, I reflect on why I chose to undertake this PhD project and what kept me going. The first thing that comes to mind is my curiosity to learn. Very quickly, I was faced with the realisation of how much I did not know. Curiosity was challenged by the fact that learning is, and was not always easy. Learning is a process which takes time. My candidature was supported by the University of Western Australia Postgraduate Award Scholarship. I am very humbled to have been surrounded by many people who have supported, encouraged and genuinely believed in me throughout this journey of learning.

The work in this thesis would not have been possible without the expertise, guidance and support from my supervisors. Murray Maybery thank you for helping me navigate my path. It’s fair to say that we could not have anticipated the obstacles encountered with this PhD project. Thank you for teaching me to be flexible, to problem-solve and guiding me when I felt overwhelmed. Your dedication to your students is evident in your pragmatic, yet detailed-approach to supervision and providing written feedback. Above all, I am extremely grateful for your care and compassion towards me. Andrew Whitehouse thank you for opening up many opportunities for learning and personal development. Our chats at the beginning of my candidature have helped nurture a sense of self-belief. I am also very appreciative of your prompt feedback on written work and your enthusiasm in my research. Thanks for teaching me scientific writing and how to verbally communicate research findings.

I have been very fortunate to have worked with several collaborators who have imparted their knowledge of brain imaging. Nicholas Badeock thank you for your input on the design of Chapters 4, 5 and 6 reported in this thesis. Thanks for the countless emails and helping me trouble shoot the imaging analyses. Katie McMahon thank you for making me feel welcomed during my visits to The University of Queensland. The back-and-forth emails and Skype meetings have been crucial for the design of Chapter 7 of this thesis. Thank you for prioritizing me as if I were one of your PhD students. Jess Reynolds navigating the imaging analyses pipeline for Chapter 7 would have been even more difficult without your help.
Thank you for scheduling regular Skype meetings with me, despite the 9-hour time difference. Thanks for always checking in on me.

A special thanks to staff members from the Sir Charles Gairdner Hospital Radiology Department, in Perth Western Australia. **Michael Bynevelt** thank you for being an advocate for the imaging research conducted in Chapter 7, and to **Lincoln Codd** for sacrificing weekends to run the scanning sessions with me. I would also like to acknowledge all the participants who have shared their time and interest in the research reported in this thesis.

My gratitude extends to colleagues and dear friends from the Cognition Autism and Neurodevelopmental lab at the University of Western Australia. **Suzanna Russell-Smith** and **Claire Mitchell** thanks for assisting with the development of test stimuli for Chapter 2 of this thesis. **Michael English** and **Doris Leung** thanks for your help with programming the tasks administered in this thesis. While the countless modifications to the tasks were understandably frustrating, you always showed optimism. **Diana Tan**, my ‘go to’ person in moments of questioning my capabilities. I cannot thank you enough for your motivational and insightful conversations. You are not just a colleague, but an incredible friend.

My journey has been made memorable by many other friendships. **Lisa Berry** and **Esha Jamnadass** thanks for giving me reasons to take breaks away from my desk. Our extended lunch breaks, conversations of the joys and woes of PhD life have been very cathartic. Thanks for reminding me that there is more to life outside PhD. **Eepin Chang** thanks for remembering me in your baking initiatives. Eating cakes and delicious treats often generated food for thought. I am so grateful for your support. ‘**The Gang**’, after years of asking “When?,” I can finally say that I have finished this!

Thanks to my family for their unwavering support. **Hayden Blanch**, my rock throughout this journey. Your unconditional love for me is clear. You have been there through my happiest and toughest of times. I cannot wait for what the future holds for us and our **Fur Baby Bruno**. To **Mum and Dad** thank you for all the sacrifices that you have made in order for our family to move to Australia. Thanks for instilling in me a curiosity for learning and bulk resilience. I might not have chosen this path if not for you.
Conference Proceedings Arising from this Thesis


Chapter 1: Cognitive and Neural Mechanisms Associated with Verbal and Visuospatial Disparities in the Autism Spectrum
1.1 Overview

Individuals with an Autism Spectrum Condition (ASC) often exhibit intact or even superior performance on visuospatial tasks, but have comparably poorer performance on verbal tasks. The aim of thesis is to understand why such disparities in verbal and visuospatial skills might develop in ASC, by using behavioural and neuroimaging methodologies to examine verbal and visuospatial characteristics in non-clinical adults with high levels of autistic-like traits. In this chapter, I provide a brief overview of ASC, and consider the possibility that disparities in verbal and visuospatial skills in ASC might be underpinned by atypical cerebral lateralisation. I then outline how early theories of ASC are limited in explaining cognitive advantages in visuospatial over verbal abilities. This is followed by a review of behavioural and neuroimaging research on a relatively recent cognitive conceptualisation of ASC, the Thinking in Pictures account, which proposes a cognitive bias towards visual thinking and away from verbal thinking. Therein, methodological gaps in the Thinking in Picture literature are identified, including: (1) limited recognition that atypical cerebral lateralisation may be present in individuals with ASC and complicate interpretation of neuroimaging data, (2) failure to consider how verbal and visuospatial abilities relate to cognitive biases, and (3) a lack of robust measures probing cognitive biases. This chapter will guide the rationale for the studies reported in this thesis by informing how behavioural and neuroimaging methodologies will be applied to examine the Thinking in Pictures account in general population adults with high levels of autistic-like traits.

1.2 Autism Spectrum Condition

Autism is the collective term for neurodevelopmental conditions characterised by impairments in social communication and interaction, which occur alongside restrictive, repetitive patterns of behaviours and interests. Since its inclusion to the Diagnostic and Statistical Manual of Mental Disorders (DSM-III, American Psychiatric Association, 1980), the diagnostic criteria of autism have undergone changes as to how the label is conceptualised and communicated. Where conditions such as Autistic Disorder, Asperger Syndrome and Pervasive Developmental Disorder — Not Otherwise Specified previously constituted separate diagnoses (DSM-IV, American Psychiatric Association, 2000), these conditions are
captured under a single diagnostic label, Autism Spectrum Disorder, in the current (fifth) edition of the DSM (DSM-V, American Psychiatric Association, 2013). This shift towards conceptualising autism along a continuous spectrum recognises substantial heterogeneity between individuals, where dyadic impairments in social communication and restrictive repetitive behaviours can range from the severe end of the continuum through to milder difficulties. While Autism Spectrum Disorder is the formal diagnostic term, the terms “Autism Spectrum Condition” (ASC) and “autistic” are often preferred by autistic people to describe autism (Baron-Cohen, 2009; Kenny et al., 2016). These terms acknowledge that autistic individuals, despite having some areas of difficulty, can possess unique cognitive strengths that form an important part of their self-identify. With this in mind, this thesis uses ASC and autistic interchangeably to refer to individuals with a clinical diagnosis of Autism Spectrum Disorder.

ASC is estimated to affect around 1 in every 59 people worldwide (Centre for Disease Control and Prevention, 2014). Clinical diagnosis of ASC most commonly occurs in the preschool period and is based on clinical observation of behavioural symptoms. Core difficulties with social communication can manifest as atypical eye contact, a lack of smiling and inappropriate use of pragmatic language or gestures during social activities, which can interfere with formation and maintenance of close relationships (for a review, see Yirmiya & Charman, 2010). Restrictive behavioural symptoms might be evident as repetitive language/motor mannerisms (e.g. echolalia, hand mannerisms), intense preoccupation with objects/interests (e.g. stacking blocks, narrow interests) or rigid adherence to non-functional routines (e.g. insistence on a fixed schedule) (for a review, see Leekam & Prior, 2011), which undoubtedly interfere with social functioning, learning and quality of living (Kirby, Boyd, Williams, Faldowski, & Baranek, 2017; Richler, Bishop, Kleinke, & Lord, 2007).

By its very definition, ASC is associated with impairments in functional abilities. However, there is also a growing recognition of the strengths and capabilities of individuals who receive an ASC diagnosis (Howlin, Goode, Hutton, & Rutter, 2009; Meilleur, Jelenie, & Mottron, 2015). For example, some autistic individuals who have a comorbid intellectual disability (i.e. IQ less than 70), develop vocational skills (Taylor & Seltzer, 2011) and actively participate in the community (Carter et al., 2015) despite requiring considerable support with independent living. Among the subset of autistic individuals without an intellectual disability (i.e. IQ
more than 70) who are able to function with some degree of independence, a
majority experience language difficulties but often excel in areas of visual arts,
architecture and route memory (Frith & Happé 1994; Grandin, 2009; Henninger &
Taylor, 2013; Howlin, Savage, Moss, Tempier, & Rutter, 2014; Selfe, 2011). Such
cognitive peaks in the visuospatial domain are particularly interesting in ASC, given
that deficits are more commonly reported in the broader realm of
neurodevelopmental conditions.

How and why such ‘unevenness’ between visuospatial and verbal abilities
develops in some but not all autistic individuals is not well understood. One problem
with research in ASC is that early cognitive theories have focused mainly on
explaining impairments and have failed to account for abilities in autistic individuals
that are cognitive advantages. While there are emerging strength-focused cognitive
frameworks of autism, such as the “Thinking in Pictures” account (Kunda & Goel,
2011), research in this area is in its infancy. This thesis is focused on investigating
cognitive and neural mechanisms which underpin disparities in verbal and
visuospatial skills to understand how the brain-behaviour relationship might be
altered in the autism spectrum.

1.3 Uneven Verbal and Visuospatial Profile

Substantial research has established that, when taken as a group, autistic
individuals tend to exhibit an uneven cognitive profile characterised by stronger
visuospatial abilities and weaker verbal abilities. Although there is currently no
unifying diagnostic cognitive profile, discrepancies between verbal and visuospatial
abilities occur around twice as frequently in people with ASC relative to their
neurotypical counterparts (Ankenman, Elgin, Sullivan, Vincent, & Bernier, 2014;
Black, Wallace, Sokoloff, & Kenworthy, 2009). When compared to other subtest
scores on the Wechsler intelligence tests, peak performance on the Block Design
subtest and comparative weaknesses on the Comprehension subtest characterises the
ASC literature (Dawson, Soulières, Gernsbacher, & Mottron, 2007; Ehlers et al.,
1997; Nader, Jelenic, & Soulières, 2015).

The Wechsler Block Design subtest requires visuospatial assembly of blocks
to match a target design, whereas, the Comprehension subtests involves verbal
reasoning to answer questions like, “What should you do if you cut your finger?.”
Some researchers have argued that weak verbal performance on Wechsler
intelligence tests might be more apparent in ASC, since the Comprehension subtest relies, in part, on the pragmatic ability to mentalise rules pertaining to social scenarios (Baron-Cohen, 2000; Happé, 1994). While there is evidence that autistic individuals with a cognitive profile of greater visuospatial than verbal abilities experience more severe social difficulties (Black et al., 2009; Joseph, Tager-Flusberg, & Lord, 2002), there is consensus that comorbid language impairments in ASC can further disrupt and interfere with social communication (for reviews, see Bishop, 2000; Tager-Flusberg & Caronna, 2007).

Beyond social pragmatic language, poor language skills in ASC can adversely affect the acquisition of semantic knowledge as well as understanding word meaning (Boucher, 2012; Minshew, Goldstein, & Siegel, 1997). Relative to their neurotypical counterparts, autistic children and adults experience difficulties understanding instructions (Howlin et al., 2014; Hudry et al., 2010), expressing themselves fluently (Howlin et al., 2014; Spek, Schatorjé, Scholte, & Berckelaer-Onnes, 2009) and remembering the names of objects and words (Joseph, Steele, Meyer, & Tager-Flusberg, 2005; Whitehouse, Maybery, & Durkin, 2006). Weak verbal performance in ASC has been linked with limitations in inner speech development where verbal labelling and rehearsal of information is diminished (Joseph et al., 2005; Whitehouse et al., 2006), although other researchers have implicated cognitive difficulties in receiving/encoding linguistic information (Minshew et al., 1997; Hudry et al., 2010). Either way, similar verbal profiles in ASC and other clinical conditions where language skills are affected (e.g. developmental language disorder, specific learning disability with reading impairments), highlights shared problems in this area, even though language deficits are not a core diagnostic feature of ASC (Tager-Flusberg, 2006; Ricketts, 2011).

Where autistic individuals typically perform with less proficiency than neurotypical individuals on verbal tasks, they often display faster or even more accurate visuospatial performance than neurotypical comparison groups during mental rotation (Soulières, Zeffiro, Girard, & Mottron, 2011), perceptual reasoning (Dawson et al., 2007; Stevenson & Gernsbacher, 2013), spatial memory (Blair, Frith, Smith, Abell, & Cipolotti, 2002) and visual search (Kaldy, Giserman, Carter, & Blaser, 2016). Common to these visuospatial tasks are mental operations involving analysing the physical form of visual images, mental construction and manipulation of spatial information, which seem to develop more proficiently in ASC, when
compared to their verbal abilities. This has prompted various researchers to speculate that such disparities between verbal and visuospatial skills in ASC might be underpinned by differences in brain biology (for reviews, see Herringshaw, Ammons, DeRamus, & Kana, 2016; Lindell & Hudry, 2013).

1.4 Atypical Cerebral Lateralisation: A Possible Mechanism for Verbal and Visuospatial Disparities in Autism

With growing advances in brain imaging, a number of structural and functional differences have been identified in the brains of children and adults with ASC, sparking suggestions that biological pathways can result in atypical brain differences that persist into adulthood (for reviews, see Amaral, Schumann, & WuNordahl, 2008; Ecker, Bookheimer, & Murphy, 2015). Relative to neurotypical comparison groups, autistic individuals show reduced grey matter (i.e. neuronal cell) volume in frontal and temporal regions subserving language (Knaus et al, 2010; McAlonan, 2008) and increased grey matter in parietal and occipital regions supporting visuospatial functions (Hyde, Samson, Evans, & Mottron, 2010). This pattern of structural abnormalities is strikingly concordant with the profile of cognition in ASC, where alterations in structural asymmetry have also been reported. While it is common for several regions of the brain (e.g. inferior frontal, superior temporal) to be anatomically larger in the left than right cerebral hemisphere, the opposite is seen in ASC where these same regions are enlarged in the right hemisphere (Gage et al., 2009; Herbert et al., 2002; Rojas, Camou, Reite, & Rogers, 2005). Such changes in structural asymmetry prompt the question of whether the divergence between verbal and visuospatial skills in ASC might reflect disruption from the normal pattern of cerebral lateralisation.

Cerebral lateralisation is a central aspect of brain organisation, where some neural functions or cognitive processes tend to be specialised to one hemisphere of the brain or the other. In a majority of people, one cerebral hemisphere is typically relatively more adept at processing and accessing language, while the other is typically more attuned to processing and accessing visuospatial information (Whitehouse & Bishop, 2009). Research examining cerebral lateralisation has employed a range of non-invasive functional imaging techniques including functional Magnetic Resonance Imaging (fMRI), functional Transcranial Doppler (fTCD) and Positron Emission Tomography (PET), which commonly measure
changes in cerebral metabolism during cognitive task performance. Although there is individual variability, brain areas supporting language functions are more commonly localised in the left cerebral hemisphere, with visuospatial functions focused in the right cerebral hemisphere (for reviews, see Ardila, Bernal, & Rosselli, 2016; Price, 2012; Thiebaut de Schotten et al., 2011).

Functional imaging studies in ASC have focused on examining the laterality of language functions, showing that weak verbal skills might be associated with a departure from the typical pattern of left hemisphere specialisation. For example, in a small pilot study using PET, Müller et al. (1999) were the first to report weakened left hemisphere frontal responses in adults with ASC compared to a neurotypical control group during auditory sentence processing. Within the area of sentence comprehension, fMRI studies have documented similar results, where autistic individuals show decreased left hemisphere activation (Anderson et al., 2010; Harris et al., 2006; Just, Cherkassky, Keller, & Minshew, 2004a), or even dominant right hemisphere activation (Eyler, Pierce, & Courchesne, 2012; Redcay & Courchesne, 2008; Takeuchi, Harada, Matsuzaki, Nishitani, & Mori, 2004) in cerebral regions supporting verbal semantic processing.

Deviations from the typical pattern of left hemisphere language lateralisation have been shown to be more prominent among autistic individuals who have severe language impairments (Anderson et al., 2010; De Fossé et al., 2004; for meta-analysis, see: Herringshaw et al., 2016). However, atypical language (i.e. reduced leftward, greater rightward) lateralisation has been reported in ASC, even in subsets of autistic individuals who display similar behavioural performance on verbal tasks to their neurotypical peers (Kenworthy et al., 2013; Kleinhans, Müller, Cohen, & Courchesne, 2008; Knaus, Silver, Lindgren, Hadjikhani, & Tager-Flusberg, 2008). These findings leave open the possibility that altered hemispheric activation in ASC might reflect cortical reorganisation of language functions, or perhaps result from engagement in alternative compensatory processing strategies.

Research on visuospatial laterality in ASC is scarce, although differences in the distribution of hemispheric activation have also been reported. Using fMRI, studies have generally documented heightened right hemisphere responses in parietal (Silk et al., 2006) and occipital (Lee et al., 2007; Manjaly et al., 2007; Ring et al., 1999) regions, along with weakened left hemisphere frontal activation in autistic individuals during visuospatial task performance (Lee et al., 2007;
Manjaly et al., 2007; Silk et al., 2006). A stronger bias towards right hemisphere parietal and occipital activation (and away from left hemisphere frontal activation) in ASC could represent augmentation of the typical pattern of visuospatial lateralisation, or reflect greater recruitment of visuospatial processing strategies (discussed more in Section 1.6). Critically, if language and/or visuospatial cerebral functions are atypically organised in ASC, it is reasonable to expect that different hemispheres or different brain regions might be activated during the completion of tasks drawing on these functions. Concurrent assessment of language and visuospatial cerebral laterality in ASC is necessary to establish whether differences in hemispheric activation reflect atypical cortical organisation, or fundamental differences in cognitive approaches on verbal and visuospatial tasks.

1.5 Early Cognitive Theories of Autism and their Limitations

Various cognitive theories of autism have been proposed and investigated, in an attempt to understand links between the brain and behaviour. Historically, theories of autism have revolved around impairments in three hypothesized aspects of cognition, namely deficits in theory of mind (for a review, see Baron-Cohen, 2000), executive dysfunction (for a review, see Hill, 2004) and weak central coherence (for reviews, see Frith & Happé 1994; Happé & Frith, 2006). The theory of mind deficit hypothesis suggests that autistic individuals experience difficulties inferring the mental state of other people, where failure to understand the thoughts, beliefs and feelings of others contributes to social and communication problems. In the executive dysfunction theory, impairments in higher-order cognitive skills, such as planning, set-shifting and inhibition are understood to underlie inflexible thinking (e.g. narrow interests, getting stuck on tasks) and rigid behaviours (e.g. adhering to non-functional routines) in ASC. While cognitive conceptualisations involving theory of mind and executive dysfunction attempt to explain symptoms of autism, these theories are deficit-focused and fail to recognise why certain cognitive functions, like visuospatial abilities, are not only spared but sometimes superior in autistic individuals (Frith & Happé 1994; Kunda & Goel, 2011).

The weak central coherence theory was the first to view cognition in ASC as reflecting a different information processing style, where a tendency to focus on local details and figural processing confers cognitive advantage on some visuospatial
tasks (e.g. Wechsler Block Design, visual search). This theory, however, also predicts performance deficits in ASC on other visuospatial tasks, particularly when global integration of perceptual information is required. Yet, autistic people often show superior scores on mental rotation and matrix reasoning tasks, which not only require attention to figural details, but also demand global integration (e.g. comparing whether a rotated figure matches a target image, generating higher-order rules confining a visual array) for successful completion (Dawson et al., 2007; Edgin & Pennington, 2005). As such, the weak central coherence theory does not adequately explain how individuals with ASC can display intact or even superior performance on visuospatial tasks that do not solely necessitate detailed-focused processing.

In 2006, Temple Grandin, an autistic adult, published a book, “Thinking in Pictures: My Life with Autism” (expanded edition) (Grandin, 2006), which provoked research interest, in that she described her thoughts as being predominantly in visuospatial images. According to Grandin, “I think in pictures. Words are like a second language to me. I translate both spoken and written words into full color movies, complete with sound, which run like a VCR tape in my head. When somebody speaks to me, his words are instantly translated into pictures.” Grandin’s VCR analogy alludes to the idea that mental imagery forms a central part of how she retrieves and processes information in her world, where incoming linguistic information elicits pictorial images, presumed to facilitate meaning. Similar accounts have since been reported in other autistic individuals (Hurlburt, Happé, & Frith, 1994; Selfe, 2011), promoting a new framework that proposes cognitive differences in the way in which people with ASC process verbal and visuospatial information.

1.6 The Thinking in Pictures Account of Autism and Methodological Considerations

Inspired by Grandin’s book, Kunda and Goel (2011) formally proposed the “Thinking in Pictures” (TiP) account, in which people on the autism spectrum are understood to display a different style of information processing, marked by a cognitive bias towards visuospatial processing. Where neurotypical individuals have a natural propensity for using both verbal and visuospatial mental representations,
autistic individuals are purported to acquire, conceptualise and process information in visuospatial ways, often with restricted or no use of verbal mental representations.

The TiP account provides a promising framework for explaining why autistic individuals perform better on visuospatial tasks and comparably worse on verbal tasks. Inherent to visual thinking is enhanced mental proficiency in accessing and utilising visuospatial processing strategies, assumed to underlie faster and/or more accurate visuospatial task performance in ASC. By contrast, deficits on verbal tasks in ASC are argued to result from spontaneous recruitment of visuospatial processing strategies, where use of ineffective strategies or limited engagement in verbal processing strategies might lead to unsuccessful performance on verbal tasks.

Behavioural support for the TiP framework has mainly been gathered from dual-task studies involving concurrent articulatory suppression or spatial tapping to shed light on the way in which thinking is represented in ASC (for a review, see Williams, Peng, & Wallace, 2016). Dual-task articulatory suppression requires repeated speech production (e.g. saying the word “Monday” continuously) and serves to block verbal encoding and rehearsal, while dual-task spatial tapping can involve continuous finger tapping (e.g. pressing a spatial sequence on a keyboard) to inhibit visuospatial encoding and rehearsal of information (Baddeley & Hitch, 1974; Logie, 1995). The logic is that if a person engages in visuospatial processing strategies to perform a primary task, concurrent spatial tapping should adversely affect their performance, whereas if they employ verbal processing strategies, concurrent articulatory suppression should lead to poorer performance.

Consistent with anecdotal reports of visual thinking (Grandin, 2006; Hurlburt et al., 1994; Selfe, 2011), cognitive task performance in autistic individuals is less affected by concurrent articulatory suppression and relatively more disrupted by concurrent spatial tapping. For instance, using a tower planning task, Wallace, Silvers, Martin and Kenworthy (2009) demonstrated that neurotypical individuals typically suffered pronounced decrements in performance accuracy under articulatory suppression, relative to their level of performance during a baseline (no-distraction) condition. In comparison, tower task performance for the autistic group remained similar under articulatory suppression and baseline conditions, where a lack of accuracy cost during articulatory suppression suggests that planning performance is less verbally mediated in ASC. Similarly, concurrent articulatory suppression has been found to exert minimal impacts on disrupting
mathematical (Whitehouse et al., 2006, Experiment 3) and rule-based set-shifting (Russell-Smith, Comerford, Maybery, & Whitehouse, 2014) performance in autistic individuals, but adversely impede performance in neurotypical participants on these same tasks. While these studies provide support for reduced reliance on verbal processing strategies in ASC, mixed findings of comparable performance disruptions in autistic and neurotypical comparisons during articulatory suppression (Williams, Happé, & Jarrold, 2008; Williams, Bowler, & Jarrold, 2012) indicate intact use of verbal processing strategies, challenging the TiP framework.

The lack of a spatial tapping condition in the previous dual-task articulatory suppression studies makes it difficult to conclude whether alternative processing approaches in ASC represent a shift towards visual thinking. One exception is work by Holland and Low (2010) which found that tower planning and mathematical performance in ASC is relatively more disrupted by spatial tapping than articulatory suppression, in contrast with their neurotypical counterparts (who were equally affected by the two dual-task interference conditions). Their results point towards favourable recruitment of visuospatial over verbal processing strategies in the autistic sample. Considering inconsistencies across the previous dual-task articulatory suppression studies, and that the only study to combine articulatory suppression and spatial tapping methodologies found relatively greater performance interferences in ASC during spatial tapping, behavioural support for the TiP account remains preliminary (Williams et al., 2016).

Functional neuroimaging has provided more direct evidence for an imbalance in neural responses in ASC favouring over participation of perceptual regions (e.g. inferior parietal, extrastriate) on visuospatial tasks (Damarla et al., 2010; Keehn, Brenner, Palmer, Lincoln, & Müller, 2008; Soulières et al., 2009), but restricted activation in core language regions (e.g. inferior frontal, superior temporal) during verbal task performance (Gaffrey et al., 2007; Gervais et al., 2004; Harris et al., 2006; Just et al., 2004a; Williams et al., 2013). During sentence comprehension, visuospatial cerebral regions in ASC seem to be recruited in a way that is not observed in neurotypical development. Where neurotypical adults display visuospatial cerebral activity when verifying content from high-imagery statements and show a characteristic shift towards increased language activation during low-imagery statements, autistic adults rely on visuospatial processing during sentence
verification of high- as well as low-imagery statements (Kana, Keller, Cherkassky, Minshew, & Just, 2006).

Results from the previous neuroimaging and dual-task investigations on the TiP framework are, nevertheless, difficult to interpret because some studies recruited the autistic and neurotypical samples to be matched on both verbal and visuospatial abilities (Damarla et al., 2010; Harris et al., 2006; Just et al., 2004a; Russell-Smith et al., 2014; Soulières et al., 2009; Wallace et al., 2009; Williams et al., 2008; Williams et al., 2012; Williams et al., 2013), while other studies did not (Gaffrey et al., 2007; Gervais et al., 2004; Holland & Low, 2010; Kana et al., 2006; Keehn et al., 2008; Whitehouse et al., 2006). On the one hand, cognitive abilities pertaining to mental aptitude, that is, uneven development of visuospatial strengths and verbal weaknesses in ASC can account for their limited capacity to draw on verbal resources (Lidstone, Fernyhough, Mein, & Whitehouse, 2009; Williams & Jarrold, 2010), or even facilitate access to visuospatial resources. On the other hand, cognitive biases towards visual thinking could render autistic individuals more likely to recruit visuospatial cerebral processing strategies and less likely to rely on verbal cerebral processing strategies when approaching verbal and visuospatial tasks.

One problem with the TiP account of autism is it does not distinguish cognitive biases from cognitive abilities, as the framework merely predicts that visuospatial information processing biases should lead to discrepant performance on verbal and visuospatial ability measures. Nevertheless, Kunda and Goel (2011) proposed that the nature of cognitive biases in ASC can be clarified from a TiP perspective, by designing and administering ambiguous verbal-visual tasks. They reasoned that if an ambiguous task is amenable to verbal or visuospatial processing strategies with equal likelihood, then it would be possible to examine the underlying representational biases based on the strategy selected by the individual. More specifically, ambiguous tasks provide a potential means of distinguishing whether autistic individuals predominantly recruit visuospatial strategies, when verbal strategies could also be applied to generate a solution, or where neurotypical individuals might approach these ambiguous tasks favouring greater use of verbal strategies. In this way, ambiguous verbal-visual tasks provide a way of objectively quantifying whether cognitive biases in ASC reflect preferential use of visuospatial over verbal processing.
To date, only a handful of neuroimaging studies have employed ambiguous verbal-visual tasks to examine cognitive biases in ASC (Koshino et al., 2005; Koshino et al., 2008; Sahyoun, Belliveaua, Soulières, Schwartza, & Modya, 2010), and while initial results are encouraging, findings should be interpreted cautiously for reasons outlined below. For example, using fMRI, Sahyoun et al. (2010), administered a fluid reasoning matrices task containing ambiguous problems, along with sets of verbal problems and visual problems. The verbal problems contained a picture array of nameable objects which were argued to encourage verbal semantic processing strategies, whereas, the visual problems contained abstract figures that were deemed difficult to name and were assumed to require visuospatial processing strategies. The ambiguous matrices problems included pictorial stimuli where verbal semantic processing could be used to label objects (e.g. slide, witches hat), or, in which visuospatial manipulations (e.g. vertical reflection) of stimuli within the matrix could be applied to solve the problem (see Figure 1, Sahyoun et al., 2010).

On the ambiguous matrices problems, Sahyoun et al. (2010) found that where the neurotypical sample showed pronounced activation in language (e.g. superior temporal) regions, the autistic group relied more on visuospatial (e.g. extrastriate cortex) regions, interpreted to reflect a cognitive bias towards visual thinking. Considering the ambiguous problems were not initially piloted to be amenable to verbal and visuospatial processing strategies, and that fluid reasoning demands executive resources, it is difficult to definitively conclude whether group differences in brain activation, in part, reflect executive deficits in ASC (predicted under the executive dysfunction theory proposed by Hill, [2004]).

Another key finding from Sahyoun et al. (2010) was that group differences in the distribution of hemispheric activation were evident on the verbal and the visual matrices problems. Unlike their neurotypical counterparts, autistic individuals showed less left hemisphere (e.g. inferior frontal) activation during completion of the verbal matrices and failed to show sufficient right hemisphere (e.g. angular gyrus) activation during the visual problems (Sahyoun et al., 2010). As noted previously, reduced hemispheric asymmetry in the autistic sample for the verbal and visual matrices could reflect either an absence in the development of language and visuospatial lateralisation, or atypical preferences in strategy use. However, given that cerebral laterality for language and visuospatial functions was not assessed in the autistic sample and established to be similar (or different) to neurotypical
individuals, it complicates interpretation of these results with reference to the TiP framework.

### 1.7 Research Challenges in Autism: Studying Autistic Traits in the General Population

Behavioural and neuroimaging studies have provided valuable insights into the TiP framework, although there are a number of challenges associated with conducting research on clinical samples with an ASC diagnosis (for reviews, see Yerys et al., 2009; Landry & Chouinard, 2016). Autistic individuals often present with a range of other comorbidities, and differences in the selection criteria have meant that while some studies excluded participants with comorbid conditions (e.g. Koshino et al., 2008; Sahyoun et al., 2010), others did not (e.g. Kana et al., 2006; Russell-Smith et al., 2014). Comorbid conditions such as developmental language disorder, for example, can further compromise verbal abilities in ASC, potentially contributing to variable findings within the TiP research. To further complicate this issue, small sample size is an inherent problem in the subset of TiP studies in which the recruited autistic participants were screened for comorbid conditions. Another challenge is behavioural compliance in that neuroimaging procedures, such as fMRI require remaining still throughout the cognitive task. Excessive in-scanner movement artefacts can compromise the quality of the neuroimaging recordings, where researchers are often limited to brief assessment batteries to shorten the duration of scanning/testing session when studying clinical populations, including ASC.

A major research advance over the previous two decades is the understanding that autistic traits present along a continuum in the general population, with clinical ASC representing one extreme end of the normal distribution (Baron-Cohen, Wheelwright, Skinner, Martin, & Clubley, 2001; Constantino & Todd, 2003; Ruzich et al., 2015). This has expanded autism-related research to individuals in the general population with sub-clinical symptoms, to understand brain-behaviour mechanisms of autism and build on existing cognitive theories (for reviews, see Sucksmith, Roth, & Hoekstra, 2011; Landry & Chouinard, 2016). The Autism Spectrum Quotient (AQ; Baron-Cohen et al., 2001) is one of the most frequently administered measures for assessing milder autistic-traits in the broader neurotypical population (Ruzich et al., 2015).
The AQ is a 50-item self-report questionnaire tapping into everyday aspects of autistic preferences and behaviours across the individual’s social skills, communication, imagination, attention switching and attention to detail. Items on the AQ are presented on a four-point Likert scale (‘definitely agree’, ‘slightly agree’, ‘slightly disagree’, and ‘definitely disagree’) and the authors of the scale proposed using binary (0-1) system, where higher scores (range =0-50) reflect more pronounced autistic-like traits (Baron-Cohen et al., 2001). More recently, a 1-4 item AQ scoring method (Austin, 2005) has been recommended for being more sensitive at discriminating individuals who endorse “slightly” agreeing or disagreeing responses on the items and includes a broader range (50-200) of scores, not captured in the binary system (Stevenson & Hart, 2017). Nevertheless, the two scoring methods on the AQ have been found to identify close relatives of autistic individuals as reporting higher scores on the AQ than control groups with unaffected relatives, consistent with a broader autism phenotype (Kose et al., 2013; Wheelwright, Auyeung, Allison, & Baron-Cohen, 2010; Whitehouse, Barry, & Bishop, 2007).

Support for the utility of the AQ has also come from general population studies. In general population studies, researchers have often screened large samples using the AQ and focused on comparing groups of individuals scoring in the high and low quintiles of the AQ distribution, as a means of increasing power in assessing the influence of autistic traits (Cribb, Olaithé, Di Lorenzo, Dunlop, & Maybery, 2016). One notable finding is that individuals scoring high on the AQ generally outperform those scoring low on the AQ during visuospatial tasks, including the Wechsler Block Design subtest (Grinter, Maybery, Van Beck, & Badcock, 2009; Stewart, Watson, Alcock, & Yaqoob, 2009), visual search (for meta-analysis, see Cribb et al., 2016) and mental rotation (Dinsdale, Hurd, Wakabayashi, Elliot, & Crespi, 2013); consistent with the differences previously reported in ASC/neurotypical comparison studies (see Section 1.3). Individuals with higher AQ scores have also been reported to perform poorer on a verbal subset of fluid reasoning items (Fugard, Stewart, & Stenning, 2011), along with showing atypical activation in temporal (e.g. superior temporal) (Nummenmaa, Engell, von dem Hagen, Henson, & Calder, 2012; von dem Hagen et al., 2011) and parietal (e.g. intraparietal, extrastriate) regions (Nummenmaa et al., 2012) on social cognitive tasks. It should be noted that these brain regions found to be differentially activated...
in individuals with high levels of autistic traits, overlap considerably with regions supporting language and visuospatial functions described previously (in Section 1.4).

From these behavioural and neuroimaging studies, it is plausible that general population individuals with high levels of autistic-like traits show subtle but similar verbal and visuospatial characteristics to those observed in autistic individuals. Given that investigations on the TiP account have focused primarily on ASC, questions remain about whether individuals scoring high on the AQ would show differences in their profile of verbal and visuospatial abilities and/or cognitive biases, compared to those with low AQ scores. Furthermore, whether such group differences in verbal and visuospatial functions stem from alterations in cerebral lateralisation is less clear.

1.8 Further Examining the Thinking in Pictures Framework

The empirical review highlights that atypical language and visuospatial cerebral activity in ASC has often been interpreted to reflect underlying differences in information processing strategies, even though functional division of language and visuospatial laterality was not established to place results in context. Little is known about whether alterations in language and/or visuospatial cerebral organisation might contribute to weaker verbal performance or enhanced visuospatial performance in autism. Furthermore, while the notion of cognitive preferences in visual (over verbal) thinking in autism provides some explanation for why visuospatial performance might be comparatively better than verbal performance, there are three outstanding questions with the TiP research, which this thesis will address.

First, the existing body of literature on the TiP account has mainly assumed that the typical pattern of left-side language and right-side visuospatial specialisation commonly seen in neurotypical development applies to all autistic individuals. Unlike their neurotypical counterparts, autistic individuals exhibit significantly less activation in left hemisphere regions and greater activation in right hemisphere regions during sentence comprehension, often interpreted to reflect visual thinking. Furthermore, where sentence verification of low-imagery statements elicits frontal-temporal language activation in neurotypical adults, heightened parietal-occipital visuospatial activation is observed in autistic adults for whom low-imagery statements seem to be solved in a similar way to high-imagery statements. What is
unclear is whether cerebral laterality of language and/or visuospatial functions might develop atypically in people on the autism spectrum, or alternatively if they preferentially process sentence information in a different way to neurotypical individuals. If cerebral lateralisation is atypical in ASC, then it is reasonable to expect that different brain regions would be activated, even if the autistic sample enlists the same information processing strategies to neurotypical individuals. Alternatively, if language and visuospatial functions are typically lateralised in ASC, neural differences could reflect the fact that autistic individuals might be approaching verbal and visuospatial tasks in a fundamentally different way to neurotypical individuals. The approach taken in this thesis is to localise the directionality of language and visuospatial functions to contextualise hemispheric differences in brain responses within the TiP framework.

Second, the TiP account of autism attributes better performance on visuospatial tasks relative to verbal tasks primarily to cognitive biases in visual thinking, although it is also plausible that cognitive abilities can influence such performance disparities. Arguably, an uneven profile of weaker verbal abilities and superior visuospatial abilities in ASC, could restrict their capacity to employ verbal processing strategies, or lead to overreliance on compensatory visuospatial processing strategies during cognitive performance. Differences in the recruitment criteria across the TiP research are problematic in that some studies have selected autistic and neurotypical participants to be matched on both verbal and visuospatial abilities, while other studies have used an unconstrained approach. One disadvantage of matching participant groups on both verbal and visuospatial abilities is that it does not permit examination of how the individual’s cognitive profile might relate to cognitive biases in verbal-visual thinking. In this thesis, I argue that fractionation of cognitive abilities and cognitive biases in the TiP account of autism can be achieved without having to match the recruited participant groups on verbal and visuospatial abilities. The approach taken in this thesis is to assess for differences in verbal and visuospatial abilities and also test for differences in verbal-visual strategy preferences, enabling consideration of relationships between the two constructs.

Finally, although Kuda and Goel (2011) have argued that test administration of ambiguous verbal-visual tasks hold potential for unravelling the extent to which thinking is verbally or visually mediated, there is no accepted behavioural task which adequately quantifies cognitive biases. Within the existing TiP studies which
incorporated ambiguous tasks (e.g. fluid reasoning, working memory), testing was not conducted to ascertain if these measures were, in fact, amenable to verbal or visuospatial processing strategies. Thus, before employing a purported ambiguous task to assess cognitive biases associated with ASC, it is necessary to first consider how neurotypical individuals drawn from the general population approach the supposed ambiguous task. To this end, the starting point for test design and development of ambiguous assessment measures would be to examine typical individual differences in verbal and visuospatial strategic approaches. The implication is that test stimuli from ambiguous tasks must be administered to an unselected sample and established to be solvable to verbal and visuospatial strategies, before examining differences in cognitive biases across ASC/neurotypical or high/low autistic trait comparison groups.

1.9 Thesis Aims and Organisation

The overarching aim of this thesis is to investigate the TiP account of autism by developing an understanding of the cognitive and neural mechanisms that contribute to verbal and visuospatial skills of adults with high versus low autistic trait levels. In particular, I examine whether individuals with high levels of autistic traits show differences compared to individuals with low levels of autistic traits, with regard to their: (1) cognitive profile of verbal and visuospatial abilities, (2) cognitive biases for visual-verbal thinking, and (3) pattern of cerebral lateralisation. Studying non-clinical samples selected for autistic traits provides a starting research platform for examining the TiP account of autism and benefits in accessing larger sample sizes and better control of comorbidities, while reducing issues associated with movement artefacts during neuroimaging. Given the extent of ASC literature reporting differences in regional and hemispheric activation during sentence processing, sentence comprehension is an appealing area for examining TiP account in individuals differing on low and high levels of autistic traits.

The six experimental studies included in this thesis can be broadly divided into two distinct arms. As discussed previously, there is clear need to develop a novel measure that could assess the degree to which individuals show cognitive biases in verbal-visual thinking within the TiP framework. To achieve this, I constructed a novel sentence verification task, which was administered to unselected adult samples drawn from an undergraduate student population to validate the newly designed
measure across three task-development studies (Experiments 1, 3, and 4). In the remaining three studies (Experiments 2, 5 and 6), the novel sentence verification task was combined with behavioural and neuroimaging methodologies to examine the TiP account in undergraduate students selected for low versus high levels of autistic traits (as measured by the AQ). As well as assessing cognitive biases (via sentence verification) in the low and high autistic trait samples, established verbal (Wechsler Vocabulary, word generation) and visuospatial (Wechsler Visual Puzzles, visual short-term memory) measures were administered to compare their ability profiles. Experiments 3 to 6 combined use of neuroimaging techniques with the novel sentence verification task. In these neuroimaging studies, gold standard laterality tasks (word generation, visual short-term memory) were also employed to characterise hemispheric organisation of language and visuospatial functions.

Experiment 1 of this thesis began with the development of an auditory sentence verification task, specifically designed to assess verbal and visuospatial functions, and to provide an objective measure for detecting cognitive preferences in verbal-visual thinking. A total of 180 verbal, visual and ambiguous verbal-visual candidate statements were created for the sentence verification task. The rationale was that statements containing verbal content and statements conveying visuospatial content could, potentially, be used to localise language and visuospatial cerebral networks, respectively, while the ambiguous statements solvable in either processing modality, could potentially provide an indication of information processing biases. In Experiment 1, candidate items on the sentence verification task were administered to an unselected young adult sample to gather normative information regarding the extent (frequency and intensity) to which verbalising or visualising strategies were reportedly used to solve each statement. Using predetermined empirical criteria, a final set of 30 verbal, 30 visual and 30 ambiguous statements were identified. All three statement conditions were matched on mean difficulty, response times and sentence length and constituted the sentence verification task, which was used in the subsequent studies.

Experiment 2 examined the TiP framework by comparing the effects of dual-task articulatory suppression and spatial tapping on sentence verification performance in young adults with low and high levels of autistic traits. Contrary to TiP predictions, the dual-task articulatory suppression and spatial tapping exerted similar interference effects on the low and high autistic trait samples across the
verbal, visual and ambiguous statements. Although participants with high autistic traits displayed superior visuospatial abilities, their verification performance on the ambiguous statements was not more affected during the visuospatial (spatial tapping) interference or, less affected by verbal (articulatory suppression) interference, relative to low autistic trait comparisons. In other words, for the high autistic trait sample, strengths in visuospatial abilities did not correspond with an overall cognitive preference towards visual thinking. One limitation was that the articulatory suppression and spatial tapping interferences failed to differentiate the verbal, visual and ambiguous statements on relative verbal and visuospatial processing demands, and this warranted further clarification on whether all three statement types might share common processing demands.

Experiments 3 and 4 then utilised non-invasive fTCD imaging to evaluate language and visuospatial mechanisms underpinning sentence comprehension in unselected young adult samples. Here, gold standard language (word generation) (Bishop, Watt, & Papadatou-Pastou, 2009) and visuospatial (visual short-term memory) (Whitehouse, Badcock, Groen, & Bishop, 2009) tasks were administered to localise respective cerebral hemisphere specialised for language functions and visuospatial function, for each participant. By individually accounting for the pattern of cerebral lateralisation, it was possible to examine how participants’ language and visuospatial hemispheres were recruited during sentence verification performance. This was done to verify if completion of the verbal statements would primarily recruit activation in the language hemisphere, and if the visual statements would primarily enlist activation in the visuospatial hemisphere. To examine whether the ambiguous statements were amenable to verbal and visuospatial processing strategies, it was predicted that some of the sample would show dominant activation in their language hemisphere with the remaining favouring activation in their visuospatial hemisphere. Findings from Experiment 3 indicated that most of the unselected sample recruited significantly greater activation in their left language hemisphere (than their right visuospatial hemisphere) across all three sets of statements. In contrast with the self-report study (Experiment 1), the fTCD results from Experiment 3 suggest that the verbal, visual and ambiguous statements might overlap substantially on linguistic processing demands.

Using a similar fTCD design as that employed for Experiment 3, the auditory sentence verification task was then modified to a reading task in Experiment 4. This
study was conducted in an attempt to reconcile the inconsistent results, and to examine the possibility that the auditory nature of the sentence task in Experiment 3 might have inadvertently encouraged verbal rehearsal across all three statement types. It was proposed that if the reading sentence verification task presented the complete statement on screen, then this could free up linguistic resources associated with temporarily rehearsal of auditory content while verifying the statement. However, changes to the task modality did not impact the results. Most of the unselected sample in Experiment 4 enlisted greater activation in their left language hemisphere (than right visuospatial hemisphere) during reading verification of the verbal, visual and ambiguous statements.

The final two studies utilised the reading verification task and focused on examining the TiP account of autism in individuals with low and high levels of autistic traits, using non-invasive functional imaging techniques including fTCD (Experiment 5) and fMRI (Experiment 6). Relative to fMRI, fTCD has higher temporal resolution and is able to detect more fine grained changes in cerebral blood flow velocity during cognitive task performance. In comparison to fTCD, fMRI has higher spatial resolution enabling more precise mapping of brain tissue oxygenation onto specific neural structures. These two imaging techniques hold potential for adding complimentary information on cerebral responses in individuals with low versus high autistic trait levels, enabling further examination of the TiP account.

Experiments 5 and 6 assessed the pattern of cerebral lateralisation for the low and high autistic trait samples using gold standard (word generation, visual short-term memory) laterality measures, before comparing the relative profile of language and visuospatial activity on the reading verification task. The findings from these fTCD and fMRI studies shed light on whether neural differences in language and visuospatial cerebral activation in individuals with low and high autistic traits stem from group differences in cerebral lateralisation, or from fundamental differences in information processing strategies under the TiP framework.

The body of work contained in this thesis expands on the TiP account of autism by outlining how verbal and visuospatial abilities, cognitive biases and cerebral lateralisation might influence verbal and visuospatial characteristics of general population individuals differing in levels of autistic traits. The results from these six experiments contained in this thesis are summarised in the final chapter, the General Discussion, where implications of the findings will also be discussed.
Chapter 2: Sentence Comprehension—A Novel Measure of Verbal and Visuospatial Strategy Approaches and Thinking Style
Introduction

Sentence comprehension is an important aspect of everyday life, serving to guide how we understand or internally represent spoken and written information. Theoretical models of sentence comprehension have traditionally emphasized a core role of language in constructing meaning (Just, Carpenter, & Keller, 1996; MacDonald, 2013; Perfetti & Stafura, 2014). One assumption is that words convey verbal content, where language is necessary for decoding individual words within a sentence, temporarily holding the information in phonological short-term memory and accessing long-term semantic knowledge to integrate their collective meaning. Yet, when answering questions like, “Is a tennis ball larger than a pear?”, or “Is a Christmas tree darker than a frozen pea?”, people typically report that they mentally “look at” the named object or “zoom in and out” to have a “closer look” (Kosslyn, 1980; Kosslyn, Thompson, & Ganis, 2006). These introspective accounts have sparked suggestions that visual imagery can be generated in the course of sentence comprehension. The experiment in this chapter examined how adults from the general population approach sentence comprehension, with the primary aim of identifying statements differing on self-reported verbal and visuospatial strategies for the verification task used in this thesis.

Functional brain imaging studies in neurotypical individuals have provided evidence that visuospatial processes are activated not only during reading, but also when listening to instructions and evaluating the truth of statements (Carpenter, Just, Keller, Eddy, & Thulborn, 1999; Desai, Binder, Conant, & Seidenberg, 2010). For example, a fMRI study by Just, Newman, Keller, McElney and Carpenter (2004b) measured brain activation using a sentence verification task that required listening to a series of statements and deciding if each statement was true or false. The task contained low-imagery and high-imagery statement types. Low-imagery statements were designed to assess general knowledge (e.g. “Although now a sport, marathons started with Greek messengers bringing news”, true), while the high-imagery statements were designed to elicit visual imagery (e.g. “The number eight when rotated 90 degrees looks like a pair of spectacles”, true). Consistent with the notion that language functions are involved with sentence comprehension, neurotypical individuals show pronounced activation in brain regions subserving verbal semantic processing (e.g. superior temporal area) during task performance on the low-imagery
statements. Interestingly, the high-imagery statements elicited marked activity in brain regions supporting visual and spatial functions (e.g. intraparietal region) even though judgements were made on auditory stimuli. Findings from the Just et al. (2004b) study demonstrate that content within a statement can influence whether verbal or visuospatial strategies are recruited to verify meaning.

Cognitive models accounting for the role of visual imagery in sentence comprehension have proposed that statements which elicit vivid imagery or convey spatial descriptions, are more likely to be mentally transformed into a visual code (Bergen, Lindsay, Matlock, & Narayanan, 2007; De Beni, Pazzaglia, Gyselinck, & Meneghetti, 2005; Verhoeven & Perfetti, 2008). For instance, when solving the high-imagery statement, “The number eight when rotated 90 degrees looks like a pair of spectacles”, auditory descriptions about the number eight are understood to be converted into a visual image that is mentally rotated. Visual short-term memory processes are then used to temporarily hold the rotated mental image within memory so that the individual can evaluate whether it resembles a visuospatial representation of spectacles. Conversely, when solving the low-imagery statement, “Although now a sport, marathons started with Greek messengers bringing news”, transformation of auditory content into a visual image of sport, marathons or Greek messengers might not be readily generated, as this imagery would not be particularly informative for verifying the truth of the statement. Individuals may, instead, engage in verbal semantic processing where access to previously learnt information about Greek history can help them generate a solution for the low-imagery statement.

Although the linguistic and visuospatial content in statements can influence whether verbal or visuospatial strategies are employed, individual differences in thinking style can also influence the likelihood which these strategies are selected (Mayer & Massa, 2003; Wyer, Hung, & Jiang, 2008). According to Childers, Houston and Heckler (1985), people who are cognitively inclined to visualise information readily generate pictorial images in mind when reading, listening or problem-solving, which helps them to elaborate meaning from incoming content. By contrast, individuals with a cognitive preference towards verbalising information spontaneously engage in verbal semantic processing and internalised speech (e.g. self-talk) to guide thinking.

It is currently understood that while people from the general population might display a preferred style processing information, they can flexibly switch between
verbalising and visualising strategies to facilitate cognitive performance (Kraemer et al., 2017; Riding, Glass, & Graeme, 1993; Riding, Glass, Butler, & Pleydell-Pearce, 1997). Unlike neurotypical individuals, the TiP account (Kunda & Goel, 2011) proposes that people on the autism spectrum are visual thinkers, relying predominantly on visualisation processing strategies and with restricted use of verbalisation processing strategies, on various behavioural (for review, see Williams et al., 2016) and neuroimaging (for review, see Herringshaw et al., 2016) measures.

Using the low- and high-imagery statements from the Just et al. (2004b) paper, a central study by Kana et al. (2006) compared neural mechanisms underlying sentence comprehension in young adults diagnosed with ASC and a neurotypical comparison group. Where the neurotypical sample demonstrated an effect of imagery, with low-imagery statements recruiting activation in language cerebral regions and the high-imagery statements solved using visuospatial cerebral regions (replicating results from the Just et al., [2004b] paper), this pattern of brain activity was not found in the autistic sample. Instead, autistic individuals appeared to solve the sets of low- and high-imagery statements similarly, with pronounced visuospatial cerebral activation evident for both statement types. Kana et al. (2006) interpreted the profile of results in the ASC sample as confirming evidence of cognitive biases towards visual thinking (and away from verbal thinking), predicted by the TiP framework (Kunda & Goel, 2011). However, such findings need to be interpreted somewhat cautiously.

Bearing in mind that individual differences in thinking style exist within the general population, the same statement can be solved differently among neurotypical individuals (Riding et al., 1993; Wyer et al, 2008). That is, it cannot be assumed that all participants from neurotypical samples in the Just et al. (2004b) and Kana et al. (2006) studies systematically solved all statements in the low-imagery condition using verbalising strategies, or that all statements in the high-imagery condition were solved using visualising strategies. Additionally, under the TiP account, it cannot be assumed that statements designed to assess language and visuospatial cognitive functions in neurotypical individuals are systematically solved the same way in people on the autism spectrum (Kunda & Goel, 2011). The implication is that sentence verification statements should be carefully piloted for relative use of visualising and verbalising strategies in a general population sample,
to ascertain whether test-tasking approaches in people on the autism spectrum reflect a shift towards visual thinking in the TiP account.

In the current experiment, I developed a novel sentence verification task containing a visualising-verbalising strategy rating scale to provide normative data on how an unselected sample of undergraduate students approach sentence comprehension. The self-report rating scale was designed to capture information pertaining to each participant’s preferred type of strategy (verbalising or visualising) for verifying any statement, along with the degree which the chosen strategy was utilised. Using predefined statistical analyses, the strategy ratings were analysed to identify sets of three distinct statements which differed systematically in the strategies they were reported to elicit.

The aim of this experiment was to identify sets of verbal, visual and ambiguous verbal-visual statements. The set of verbal statements were, respectively, selected based on high rates of reporting verbalising strategies, while the visual statement were selected based on high rates of reporting visualising strategies. These sets of statements could then be used to assess language and visuospatial functions in subsequent studies examining the TiP framework. In contrast to Just et al. (2004b) and Kana et al. (2006), and as recommended by Kunda and Goel (2011), the verification task in this thesis incorporated a third set of ambiguous verbal-visual statements that would be amenable to either verbalising or visualising processing strategies. By creating ambiguous statements for which verbal and visuospatial processing solutions could be employed with equal effectiveness, I sought to develop a behavioural measure to quantify the nature of cognitive biases in individuals selected for high versus low levels of autistic-like traits, in subsequent experiments.

In the course of developing sets of verbal, visual and ambiguous verbal-visual statements for the verification task, I reviewed the cognitive literature on language and visuospatial processing to identify candidate statement types (for details, see Tables 1.1, 1.2 and 1.3).
Table 1.1. *Five subtypes of statements developed for the verbal condition.*

<table>
<thead>
<tr>
<th>Verbal statements</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Anagrams</strong></td>
</tr>
<tr>
<td>The anagrams in this study involved presenting a string of four letters, which required participants to determine if the letters could be rearranged to spell a target word. When generating solutions to anagrams, semantic knowledge and an understanding of the sequential constraints of alphabet combinations is required to decide whether the presented letters form the target word (Novac &amp; Sherman, 2008; Tuffiash, Roring, &amp; Anders, 2007). In addition, verbal strategies such as using inner speech and verbal working memory can be drawn on to subvocally rehearse the list and manipulate the letters in mind (Baddeley &amp; Hitch, 1974; Vallar, Papagno, &amp; Baddeley, 1991).</td>
</tr>
<tr>
<td><strong>Double-negatives</strong></td>
</tr>
<tr>
<td>Double-negatives comprise of statements where two forms of negation are present. The inclusion of double-negatives was expected to increase the likelihood that verbal deductive processes would be employed to verify the truth of the statements (Carpenter &amp; Just, 1975; Ye &amp; Zhou, 2009).</td>
</tr>
<tr>
<td><strong>Verbal analogies</strong></td>
</tr>
<tr>
<td>The verbal analogy statements contained two pairs of abstract words and required determining whether the relationship between the first pair of words is conceptually the same as the relationship between the second pair of words. To successfully solve the verbal analogy, individuals must comprehend the semantic meaning of each word, infer abstract relationships between the words in each pair and verify whether the relationships are the same or different (Bunge, Wendelken, Badre, &amp; Wagner, 2005; Hummel &amp; Holyoak, 1997).</td>
</tr>
<tr>
<td><strong>Word oddities</strong></td>
</tr>
<tr>
<td>The word oddity statements contained a set of three words, two sharing the same meaning and one having a different meaning. Solving word oddities involves identifying whether a target word has a distinct meaning from the other two words. Determining the odd word from the list requires use of semantic knowledge to understand the individual words and discern whether the target word has a distinct meaning (Crutch, Connell, &amp; Warrington, 2009; Murphy, 2003).</td>
</tr>
<tr>
<td><strong>Word synonyms</strong></td>
</tr>
<tr>
<td>Word synonyms are similar to word oddity statements where a set of three words were presented, two with the same meaning and one with a different meaning. The main difference is that word synonyms require identifying whether two words are more similar in meaning to each other, than one of them is to a third word. Verbal comprehension of the word list and retrieval of semantic knowledge is understood to be involved when verifying which pairs of words have similar meanings (Häberling, Steinemann, &amp; Corballis, 2016; Murphy, 2003).</td>
</tr>
</tbody>
</table>
Table 1.2. *Four subtypes of statements developed for the visual condition.*

<table>
<thead>
<tr>
<th><strong>Visual statements</strong></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Alphanumeric manipulations</strong></td>
<td>Alphanumeric manipulations are statements that involve constructing an image of a target number or letter, and visually manipulating it in some way. These statements require visuospatial mental operations, such as 2-D rotation, visual superimposition (e.g., perceptually superimposing elements) and visual cancellation (e.g. perceptually removing elements) (DeShon, Chan, &amp; Weissbein, 1995; Tomasino &amp; Greseme, 2016). When solving alphanumeric manipulations, participants visualise a mental image of a target number or letter, transform it, and subsequently compare whether the resultant image resembles a target image.</td>
</tr>
<tr>
<td><strong>Clock positions</strong></td>
<td></td>
</tr>
<tr>
<td>Clock position statements require a judgement about the spatial relationships among elements within the analogue clock face (e.g. direction of clock hands or numerical position). It is understood that visuospatial strategies are required to access spatial positions of the clock face from long-term visual memory and temporarily hold the mental image so that spatial comparisons can be made (Sack, Camprodon, Pascual-leone, &amp; Goebel, 2005; Trojano et al., 2002).</td>
<td></td>
</tr>
<tr>
<td><strong>Map representations</strong></td>
<td></td>
</tr>
<tr>
<td>Map representations consist of statements designed to assess mental retrieval of basic geographical information of the continents on a World map and understanding of large-scale visuospatial relationships (e.g. shape or relative position of continents). Since the ability to systematically assess spatial locations and relationships on maps requires access to long-term visual memory, visuospatial strategies are likely to enhance comprehension (Gyselinck, De Beni, Pazzaglia, Meneghetti, &amp; Mondoloni, 2007; Meneghetti, Labate, Pazzaglia, Hamilton, &amp; Gyselinck, 2016).</td>
<td></td>
</tr>
<tr>
<td><strong>Telephone keypad</strong></td>
<td></td>
</tr>
<tr>
<td>These statements involve generating an image of a telephone keypad, listening to a series of three numbers, and visually navigating the keyboard layout to establish whether the number transitions produce the spatial outline of a target shape. Successful navigation of this type of statement requires access to a long-term visual representation of the telephone keypad, spatial relationships between the numbers, along with maintaining the sequence pattern in visual short-term memory (Pak, Sharit, Czaja, &amp; Rogers, 2003).</td>
<td></td>
</tr>
</tbody>
</table>
Table 1.3. Four subtypes of statements developed for the ambiguous verbal-visual condition.

<table>
<thead>
<tr>
<th>Ambiguous verbal-visual statements</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Alphabet representations</strong></td>
</tr>
<tr>
<td>These statements require verifying the number of serial positions between two target letters from the English alphabet. The alphabet is thought to have a highly practiced linear order that can be mentally represented either verbally or visually. Individuals might use verbalising strategies such as inner speech to subvocally rehearse the alphabet and count the number of serial positions between target letter pairs (Baddeley &amp; Hitch, 1974; Zhou et al., 2006), or use visualising strategies to visualise the letters from memory and retrieve metric information pertaining to the serial positions between the target letters (Gevers, Reynvoet, &amp; Fias, 2003; Jou &amp; Aldridge, 1999).</td>
</tr>
<tr>
<td><strong>Mental arithmetic</strong></td>
</tr>
<tr>
<td>Mental arithmetic statements require solving two-digit addition or subtraction problems with “carry over” mental operations (e.g. where the sum of the digits in the unit’s place is more than 9). These problems are thought to require either verbal or visual working processes to retain numerical information during calculation and carry of digits across columns (Clearman, Klinger, &amp; Szűcs, 2017). Verbal working memory and semantic elaboration strategies may help individuals to temporarily hold (lexical/phonological) information in memory and self-monitor counting during simple addition and subtraction (Ashcraft, Donley, Halas, &amp; Vakali, 1992; Hecht, 2002). Conversely, visuospatial working memory may be enlisted if individuals visualise the numbers and operands as a string of Arabic numerals and symbols (Heathcote, 1994; Ward, Sagiv, &amp; Butterworth, 2009).</td>
</tr>
<tr>
<td><strong>Syllogisms</strong></td>
</tr>
<tr>
<td>Syllogisms are logical deductive reasoning problems. The syllogism statements in this study consisted of a three-term series problem in the format of “If A &gt; B, and B &gt; C, then A &gt; C”. These statements require participants to evaluate relationships among three characters, to decide whether the proposition is true or false. It is has been suggested that visuospatial strategies can be enlisted to solve syllogisms, through the use of an image that orders the three terms, from left-to-right or top-to-bottom using visuospatial working memory (Bacon, Handley, Dennis, &amp; Newstead, 2008; Capon, Handley, &amp; Dennis, 2003). Alternatively, syllogisms can be processed verbally, particularly if the individual imposes linguistic-based relations on the terms in each statement and uses verbal working memory to verify if the conclusion is congruent with the premises (Bacon et al., 2008; Capon et al., 2003).</td>
</tr>
<tr>
<td><strong>Verbal-visual oddities</strong></td>
</tr>
<tr>
<td>In these statements, participants are presented with three words. Two words are closely related both semantically and physically in appearance (e.g. guitar, violin), while the other word is less similar either semantically or physically (e.g. trumpet). The goal is to identify which two words are most similar to each other than the third word. These statements were manipulated such that the two words that were most similar could be identified by conceptually linking them using either verbal abstraction (e.g. guitar and violin are string instruments) or by mentally visualising their shapes (e.g. guitar and violin are pear-shaped instruments).</td>
</tr>
</tbody>
</table>
Statements in the verbal category (verbal analogies, word synonyms, word oddities, anagrams, double-negatives) were designed to draw on verbalisation strategies in the form of inner speech, verbal working memory, conceptual reasoning, syntactic processing and semantic knowledge. Statements in the visual category (alphanumeric manipulations, clock positions, telephone keypad, map representations) were designed to be solved predominantly by using visualisation strategies, through the enlistment of imagery, visual short-term memory, visual long-term memory and visuospatial mental operations. The set of ambiguous verbal-visual statements (alphabet representations, mental arithmetic, syllogisms and verbal-visual oddities) were designed to be solvable using either a verbalising or visualising processing strategy, with the two types of strategy applicable to each statement.

A pool of 180 statements were created, with 60 statements for each of the verbal, visual and ambiguous verbal-visual conditions (half true, half false). The primary aim was to identify, using predetermined statistical criteria, three distinct types of statements: (1) verbal statements, for each of which a majority of the sample report using verbalising strategies, (2) visual statements, for each of which a majority of the sample report using visualising strategies, and, (3) ambiguous verbal-visual statements, for each of which, approximately half the sample report using verbalising strategies and the remaining half report visualising strategies.

A secondary aim was to examine the accuracy and response-time profiles of the verbal, visuospatial and ambiguous statements to further characterise their psychometric properties in a young adult sample. Analyses were conducted to ensure that the three sets of statements are approximately matched on item difficulty and processing speed demands. The best verbal, visual and ambiguous verbal-visual statements (30 per condition, half true and half false) were subsequently selected to form a refined version of the sentence verification task.

Three hypotheses were generated in this experiment. First, it was predicted that the verbal analogies, word synonyms, word oddities, anagrams and double-negative statements would be predominantly solved using verbalising strategies and would mainly constitute the final set of verbal statements. Second, it was expected that statements conveying alphanumeric manipulations, clock positions, telephone keypad, map representations would be primarily solved using visualising strategies and would mainly comprise the final set of visual statements. Third, it was
hypothesized that the alphabet representations, mental arithmetic, syllogisms and verbal-visual oddity statements would be approximately equally open to visualising and verbalising strategies and would mainly constitute the final set of ambiguous verbal-visual statements.

**Experiment 1**

2.1 Methods

**Participants**

Twenty undergraduate students ($M_{\text{age}} = 22.95$ years, $SD = 8.11$ years) from the University of Western Australia participated in this study. There were 8 males and 12 females. When asked, no participant reported any psychiatric, neurodevelopmental or significant medical condition. Informed consent was obtained prior to each participant’s inclusion in the study.

**Apparatus and Stimuli**

The sentence verification task was presented on a 1.8GHz Intel PC monitor fitted to a LG L1730SF 271 mm by 340 mm resistive touch screen. Statement stimuli for the sentence verification task were auditorily presented to participants through Sennheiser HD205 headphones, under computer control. Accuracy and response time (RT) data were recorded via touch screen monitor. The task was programmed in E-prime (Schneider, Eschman, & Zuccolotto, 2002).

An extensive computer assisted literature search was conducted using keywords for published articles on Google Scholar to identify candidate verbal, visual and ambiguous verbal-visual statement stimuli. For verbal items, the search terms ‘Verbal OR Language’ were combined with ‘Cognition OR Brain Imaging OR Cerebral Lateralisation OR Comprehension.’ For visual items, the terms ‘Visual OR Visuospatial OR Imagery’ were combined with ‘Cognition OR Brain Imaging OR Cerebral Lateralisation OR Comprehension.’ For the ambiguous items, the terms ‘Dual-route OR ‘Alternate Processing’ were combined with search terms for the verbal and visual stimuli (‘Verbal OR Language’ AND ‘Visual OR Visuospatial OR Imagery’ AND ‘Cognition OR Brain Imaging OR Cerebral Lateralisation OR Comprehension’). For each statement type, potential items were discussed with my supervisor, and the final sets of candidate statements were then designed by the
current author and colleagues. Examples of the true and false verbal, visual and ambiguous statements are presented in Table 1.4.

Stimuli consisted of 186 audio statements spoken in English by an Australian woman for whom English was her first language. A total of 6 practice and 180 test statements were used, with 2 practice and 60 test trials (half true, half false) for each of the verbal, visual and ambiguous verbal-visual statement conditions. The statements varied from 9 to 15 words in length, were digitized at 16 bits with a 44 kHz sampling rate, and were presented in a true or false format. All three statement types were approximately balanced on word length, $F(2, 177) = .20, p = .82, d = .05$, and auditory recording length, $F(2, 177) = 2.66, p = .08, d = .17$.
### Table 1.4. Examples of candidate verbal, visual and ambiguous statement stimuli for the sentence verification task.

<table>
<thead>
<tr>
<th><strong>Verbal statements (n = 60)</strong></th>
<th><strong>True</strong></th>
<th><strong>False</strong></th>
</tr>
</thead>
<tbody>
<tr>
<td>Anagrams (n = 12)</td>
<td>The letters O, T, M, B can be rearranged to spell “tomb.”</td>
<td>The letters S, Y, I, N can be rearranged to spell “sign.”</td>
</tr>
<tr>
<td>Double-negatives (n = 12)</td>
<td>There is not a living being that would survive without water.</td>
<td>Drink driving decreases chances of not being in a car accident.</td>
</tr>
<tr>
<td>Verbal analogies (n = 12)</td>
<td>Frustration is to calm as revenge is to forgive.</td>
<td>Freedom is to incarcerate as liberate is to release.</td>
</tr>
<tr>
<td>Word oddities (n = 12)</td>
<td>Of the words conventional, traditional and atypical, atypical is the odd one out.</td>
<td>Of the words outstanding, spectacular and famous, outstanding is the odd one out.</td>
</tr>
<tr>
<td>Word synonyms (n = 12)</td>
<td>Of the words separate, connect and attach, attach is most similar to connect.</td>
<td>Of the words blame, admit and confess, admit is most similar to blame.</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th><strong>Visual statements (n = 60)</strong></th>
<th><strong>True</strong></th>
<th><strong>False</strong></th>
</tr>
</thead>
<tbody>
<tr>
<td>Alphanumeric manipulations (n = 24)</td>
<td>The number 9 when flipped upside-down looks like small letter d.</td>
<td>Erasing the left-half of the number 8 forms capital letter E.</td>
</tr>
<tr>
<td>Clock positions (n = 12)</td>
<td>On a clock, number 1 is North of number 5.</td>
<td>On a clock, number 11 is South of number 7.</td>
</tr>
<tr>
<td>Map representations (n = 12)</td>
<td>On the world map, North America is closer to Europe than Asia.</td>
<td>Turning the world map upside down, Australia is below Asia.</td>
</tr>
<tr>
<td>Telephone keypad (n = 12)</td>
<td>On a telephone keypad, pressing 1,8,3 forms a “V” shape.</td>
<td>On a telephone keypad, pressing 1,5,7 forms a vertical line.</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th><strong>Ambiguous statements (n = 60)</strong></th>
<th><strong>True</strong></th>
<th><strong>False</strong></th>
</tr>
</thead>
<tbody>
<tr>
<td>Alphabet representations (n = 24)</td>
<td>In the alphabet, M is three letters before P.</td>
<td>In the alphabet, Q is three letters after O.</td>
</tr>
<tr>
<td>Mental arithmetic (n = 12)</td>
<td>The number 25 plus the number 27 is equal to 52.</td>
<td>The number 62 minus the number 15 is equal to 48.</td>
</tr>
<tr>
<td>Syllogisms (n = 12)</td>
<td>If Pete is hairier than Craig, and Craig is hairier than Luke, Pete is hairiest.</td>
<td>If Meg is thinner than Trish and Meg is thinner than Liz, Trish is thinnest.</td>
</tr>
<tr>
<td>Verbal-visual oddities (n = 12)</td>
<td>Among guitar, trumpet and violin, trumpet is the odd one out.</td>
<td>Among basil, onion and mint, mint is the odd one out.</td>
</tr>
</tbody>
</table>

**Task Design**

The sentence verification task required participants to listen to a statement, decide as to whether it is true or false, and then introspect about the strategy used by rating the strategy on a visualising-verbalising scale. At the start of each trial, participants viewed a blank screen and were cued by a tone to attend to the auditory statement. Immediately after the auditory statement was presented, true and false response buttons appeared side-by-side on the touch-screen monitor to prompt a
response. All responses were made with the participant’s dominant hand and could not be corrected. After the touch response was made, a 20-point visualising-verbalising Likert scale was presented on the screen. The scale comprised of numbers ranging from -10 to +10 (including 0), displayed horizontally in increasing order. Displayed below the scale were the words “visualising” and “verbalising”, presented on the left- and right-sides, respectively.

Negative values on the visualising-verbalising scale denoted use of visualising strategies (i.e. ratings from -10 to -1), while positive values indicated use of verbalising strategies (i.e. ratings from 1 to 10). Numbers on each extreme of the continuum represented pronounced reliance, while ratings closer to -1 and +1 indicate poorer reliance on the selected strategy. Participants were instructed to press ‘0’ on the scale if they could not decide which strategy they had recruited to solve the statement. Once a strategy rating was made using the touch screen, a tone cued the start of a new statement presented through the headphones.

Procedure

All participants were instructed to complete the sentence verification task to their best ability and to reflect on the main type of strategy used to generate the solution for each statement. Prior to completing the sentence verification task, they were informed that verbalising strategies referred to “word-based” strategies in which language was used to conceptualise meaning and/or elaborate on the content of thinking. Conversely, they were told that visualising strategies encompassed “picture-based” strategies where visual imagery was used to reconstruct the content conveyed and/or mentally manipulate images to verify meaning of the presented statement. For each statement, response accuracy and RT were recorded, with RT measured in milliseconds from the end of the auditory statement to the touch-screen response. The sentence verification task was administered over 3 blocks, with 60 test trials in each block. Each block contained 20 statements for each of the verbal, visual and ambiguous conditions (half true, half false). Apart from these restrictions, the 180 statements were presented in a randomised order for each participant. The six practice statements, two from each condition (one true, one false), were presented at the start of the first block.
Statement Selection Analyses

Strategy ratings for the 180 statements were analysed using predetermined selection criteria to identify sets of verbal, visual or ambiguous verbal-visual statements. Items for which criteria were not met for any of these categories were understood to have poor content validity and were discarded.

The selection process involved firstly selecting statements where no more than 2 participants provided a ‘0’ strategy rating on the visualising-verbalising scale. This criterion was applied to eliminate statements in which more than 10% of the participants were uncertain about the strategy used to generate a solution. Binomial distribution analyses were then conducted to evaluate the frequency distribution of verbalising and visualising strategy reports in the sample, for each item. For the binomial analyses, the strategy ratings were re-coded into a dichotomous variable to identify how many people utilized visualising strategies (i.e. negative ratings) and how many employed verbalising strategies (i.e. positive ratings). In addition, kurtosis and single-sample t-test analyses were computed on the numerical rating scores (range -10 to 10) for each item to examine the distribution of self-reported strategies in the recruited sample.

In selecting statements for the verbal and visual categories, first, binomial distribution tests were conducted to identify items for which a significant number of participants reported verbalising strategies and items where a significant number of participants reported visualising strategies. The criterion adopted was that 15 or more (out of 20) participants favoured a verbalising strategy, or alternatively a visualising strategy (for \( p < .05 \) based on the binomial distribution and assuming an equal likelihood for selecting each strategy type). The second criterion for validating statements for the verbal and visual categories involved the t-tests conducted on the numerical rating scores. Based on the single-sample t-test, items with mean strategy ratings significantly smaller than -1 (\( p < .05 \)) were selected as visual statements, whereas, items with mean ratings significantly greater than +1 (\( p < .05 \)) were identified as verbal statements. Statements that satisfied these two criteria were classified into the verbal or visual categories.

Selection criteria for the ambiguous verbal-visual categories involved identifying statements in which approximately half the sample reported use of verbalising strategies and the other half reported visualising strategies. Binomial distribution tests (50% probability outcome, \( n \) of 20) were used to identify statements...
with non-significant \( p \)-values \((p > .05)\). By applying this criterion, statements in which fewer than 15 participants reported using each particular strategy, were selected as potential verbal-visual ambiguous statements. The second criterion for the ambiguous verbal-visual category used single-sample t-tests to select statements with mean strategy ratings that were not significantly different from -1 or +1 \((p > .05)\) on the visualising-verbalising scale. The rationale for using this criterion is that if around half the participants reported use of verbalising strategies and the other half reported verbalising strategies, then their overall mean strategy ratings should be within the boundaries of -1 and +1 scores. Two additional criteria were employed to select ambiguous verbal-visual statements likely to have two characteristic peaks in the distribution of strategy ratings on the visualising-verbalising scale. These were the criteria of a kurtosis value < -1 and Ashman’s \( D \) value > 2, based on Ashman’s test of bimodality (Ashman, Bird, & Zepf, 1994). Collectively these criteria were designed to select ambiguous verbal-visual statements amenable to either type of strategy.

**Behavioural Analyses**

Behavioural analyses were conducted to examine item-difficulty and RT characteristics of the statements in the verbal, visual and ambiguous verbal-visual categories. As this study sought to select the best 30 verbal, visual and ambiguous verbal-visual statements for the refined sentence verification task, it was necessary to ensure that: (1) task performance on the selected items was above ‘chance’ and that (2) the three sets of statements were equated as closely as possible on mean accuracy and mean completion times. Consequently, statements with a mean accuracy below 70% were removed. Mean RTs were then calculated (based on correctly answered trials) for the remaining items.

Accuracy and RT data for the true and false verbal, visual and ambiguous verbal-visual statements were visually inspected and individually matched across the three statement categories in the refined sentence verification task. Considering the design of this study, strategy ratings on the visualising-verbalising strategy rating scale were not expected to be normality distributed. However, accuracy and RT data for the final sets of 30 verbal, visual and ambiguous statements were assessed using box-plots to ensure that most data points fell within \( \pm 2.5 \) SD from the mean.
For the final set of items in the verbal and the visual statement conditions, internal consistency of participants’ strategy ratings on the visualising-verbalising scale were analysed using Cronbach’s alpha. Internal consistency for the final set of items in the ambiguous condition were analysed slightly differently. Participants’ strategy ratings on the visualising-verbalising scale were re-coded using binary (1-0) scoring, to denote use of either visualising processes (ratings from -10 to -1 re-coded to a score of -1) or verbalising processes (ratings from 1 to 10 were recoded to a score of 1). The binary scoring method provided a way of assessing intra-individual consistency relating to the nature of the selected strategy, with Cronbach’s alpha calculated across items in the ambiguous statement condition.

2.2 Results

Sentence Selection Analyses

Strategy ratings for the 180 statements were first screened to remove items in which more than two participants indicated a ‘0’ (unsure) rating on the visualising-verbalising scale. No statements were removed on the basis of this criterion. Next, each of the 180 items was considered to determine if it could be categorised into verbal, visual or ambiguous verbal-visual statement conditions using the binomial distribution selection criteria, as described above. This yielded potential pools of 43 verbal statements, 63 visual statements and 74 ambiguous verbal-visual statements.

A single-sample t-test was subsequently conducted on the mean strategy ratings for each item to check if the item continued to meet criteria for the verbal, visual and ambiguous verbal-visual statement categories. All of the 43 (20 true, 23 false) verbal statements had mean strategy ratings significantly greater than +1 (all \( ps < .05 \)), and were retained. Among the set of the 63 visual statements, 62 (30 true, 32 false) had mean strategy ratings significantly smaller than -1 (all \( ps < .05 \)), with one item removed. Figure 1.1 depicts a breakdown in the proportion of strategy ratings in the sample, collapsed for the set of 43 verbal and 62 visual statements. Figure 1.1 shows that participants primarily reported pronounced use of verbalising strategies for solving items identified as verbal statements and predominant use of visualising strategies for the items characterised as visual statements.
Figure 1.1. Proportion of self-reported strategy ratings in the sample \((n = 20)\), collapsed across the 43 statements in the verbal category and 62 statements in the visual category.

Figure 1.2. Proportion of self-reported strategy ratings in the sample \((n = 20)\), collapsed across the 50 statements that fell in the ambiguous verbal-visual category.

For the 74 potential ambiguous verbal-visual statements, the single-sample t-test selection criterion was applied to ensure that mean strategy ratings were not significantly different from -1 and +1 on the visualising-verbalising scale. This criterion resulted in the elimination of 20 statements. Distribution of strategy ratings for the remaining 54 ambiguous statements were then analysed using kurtosis \((K < -1)\) and Ashman \((D > 2)\) bimodal criteria, where 4 statements were removed. Figure 1.2 displays participant strategy ratings for the 50 ambiguous statements (26 true, 24 false) where two peaks can be seen on each side of the
visualising-verbalising scale. These results suggest that the ambiguous verbal-visual statements were amenable to either modality of processing.

**Behavioural Analyses**

Item-difficulty for each of the 43 verbal, 62 visual and 50 ambiguous verbal-visual statements were then considered, where statements with a mean performance accuracy below 70% were eliminated. This criterion resulted in the removal of 10 verbal, 19 visual and 3 ambiguous statements. Item difficulty and RT profiles for the remaining 33 verbal (16 true, 17 false), 43 visual (23 true, 20 false) and 47 ambiguous statements (26 true, 21 false) were examined using scatter plots of mean accuracy and mean (of median) RTs. Visual inspection of the distribution of item RTs suggested that the verbal and ambiguous statements were slightly more dispersed compared to the visual statements. This was further confirmed from significant differences on Levene’s test of homogeneity regarding the variance in RT across the three statement conditions \( (p < .05) \). Consequently, the items were individually selected across the three statement categories so that the final three sets of 30 items (15 true, 15 false) were matched as closely as possible on both accuracy and RT.

To verify whether the three statement conditions were appropriately matched, two one-way ANOVAs were conducted on the accuracy and RT data. The verbal, visual and ambiguous statements were comparable on accuracy \( F(2, 87) = .69, \ p = .51, \ d = .12 \), and RT, \( F(2, 87) = .62, \ p = .54, \ d = .12 \) (see Table 1.5 for descriptive statistics). All three statement types were also balanced on word length, \( F(2, 87) = .17, \ p = .85, \ d = .06 \), and auditory recording length, \( F(2, 87) = 2.18, \ p = .12, \ d = .20 \).

Table 1.5. *Summary statistics (means, with standard deviations in parentheses) for the three types of statements in the refined sentence verification task.*

<table>
<thead>
<tr>
<th>Statement Type</th>
<th>Mean accuracy (out of 30)</th>
<th>Mean RT (s)</th>
<th>Statement length (no. words)</th>
<th>Recording length (s)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Verbal statements</td>
<td>26.90 (3.00)</td>
<td>3.84 (1.70)</td>
<td>11.67 (1.65)</td>
<td>6.15 (1.04)</td>
</tr>
<tr>
<td>Visual statements</td>
<td>26.15 (2.72)</td>
<td>4.15 (1.36)</td>
<td>11.73 (1.17)</td>
<td>5.94 (.97)</td>
</tr>
<tr>
<td>Ambiguous statements</td>
<td>26.35 (3.22)</td>
<td>3.91 (1.67)</td>
<td>11.57 (1.96)</td>
<td>6.53 (1.12)</td>
</tr>
</tbody>
</table>
The complete list of verbal, visual and ambiguous verbal-visual statements selected for the refined sentence verification task are presented in Appendix A. The final set of 30 verbal statements comprised of 11 word synonyms, 8 double-negatives, 6 verbal analogies, 4 word oddities and 1 verbal-visual oddity statement. The set of 30 visual statements contained 10 alphanumeric manipulation, 8 clock manipulation, 7 telephone keypad, 3 map representation and 2 verbal-visual oddity statements. The final set of 30 ambiguous verbal-visual statements consisted of 8 anagram, 7 syllogism, 6 alphabet representation, 4 mental arithmetic and 7 verbal-visual oddity statements. Internal consistency of strategy ratings for the verbal ($\alpha = .96$), visual ($\alpha = .89$) and ambiguous ($\alpha = .90$) statement stimuli for the verification task were high.

2.3 Discussion

Experiment 1 sought to design a novel sentence verification task and used a visualising-verbalising strategy rating scale to evaluate how neurotypical adults from the general population approach listening comprehension. Using predetermined criteria, participant strategy ratings were analysed for the selected strategy (visualising versus verbalising) and degree to which the strategy was recruited to categorise auditory statements as being verbal, visual or ambiguous verbal-visual in nature. It was reasoned that such a task could provide a potential measure for assessing language and visuospatial cognitive functions, and also capture the degree to which people show a preference towards verbal-visual thinking within the TiP framework.

A unique set of verbal, visual and ambiguous statements were successfully identified from an initial pool of 180 auditory statements. Although our statement stimuli were operationally defined and constructed following a review of cognitive literature (Tables 1.1 to 1.3), there was marked variability in the modality and strength of visualising-verbalising strategy reports within the recruited sample. The predetermined selection criteria in this study resulted in removal of 25 (of the 180; 13.88%) items from the sentence verification task. These results highlight that individual variability in test-taking strategies must be considered in test development, and, reinforce the importance of piloting statements for preferred strategy approaches to ensure that newly developed stimuli tap reliably into the constructs they are assumed to measure (John & Benet-Martínez, 2000). To my
knowledge, this study is the first study to directly investigate self-reported strategies in sentence comprehension and to use a systematic statistical approach to classify statement stimuli into verbal, visual and ambiguous verbal-visual categories.

In terms of the breakdown of test-items in the refined sentence verification task, three hypotheses were made. The first hypothesis was that the set of verbal statements would consist of anagram, double-negative, verbal analogy, word oddity and word synonym statements. As expected, the final set of verbal items mainly contained word synonym \((n = 11)\), double-negative \((n = 8)\), verbal analogy \((n = 6)\) and word oddity \((n = 4)\) statements, suggesting that underlying cognitive mechanisms involved with processing these sentences are predominantly verbally mediated (Bunge et al., 2005; Crutch et al., 2009; Häberling et al., 2016; Ye & Zhou, 2009). Intriguingly, the final set of verbal statements did not contain any anagram items. Instead, the set contained one visual-verbal oddity item (“Among perfume, incense and candle, incense is the odd one out”; false), which was initially hypothesized to be ambiguous verbal-visual in nature. It would appear that most participants in the sample primarily encoded verbal abstract concepts of the three terms (e.g. incense and candles can both be burnt and release scents, but perfume releases scent without burning), with little reliance on visualising strategies to generate a solution (e.g. constructing an image of candles and incense as being tall or emitting light, in contrast to perfume).

The second hypothesis was that the final set of 30 visual statements would comprise alphanumeric manipulation, clock position, map representation and telephone keypad statements. In line with these predictions, most participants in the study reported use of visualising strategies to solve these four subtypes of statements. Auditory information conveying alphanumeric manipulations \((n = 10)\), clock positions \((n = 8)\), map representations \((n = 3)\) and telephone keypad \((n = 7)\) information commonly convey vivid imagery and spatial descriptions which are likely transformed into visual codes in the course of comprehension (Meneghetti et al., 2016; Pak et al., 2003; Sack et al., 2005; Tomasino & Gremese, 2016). It is important to acknowledge that while some degree of verbal processing (e.g. word recognition) is required for decoding content of visual statements (for review, see Hubbard, 2010), the cerebral contribution of language activation for visual statements is considerably less than that involved with verifying verbal statements (Binder, Desai, Graves, & Conant, 2009; Hoffman, Binney, &
Lambon Ralph, 2015; Just et al., 2004b). Thus, the recruited sample is likely to have reported use of visualisation to solve the set of visual statements because such processes were more salient than verbalisation processes.

An unexpected finding was that two oddity statements ("Among donut, pie and bagel, bagel is the odd one out"; false, “Among wrist, ankle and chin, ankle is the odd one out”; false), predicted to be ambiguous in nature, were classified in the visual statement category. These results suggest that a majority of the sample encoded pictorial representations of the auditorily presented objects or body parts. For instance, participants might have engaged in spatial comparisons by retrieving memories of donuts, crackers and bagels (or wrist, neck and ankle) to check for similarities among the shape or appearance of these objects.

The third hypothesis was that the final set of 30 ambiguous verbal-visual statements would mainly contain alphabet representation, mental arithmetic, syllogism, and verbal-visual oddity statements. Consistent with this, statements in the ambiguous category comprised of alphabet representation ($n = 6$), syllogism ($n = 7$), mental arithmetic ($n = 4$) and verbal-visual oddity ($n = 5$) statements. Given that the verbal-visual oddity items were developed by the current author and colleagues, the specific cognitive mechanisms underpinning verification of this statement subtype is poorly understood. Nevertheless, it was reasoned that if a list of two (of three) words are linked both semantically and visually, and a third word is less closely related (both semantically and visually), identifying the odd-one-out might be possible using verbalising or visualising strategies. For the alphabet and syllogism statements, it is understood that the sequential or ordered nature can render such information amenable to verbal or visuospatial representations (Bacon et al., 2008; Gevers et al., 2003; Capon et al., 2003).

Regarding the mental arithmetic statements, Seron, Pesenti, Noël, Deloche and Cornet (1992), using introspective reports, found that during addition and subtraction problems, some people reported visualising numbers in spatial arrays (e.g. picturing Arabic numerals, manipulating the numbers in columns), whereas others reported verbalising strategies for the same problem (e.g. retrieving arithmetical facts, counting). Our study extends from the Seron et al. (1992) study, by capturing the distribution of strategic approaches using a visualising-verbalising scale and systematically identifying ambiguous mental arithmetic items using predefined criteria.
Contrary to predictions, a sizable number of anagram \((n = 8)\) statements were identified in the ambiguous verbal-visual category. Verbalising strategies such as using semantic knowledge, knowledge of spelling rules and inner speech have been shown previously to be helpful for generating solutions to anagrams (Novac & Sherman, 2008; Tuffiash et al., 2007). The novel finding is that approximately half of our sample reported use of verbalising strategies to generate a solution to anagram statements, while the rest of the sample reported use of visualising strategies for the same statements. By manipulating the final solution of anagrams for imagery, Dewing and Hetherington (1974) demonstrated that items containing “high-imagery” words (e.g. storm) were solved faster than those containing “low-imagery” words (e.g. shame). Their findings suggest that the content of anagrams could potentially influence test-taking strategies, such that visual imagery provides additional clues for efficiently accessing or generating solutions.

Although it is possible that a subset of our anagram statements with imaginable words were solved using primarily visualising strategies (e.g. tomb, sign, knit, gnaw), while anagrams containing abstract concepts were solved primarily using verbalising strategies (e.g. sour, debt, myth), this was not the case. By using stringent criteria to analyse strategy ratings for our set of ambiguous verbal-visual statements, each anagram item was identified on the premise that approximately half the sample reported verbalising and half reported visualising strategies. It is more likely that our findings of visualising reports for anagram items could relate to constructing an orthographic form of the letters in mind. For instance, when solving the anagram statement, “The letters O, T, M, B can be rearranged to spell tomb”, some participants might generate an image of the letters in the list and manipulate the serial positions of the letters in mind (e.g. reordering serial positions of letters O and T) to verify truth of the statement.

Given the self-report design of this study, it is difficult to pinpoint specific cognitive mechanisms involved with completing the verbal, visual and ambiguous verification statements. One possible extension of this current research is to conduct a dual-task study comparing the effect of dual-task articulatory suppression (which selectively blocks verbal processing) and spatial tapping (which selectively impedes visuospatial processing) across the three statement conditions. If the verbal statements suffer pronounced performance reductions during articulatory suppression relative to the ambiguous and visual statements, such findings would provide
confirmatory support for construct validity of the verbal statements. If task performance on the visual statements incurs greater performance decrements relative to the verbal and ambiguous statements during concurrent spatial tapping, this would add support to the idea that the visual statements are mainly solved using visualising strategies. Furthermore, the dual-task methods could also be used to confirm whether verification performance on ambiguous statements is equally affected under articulatory suppression and spatial tapping conditions, but less affected by either interference condition than the verbal or the visual statements.

In the next chapter, the refined sentence verification task was administered under dual-task articulatory suppression and spatial tapping conditions to explore the extent to which adults with low versus high levels of autistic traits rely on verbal and visuospatial processing, from a TiP standpoint. As discussed, Kana et al. (2006) documented cerebral differences in verbal and visuospatial processing between ASC and neurotypical comparison participants, where the autistic sample showed dominant visuospatial activation during verification of low- and high-imagery statements. Having piloted statements for strategy use, our verbal and visual statements should provide a more robust assessment of verbal and visuospatial processes. Additionally, our ambiguous statements were administered to assess preferences for verbal-visual thinking, specifically examining whether the high autistic trait group primarily verify these statements using visuospatial processing strategies, while the low autistic trait group primarily enlist verbal processing strategies.
Chapter 3: A Dual-Task Investigation of Sentence Comprehension in Adults with Autistic-Like Traits
Introduction

Despite developing spoken language, most autistic adults continue to experience difficulties with aspects of verbal comprehension, vocabulary and grammar (for reviews, see Andrés-Roqueta & Katos, 2017; Boucher, 2012; Howlin et al., 2014). Conversely, advantages in the visuospatial domain are prominent in autistic adults, where they often outperform their neurotypical counterparts on measures assessing perceptual reasoning, visual search and spatial construction (for reviews, see Kaldy et al., 2016; Muth, Hönekopp, & Falter, 2014).

One emerging explanation for this phenomenon comes from the TiP account (Kunda & Goel, 2011), where people on the autism spectrum are predicted to display a bias towards visual thinking and away from verbal thinking. Such assumptions of visual thinking align closely with introspective descriptions from individuals with ASC who commonly describe the frequent use of visual imagery in course of understanding meaning from words, remembering incoming information and problem-solving in their daily activities (Grandin, 2009; Hurlburt et al., 1994; Selfe, 2011).

From a TiP standpoint, visual thinking biases influence strategy selection, such that autistic individuals favour the use of visualising strategies and/or become less reliant on verbalising strategies, leading to better performance on visuospatial tasks and worse performance on verbal tasks. Another consideration is that underlying cognitive abilities\(^1\) can influence strategy preferences. Where autistic individuals often exhibit an uneven cognitive profile\(^2\) favouring stronger visuospatial than verbal abilities, they may possess enhanced proficiency in accessing and recruiting visualising strategies, or have restricted access to verbalising strategies (Lidstone et al., 2009; Williams et al., 2008; Williams et al., 2010). Consequently, there seems to be two alternative routes for which individuals with ASC might achieve superior performance on visuospatial tasks in comparison to verbal tasks.

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\(^1\)The term cognitive ability refers to a person’s mental capability. Cognitive abilities are measured by evaluating how well the individual (or selected sample) performs on a test in an absolute sense, or based on standardised norms gathered from peers their age.

\(^2\) The term cognitive profile refers to the pattern of strengths and weaknesses in the individual’s abilities, and is a relative term comparing two or more domains of thinking. In this thesis, the term cognitive profile has been used to describe the individual’s pattern of performance on cognitive ability tests.
Causal relationships between cognitive abilities and cognitive biases are difficult to disentangle in the TiP framework. It is possible that autistic individuals preferentially engage in visuospatial instead of verbal information processing strategies, without showing better visuospatial than verbal abilities. Alternatively, it is possible that autistic individuals exhibit a relative strength in visuospatial compared to verbal ability, yet not show a bias towards recruiting visuospatial over verbal information processing modalities across all cognitive tasks. The implication is that research investigations on the TiP account must consider the influence of cognitive abilities and cognitive biases to better understand how these factors contribute to a divergence between verbal and visuospatial performance in people on the autism spectrum.

According to Kunda and Goel (2011), one approach for objectively assessing cognitive biases is by administering tasks amenable to verbalisation or visualisation processing strategies, such as the ambiguous verification statements developed previously in Chapter 2 (Experiment 1). The experiment reported in this chapter examined the role of verbal and visuospatial abilities and cognitive biases in the TiP framework in non-clinical adult samples with low and high levels of autistic-like traits, and employed dual-task methodologies.

Dual-task studies have generally involved use of articulatory suppression and spatial tapping methodologies to examine the degree to which cognitive performance in ASC is contingent on verbal and visuospatial information processing. Where concurrent articulatory suppression disrupts verbal processing and adversely affects planning, task-switching and set-shifting performance in neurotypical samples, task performance on these same measures has been shown to be unaffected by articulatory suppression in autistic individuals (Holland & Low, 2010; Russell-Smith et al., 2014; Wallace et al., 2009; Whitehouse et al., 2006; Williams et al., 2012). The presence of pronounced accuracy costs in the neurotypical group during articulatory suppression suggests that planning, task-switching and set-shifting performance is generally verbally mediated. Whereas, the lack of articulatory suppression inference in autistic samples suggests limited reliance on verbal processing to facilitate task performance, and is consistent with the TiP account.

There is, however, considerable debate as to whether autistic individuals are solely reliant on visuospatial information processing modalities to support thinking. This evidence comes from finding similar patterns of dual-task articulatory
suppression interference in autistic and neurotypical comparison groups, particularly on short-term memory tasks (Williams et al., 2008; Williams et al., 2012). Such findings challenge the TiP assumption of visual thinking, as it indicates that autistic individuals are able to recruit verbal information processes just as effectively as neurotypical individuals to support cognitive performance.

One limitation of the aforementioned dual-task studies (Holland & Low, 2010; Russell-Smith et al., 2014; Wallace et al., 2009; Whitehouse et al., 2006; Williams et al., 2008; Williams et al., 2012; Winsler et al., 2007) is that cognitive performance in the autistic and neurotypical samples was examined only under an articulatory suppression condition and compared against a control baseline condition for which there was no concurrent task. Without a concurrent spatial tapping condition that suppresses visuospatial cognitive resources, these studies did not directly examine whether autistic individuals were more likely to favour use of visualisation processing strategies to approach task performance, relative to their neurotypical counterparts (Williams et al., 2016).

Work by Holland and Low (2010) is the only study to have combined dual-task spatial tapping and articulatory suppression methodologies, enabling further assessment of the TiP framework in ASC. Holland and Low (2010) compared mathematical performance in autistic and neurotypical participants under these two dual-task conditions, relative to their performances during a standard single-task baseline condition. The mathematical task involved solving problems with either blocked operations (i.e. adding (or subtracting) a pair of numbers throughout a list of problems) or with alternating operations (i.e. switching between adding and then subtracting the number pairs). Under concurrent articulatory suppression, the neurotypical group took longer to complete both the blocked and alternating numerical operations (compared to the baseline condition), while articulatory suppression did not impede mathematical performance in the autistic group. By contrast, concurrent spatial tapping incurred a more pronounced RT cost (relative to articulatory suppression) in the autistic sample, in comparison to their neurotypical counterparts. Taken together, the pattern of dual-task interference in ASC suggests an over reliance on visuospatial processing, accompanied also by under reliance on verbal processing during mathematical problem-solving, in line with the TiP account.

Another interesting finding from the Holland and Low (2010) paper was that the relationship between verbal ability and use of verbal processing on the
mathematical task was shown to be different for the autistic and neurotypical samples. If cognitive profile is related to strategy preference, it is reasonable to expect that stronger verbal ability might be associated with greater engagement in verbal processing strategies and result in greater interference during articulatory suppression. Instead, within the neurotypical sample, participants with stronger language abilities showed less articulatory suppression interference on the alternating math problems. Due to the alternating nature of the mathematical task, these results suggest that neurotypical individuals who had stronger verbal skills were perhaps better at switching to alternative strategies without incurring performance costs. No such relationships were found in the ASC group. Holland and Low (2010) interpreted these findings to indicate that autistic individuals generally do not enlist verbal processing to facilitate cognitive performance, even in those who have stronger verbal abilities. While correlations between visuospatial ability and degree of visuospatial (spatial tapping) interference were non-significant for the autistic and neurotypical samples, the findings by Holland and Low (2010) illustrate the idea that restricted verbal processing in ASC is not underpinned by limitations in verbal abilities.

To my knowledge, there has been no reported investigation of whether visual thinking biases and cognitive advantages in visuospatial abilities claimed for ASC extend along the broader autism continuum. Furthermore, it is unclear how cognitive preferences might relate to the relative profile of visuospatial and verbal abilities in general population individuals with sub-clinical, but high levels of autistic-like traits. Previous studies involving samples with high autistic traits have mostly examined visuospatial abilities, typically revealing an advantage in visual search relative to their low autistic trait counterparts (for meta-analysis, see Cribb et al., 2016).

There is, however, preliminary evidence for cognitive disparities in verbal and visuospatial abilities in individuals with high levels of autistic traits, as measured by the AQ. Using a measure of fluid reasoning, the Raven’s Advanced Progressive Matrices, Fugard et al. (2011) found that undergraduate students scoring on the higher end of the AQ performed better on subsets of visuospatial items (requiring perceptual rules) and worse on verbal items (requiring abstract conceptual rules). In comparison, participants scoring on the lower end of the AQ performed relatively better on the verbal items than on the visuospatial matrices problems. Given that Fugard et al. (2011) did not also administer a set of ambiguous verbal-visual
problems, it was unclear as to whether visuospatial information processing biases in
the high autistic trait sample might have influenced performance differences on the
verbal and visual problems.

In the current experiment, undergraduate students selected for low versus
high levels of autistic traits were recruited to investigate the role of cognitive abilities
and biases in the TiP framework. Using standardised Wechsler (Vocabulary and
Visual Puzzles) subtests, the relative profile of verbal and visuospatial abilities was
assessed among the low and high autistic trait groups. To discern the nature of
strategy choices during auditory comprehension, the sentence verification task
(from Chapter 2) was administered to participants under dual-task articulatory
suppression and spatial tapping conditions. More specifically, the pattern of dual-task
interference during verification of verbal, visual and ambiguous statements was
examined for the low and high autistic trait groups.

Participants’ verification performance during concurrent articulatory
suppression and spatial tapping were compared to task performance under a single-
task baseline condition. Based on the TiP account, participants with high levels of
autistic traits were hypothesized to rely more heavily on visuospatial than verbal
processes during sentence verification relative to those with low autistic traits. It was
predicted that spatial tapping would incur more pronounced accuracy and/or RT
costs in the high autistic trait group, relative to the cost incurred in the low autistic
trait group. Correspondingly, articulatory suppression was predicted to interfere less
with sentence verification performance (accuracy and/or RT) for the high autistic
trait group relative to the low autistic trait group.

The dual-task interferences effects were expected to be most pronounced on
the set of ambiguous verification statements, where group differences in verbal-
visual thinking biases are identified. Additionally, under the TiP account,
participants with high levels of autistic traits were predicted to perform better on the
Wechsler Visual Puzzles subtest and worse on the Wechsler Vocabulary subtest
relative to their low autistic trait counterparts. Finally, the relationship between
verbal and visuospatial abilities and strategy preferences on the verification task
were explored for the low and high autistic trait groups to further examine how these
constructs are linked within the TiP framework.
Experiment 2

3.1 Method

Participants

A total of 976 undergraduate students ($M_{age} = 19.19$ years, $SD = 4.10$ years) from the University of Western Australia completed the AQ in the screening phase of this study. Those individuals who scored in the bottom quintile (AQ score ≤ 95) or top quintile (AQ score ≥ 125) of the AQ distribution were invited to participate in the experimental phase of the study. There were 36 people recruited in the low AQ group and 36 in the high AQ group, all fluent in English and reporting no history of any neurodevelopmental, psychiatric or medical condition. Table 2.1 provides a summary of participant characteristics for the low and high autistic trait samples. Written informed consent was obtained from participants prior to their inclusion in this study.

Table 2.1. Participant characteristics (means, with standard deviations presented in parentheses).

<table>
<thead>
<tr>
<th></th>
<th>Low AQ ($n = 36$)</th>
<th>High AQ ($n = 36$)</th>
<th>Group comparison statistics</th>
</tr>
</thead>
<tbody>
<tr>
<td>Gender (female: male)</td>
<td>23:13</td>
<td>21:15</td>
<td>$\chi^2(1) = 0.23, p = .63, \phi = .06$</td>
</tr>
<tr>
<td>Age (years)</td>
<td>19.83 (4.76)</td>
<td>19.06 (3.71)</td>
<td>$t(70) = .77, p = .44, d = .18$</td>
</tr>
<tr>
<td>AQ score</td>
<td>82.56 (4.57)</td>
<td>128.86 (9.37)</td>
<td>$t(70) = 26.65, p &lt; .05, d = 6.37$</td>
</tr>
<tr>
<td>WAIS-IV Vocabulary</td>
<td>13.00 (1.94)</td>
<td>13.50 (1.80)</td>
<td>$t(70) = 1.01, p = .32, d = .24$</td>
</tr>
<tr>
<td>WAIS-IV Visual Puzzles</td>
<td>11.50 (2.09)</td>
<td>12.56 (2.14)</td>
<td>$t(70) = 2.12, p &lt; .05, d = .51$</td>
</tr>
</tbody>
</table>

Apparatus and Stimuli

The apparatus is the same as described in Chapter 2, except a keyboard was also used during the spatial tapping condition for pressing a spatial sequence. Stimuli for the sentence verification task were the 30 verbal, 30 visual and 30 ambiguous verbal-visual auditory statements developed in Chapter 2 (see Appendix A). Practice stimuli comprised of 6 additional statements (3 true, 3 false).

Materials

The Autism Spectrum Quotient is a 50-item self-report questionnaire designed to assess milder levels of autistic-like traits in the general population (Baron-Cohen et al., 2001). Items on the AQ assess autistic traits and behaviours
across aspects of social skills, attention switching, attention to detail, communication and imagination. Each item on the AQ was rated using a 4-point scale, marked by “definitely agree”, “slightly agree”, “slightly disagree” and “definitely disagree.” Each item was scored 1-4 to compute a total AQ score as recommended by Austin (2005). Compared to the binary (0-1) scoring system for each item on the AQ proposed initially by Baron-Cohen et al. (2001) (\(\alpha = .74\), weighted \(\kappa = .53\) to .63), the 1-4 scoring system has been shown to provide a more reliable (\(\alpha = .79\)) and sensitive (weighted \(\kappa = .57\) to .72) method for discriminating individuals with low versus high levels of autistic-like traits (Stevenson & Hart., 2017). Total AQ scores under the 1-4 method can range from 50 to 200, where higher scores indicate more pronounced autistic-like traits.

The Vocabulary and Visual Puzzles subtests from the Wechsler Adult Intelligence Scale - Fourth Edition (WAIS-IV) were used to provide information regarding verbal and visuospatial cognitive abilities, respectively (Wechsler, 2008). The Vocabulary subtest measures semantic knowledge of word meaning. Target words on the Vocabulary subtest were presented visually on a stimulus booklet and read aloud to participants, requiring them to verbally express the definitions of those words. Participants’ responses were scored 0, 1 or 2 points depending on the accuracy of their word definitions, as described in the WAIS-IV manual. Scores on the Vocabulary subtest have been shown to correlate with the WAIS-IV Verbal Comprehension Index \((r = .88)\).

The Visual Puzzle task measures visuospatial reasoning by examining the ability to analyse and manipulate (rotate, move) fragmented pieces in mind to create a target design. On the Visual Puzzle task, participants were asked to identify three fragmented figures (from an array of 6 response options) which, when combined, reconstruct the target design. Each trial had a 20 s time limit. For each trial, 1 point was awarded for correctly identifying all three figures and within the time limit. Participants were scored 0 points otherwise. Scores on the Visual Puzzle subtest have been shown to correlate with the WAIS-IV Perceptual Reasoning Index \((r = .76)\). Raw scores for the Vocabulary and Visual Puzzles subtests were converted into scaled scores using WAIS-IV Australian norms (Wechsler, 2008).
Task and Procedure

The sentence verification task contained 96 trials (6 practice, 90 test trials) completed under three different interference conditions: articulatory suppression, spatial tapping and a baseline condition without having to perform a concurrent task. Participants completed 6 practice statements, over 3 blocks of 2 trials under each interference condition. Then the test statements were administered over 3 blocks of 30 trials. In each experimental block, participants completed 10 verbal, 10 visual and 10 ambiguous verbal-visual statements (half true, half false for each statement type), under one of the three conditions. For each participant, accuracy (number correct) and median RT for correct responses were computed for each statement condition under each interference condition. The three types of statement were presented in random order in each interference condition. The order of the three interference conditions was counterbalanced across participants in each AQ group, as was the allocation of the particular verbal, visual and ambiguous statements to the three interference conditions.

Each trial of the sentence verification task began with a “beep” tone that cued participants to attend to the task and immediately after, an auditory statement was presented. In the baseline condition, participants were instructed to solve the statements to their best ability. Participants viewed a blank screen while they listened to the each auditory statement. After the statement was auditorily presented, true and false response buttons appeared on the bottom left and bottom right of the computer screen to cue a response by pressing the appropriate button on the touch screen.

In the articulatory suppression condition, participants were required to say the word “Monday” aloud repeatedly (Russell-Smith et al., 2014), in time with a visual dot display set to 80 pulses per minute, while completing the block of sentence verification trials. To cue participants to continuously say “Monday”, the pulsing dot was presented the centre of the screen throughout the trials in the articulatory suppression condition (prior to the stimulus onset, during auditory statement presentation and during the response phase). After each statement was auditorily administered, the true and false buttons appeared to prompt a response.

Under the spatial tapping condition, participants were asked to use their dominant index finger to press a sequence on the keyboard, in time with a visual dot display (set to 80 pulses per minute). The keyboard sequence involved pressing a “Z” shaped pattern (Eysenck, Payne, & Derakshan, 2005) on the four corners of the
numeric keypad, starting with the top left, and moving to the top right, to the bottom left and bottom right. As in the articulatory suppression condition, the visual dot continued to pulse in the middle of the screen throughout trials in the spatial tapping condition and the true and false buttons appeared on screen to prompt a response.

Sufficient practice was given for the two dual-task conditions to ensure that participants could sustain saying “Monday” or pressing the “Z” shaped sequence in time with the pulsing dot. The experimenter was seated in the testing room while participants performed the tasks. Where there was a prolonged period of off-task behaviour during the dual-task conditions, the experimenter encouraged participants to continue saying “Monday” or tap the “Z” sequence. All participants were able to complete the dual-task conditions during sentence verification. After performing all three dual-task interference conditions on the sentence verification task, participants completed the WAIS-IV Vocabulary and Visual Puzzles subtests.

3.2 Results

Preliminary Data Analyses

Data for each AQ group were screened for normality. Normal P-plots and Q-plots revealed that all variables were normally distributed, except mean RT data for the sentence verification task, which was positively skewed. Since normal P-plots and Q-plots of participants’ median response time data showed a more normal distribution, analyses used the median reaction times calculated for each participant, for the three statement conditions.

Data were also screened for univariate outliers using a z-score cut-off of ±2.5 (Tabachnick & Fidell, 2007), with outlier data points curtailed by adjusting the raw score to the value that corresponded to the z-score of ±2.5. Multivariate outliers were inspected using a Mahalanobis Distance criterion value of 5.99 (p <.05). None of the values exceeded the critical chi-square value.

Verbal and Visuospatial Abilities

Group comparisons of verbal and visuospatial abilities on the WAIS-IV Vocabulary and Visual Puzzle subtests were assessed using independent samples t-tests. These results are summarised in Table 2.1. Participants with low and high AQ scores did not exhibit significant differences in verbal abilities. However, the high
AQ group demonstrated significantly better visuospatial abilities relative to the low AQ group.

**Sentence Verification Accuracy**

A 2 (AQ group) x 3 (interference condition) x 3 (statement type) ANOVA was conducted on sentence verification accuracy, with autistic trait group entered as a between-subjects factor and interference condition and statement type repeated measures factors. The main effect of interference condition, $F(2, 280) = 19.13$, $p < .05$, $\eta^2_p = .22$ was significant. Bonferroni adjusted post-hoc analyses ($\alpha = .017$) revealed that overall, participants performed sentence verification less accurately under articulatory suppression ($M = 8.06$, $SD = .91$), relative to their performances on both the baseline ($M = 8.73$, $SD = .62$) and spatial tapping ($M = 8.48$, $SD = .77$) conditions.

There was a significant main effect of statement type, $F(2, 140) = 13.40$, $p < .05$, $\eta^2_p = .16$ and post hoc Bonferroni comparisons ($\alpha = .017$) revealed that accuracy was higher for the verbal ($M = 8.74$, $SD = .51$) statements, relative to the visual ($M = 8.28$, $SD = .54$) and the ambiguous ($M = 8.25$, $SD = .57$) statements (see Figure 2.1, left panel). However, the interaction between interference condition and statement type was non-significant, $F(4, 140) = 2.13$, $p = .08$, $\eta^2_p = .03$. None of the main effects or interactions involving the AQ group factor were significant (largest, $F(2, 280) = 1.79$, $p = .17$, $\eta^2_p = .03$). Relative to their performance in the baseline condition, participants with low and high levels of autistic traits showed considerable overlap in their pattern of accuracy costs on the verbal, visual and ambiguous statements during concurrent articulatory suppression and concurrent spatial tapping.
Figure 2.1. Dual-task effects on sentence verification accuracy (left panel) and completion times (right panel), collapsed for the low and high AQ groups.

Figure 2.2. Sentence verification accuracy (left panel) and completion times (right panel) for participants with low and high AQ scores. Error bars denote 95% confidence intervals, and show considerable overlap between the two AQ groups.
**Sentence Verification Completion Time**

Median RT data were then submitted to a 2 (AQ group) x 3 (interference condition) x 3 (statement type) ANOVA. This analysis revealed significant main effects of interference condition, $F(2, 140) = 8.26, p < .05, \eta_p^2 = .11$, and statement type, $F(2, 140) = 54.86, p < .05, \eta_p^2 = .44$. However, these effects were qualified by a significant interaction between these two factors, $F(4, 140) = 6.10, p < .05, \eta_p^2 = .08$. To further explore the nature of the interaction, a series of one-way ANOVAs were used to test the simple effect of interference condition for each of the three statement types. There was a significant effect of interference condition for the visual statements, $F(2, 215) = 8.93, p < .05, \eta_p^2 = .29$. In particular, performance on the visual statements suffered a greater RT cost during spatial tapping compared to the baseline, $t(71) = 4.12, p < .05, d = .49$, and the articulatory suppression conditions, $t(71) = 4.99, p < .05, d = .59$ (see Figure 2.1, right panel), indicating that the visual statements were substantially open to visuospatial processing strategies. However, for the verbal and the ambiguous statements, completion times were similar during spatial tapping and articulatory suppression, and no different to the RTs for the baseline condition, largest $F(2, 215) = 2.61, p = .08, \eta_p^2 = .16$ (see Figure 2.1, right panel).

There was a significant interaction between AQ group and statement type, $F(2, 140) = 6.81, p < .05, \eta_p^2 = .09$, with t-tests then conducted to examine the simple effect of AQ group for each statement type. However, the effect of AQ group fell short of significance for the verbal statement condition, $t(70) = 1.85, p = .07, d = .44$ (see Figure 2.2, right panel), and was also non-significant for the visual and the ambiguous statement conditions, largest $t(70) = .90, p = .37, d = 21$. Neither the two-way AQ group x interference condition interaction, nor the three-way AQ group x sentence type x interference condition interaction yielded a significant finding, largest $F(2, 140) = 1.15, p = .32, \eta_p^2 = .02$. Across the articulatory suppression and spatial tapping conditions, participants in the low and high autistic trait samples suffered equivalent patterns of RT costs on the verbal, visual and ambiguous verification statements.

**Associations between Cognitive Abilities and Strategy Preferences**

The relationship between verbal and visuospatial ability profile and strategy preferences on the ambiguous statements was further explored for the low and high
AQ groups. This was done by correlating participants’ WAIS-IV scaled scores on the verbal (Vocabulary) and visuospatial (Visual Puzzles) ability measures with degree of dual-task interference on the ambiguous statements. Interference effects were assessed by examining accuracy and latency costs associated with articulatory suppression and spatial tapping to provide an indication of verbal-visual strategy preferences. For these analyses, accuracy cost (i.e. accuracy on the baseline subtract mean accuracy in each dual-task condition) and RT cost (i.e. mean RT in each dual-task condition minus mean RT on the baseline control) were computed for the two AQ groups, where positive values denote greater interference.

Table 2.2 summarises the associations between participants’ verbal and visual ability profile and dual-task interference on the ambiguous statements, for the low and high AQ groups. In the high autistic trait sample, participants with stronger visuospatial abilities were more affected by the articulatory suppression interference, showing greater accuracy costs. In the low autistic trait sample, participants with stronger language abilities were more affected by the spatial tapping interference, showing greater latency costs.

Table 2.2. Pearson correlations between Wechsler verbal (Vocabulary) and visuospatial (Visual Puzzles) ability with dual-task interference on the ambiguous verification statements for participants with low and high AQ scores.

<table>
<thead>
<tr>
<th></th>
<th>Low AQ (n = 36)</th>
<th>High AQ (n = 36)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Verbal abilities</td>
<td>Visuospatial abilities</td>
</tr>
<tr>
<td><strong>Accuracy cost on ambiguous statements</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Articulatory suppression</td>
<td>.17</td>
<td>.28</td>
</tr>
<tr>
<td>Spatial tapping</td>
<td>.03</td>
<td>.02</td>
</tr>
<tr>
<td><strong>RT cost on ambiguous statements</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Articulatory suppression</td>
<td>.23</td>
<td>.04</td>
</tr>
<tr>
<td>Spatial tapping</td>
<td>.37*</td>
<td>.01</td>
</tr>
</tbody>
</table>

*p < .05, two-tailed.

### 3.3 Discussion

Building on the TiP account (Kunda & Goel, 2011), *Experiment 2* examined whether cognitive advantages in visuospatial abilities and preferences for visuospatial information processing found in ASC also extend to non-clinical individuals with high levels of autistic traits. Despite showing superior visuospatial abilities, the high autistic trait sample recruited verbal and visuospatial information...
processing to a similar extent as their low autistic trait counterparts during sentence verification performance. This was evidenced by finding equivalent dual-task interference effects for the low and high AQ groups under articulatory suppression and spatial tapping, across the verbal, visual and ambiguous statements. Critically, when the pattern of dual-task interference on the ambiguous statements was analysed within each AQ group, participants with high levels of autistic traits who had stronger visuospatial abilities tended to experience greater performance interference under articulatory suppression. These results suggest that stronger visuospatial abilities in the high autistic trait sample were associated with a corresponding vulnerability in engaging verbal processing to verify ambiguous content, providing preliminary links between cognitive abilities and strategy preferences within the TiP framework.

Finding a strength in visuospatial ability in the high AQ group on the Wechsler Visual Puzzles subtest echoes with previous reports showing enhanced visuospatial skills not only in ASC cohorts (e.g. Kaldy et al., 2016; Muth et al., 2014), but also in those who self-report high levels of autistic traits (e.g. Almeida, Dickinson, Maybery, Badcock, & Badcock, 2013, 2014; Cribb, et al., 2016; Grinter et al., 2009; Stewart et al., 2009). Fugard et al. (2011), for instance, demonstrated that individuals scoring higher on the AQ performed better on visual items, but worse on verbal items on Raven’s Advanced Progressive Matrices. The relative profiles of verbal and visuospatial abilities found in the recruited high autistic trait sample in the present study differs from the profile reported by Fugard et al. (2011) in two main ways. Firstly, although our high AQ group showed superior scores on the Wechsler Visual Puzzles subtest, they were not also found to be faster or more accurate at solving the visual statements on the verification task compared to the low AQ group. Secondly, the high AQ sample in this study did not display poorer verbal performance on either the Wechsler Vocabulary subtest or on the set of verbal verification statements, relative to the low AQ sample. While the cognitive profile of our high autistic trait sample was not characterised by relative weaknesses in verbal abilities, there was some indication of visuospatial strengths. Nevertheless, further work is required to determine whether such a profile represents a meaningful phenotypic expression within the TiP framework.

In contrast with TiP predictions of visual thinking, the high autistic trait sample were not primarily dependent on visuospatial information processes to
service comprehension. Relative to their task performance in the baseline condition, similar patterns of accuracy and RT costs were observed in the two AQ groups across all three statement types during concurrent spatial tapping and articulatory suppression. More specifically, articulatory suppression commonly impeded sentence verification accuracy, while spatial tapping contributed to significant latency costs for participants irrespective of their low or high AQ status. This pattern of dual-task interference indicates that individuals with high levels of autistic traits are able to draw on visuospatial as well as verbal processes to facilitate sentence comprehension, and do so in a similar way to their low autistic trait counterparts.

Given that the ambiguous verification statements were designed to evaluate verbal-visual thinking bias among the low and high autistic trait samples, the lack of group differences in dual-task interference on the ambiguous statements is particularly noteworthy. Finding significant but equivalent interference effects of articulatory suppression during ambiguous verification performance in our high autistic trait sample lends support to the conflicting view that verbal thinking might be intact (Williams et al., 2008, 2012), rather than impaired in ASC (Russell-Smith et al., 2014; Wallace et al., 2009; Whitehouse et al., 2006; Williams et al., 2012). Where Holland and Low (2010) found that mathematical problem solving in ASC is significantly more disrupted by spatial tapping in comparison to neurotypical controls, there was limited support for visuospatial information processing playing a predominant role in how our high AQ group solved the ambiguous statements. In other words, even on tasks designed to be solvable to verbal and visuospatial processing, individuals with high levels of autistic traits in this study did not favour visuospatial representations or show a bias against recruiting verbal mental representations, relative to their low autistic trait counterparts.

Methodological differences between this study and the previous studies involving autistic samples, could, in part, explain the lack of group differences in verbal-visual strategies on our ambiguous statements, and also on the other statements from the verification task. Dual-task studies in ASC have primarily focused on assessing cognitive domains including planning, task-switching, set-shifting and short-term/working memory (for a review, see Williams, et al., 2016). There is, however, some suggestion that verbal mediation in autistic individuals varies depending on the cognitive domain assessed.
Williams et al. (2012), for instance, found that autistic individuals were less affected by articulatory suppression during rule-based tasks (e.g. planning, task-switching), but relatively more affected by articulatory suppression (at a level similar to neurotypical comparisons) during short-term memory tasks (e.g. recalling a series of pictures). Williams et al. (2012) interpreted these findings to indicate that autistic individuals can sufficiently draw on verbal processing to service performance on short-term memory tasks, but preferentially engage in visuospatial processing as task demands require cognitive flexibility or become more complex. Thus, if the mathematical task in Holland and Low (2010) taps more into aspects of cognitive flexibility (e.g. alternating between adding and subtracting numerical operations) or is more complex, the autistic sample might rely more on visuospatial processing, potentially explain why they were more affected by spatial tapping. Conversely, if our verification task taps more into aspects of short-term memory (e.g. temporarily storing auditory information in short-term memory to verify the content) or is not sufficiently complex, the high AQ sample might have recruited verbal processing without having to resort to visuospatial compensatory processing to support comprehension. This explanation could potentially account for why participants with high levels of autistic traits showed overlapping patterns of articulatory suppression interference to those with low levels of autistic traits across all three statement conditions.

One important finding was the disparate relationship between cognitive profile and degree of dual-task articulatory suppression and spatial tapping interference on the ambiguous statements for participants with low versus the high autistic traits. Within the high AQ group, correlations between stronger visuospatial ability (Wechsler Visual Puzzles scores) and greater verification accuracy costs were found when verbal processing was impeded (via articulatory suppression). Whereas, for the low AQ group, associations between stronger verbal ability (Wechsler Vocabulary scores) and greater RT costs were found when visuospatial processing was impeded (via spatial tapping). It is possible that where the two AQ groups show relative strengths in one cognitive domain (verbal or visuospatial abilities), they were more likely to suffer performance costs when information processing resources in the opposite (weaker) cognitive domain was blocked via dual-task interference. While the findings from this study show some association between cognitive abilities and biases in the TiP framework, relative advantages in visuospatial abilities in high AQ
group were, nevertheless, not also accompanied by augmented or preferential use visuospatial processing on the ambiguous statements.

When interpreting the presence (or absence) of any AQ group differences in dual-task interference in this study, caution should be exercised since the dual-task effects across the three statement conditions only partly supported our expectations, potentially raising questions regarding content validity of the stimuli. While the imposition of spatial tapping did differentially affect verification performance (by way of latency costs) across the three statement conditions, it only revealed greater involvement of visuospatial processing on the visual statements relative to the verbal and the ambiguous statements. Despite developing our ambiguous statements to be partially amenable to visuospatial (and verbal) processing strategies, there were no significant differences in spatial tapping interference between the ambiguous and the verbal statements. Furthermore, when the effects of articulatory suppression were compared for the verbal, visual and ambiguous statements, there was no support for greater involvement of verbal processing in the solution of the verbal statements relative to the ambiguous and visual statements.

The lack of simple effects of statement type under the articulatory suppression condition could relate to verbal processing resources commonly associated with encoding the verbal, visual and ambiguous statements. Since statement stimuli from the verification task were presented in an auditory format, participants may subvocally rehearse the statements into short-term memory, at least in the initial stages to hold the complete statement in mind, before verifying its content. This early stage of verbal encoding might have masked subtle differences in the effects of articulatory suppression on subsequent stages of processing (e.g. during the verification phase when a true/false decision is made) for the three statement types. It is also plausible that dual-task methods employed in this study might also be less sensitive in capturing differences in verbal and visuospatial processing during sentence comprehension, in comparison with neuroimaging techniques such as fTCD or fMRI. For instance, using fMRI, Kana et al. (2006) documented pronounced activity in cerebral regions associated with language functions during the completion of low-imagery statements, and a shift towards greater cerebral activity in visuospatial regions for high-imagery statements in their neurotypical sample.

Using fTCD imaging, the next chapter examined the neural mechanisms underlying auditory comprehension of verbal, visual and ambiguous verification
statements in an unselected sample of neurotypical adults. Of central interest was whether the set of verbal statements enlist dominant activation in the cerebral hemisphere specialised for language functions, while the visual statements recruit dominant activation in the cerebral hemisphere specialised for visuospatial functions. If the ambiguous statements are equally amenable to verbal and visuospatial processing solutions, it was predicted that approximately half the sample would show dominant activity in their visuospatial cerebral hemisphere, while the remaining half would show dominant activity in their language cerebral hemisphere.
Chapter 4: Testing Utility of the Auditory Sentence Verification task in Assessing Cerebral Lateralisation and Thinking Style
Introduction

In a majority of people, brain regions that subserve language functions are lateralised in the left cerebral hemisphere, with visuospatial functions more likely to be focused in the right cerebral hemisphere (Price, 2012; Thiebaut de Schotten et al., 2011; Whitehouse & Bishop, 2009). This characteristic pattern of left-side language and right-side visuospatial functions has been confirmed using a range of neuroimaging methods, including fTCD and fMRI. These techniques have generally revealed greater blood flow to the left hemisphere during verbal tasks (e.g. verbal short-term memory, verbal fluency, semantic knowledge) (Gaillard et al., 2003; Henson, Burgess, & Frith, 2000; Stroobant, Buijs, & Vingerhoets, 2009), and more pronounced perfusion in the right hemisphere during visuospatial tasks (e.g. visual search, visual short-term memory, line bisection) (Flöel et al., 2002; Hage et al., 2016; Thomason et al., 2008). Such division of functional labour between the two hemispheres is understood to reduce cognitive redundancy and ensure efficient processing of language and visuospatial information (Hugdahl, 2011).

Capitalising on the notion of functional specialisation, the current experiment examined how the two cerebral hemispheres process language and visuospatial content conveyed in speech. As discussed previously in Chapter 2, during listening comprehension, verbal processes can be used to make semantic meaning from words, while visuospatial processes can be used to construct a mental picture of the same oral description. Although language and visuospatial cortical networks underpinning listening comprehension have been extensively studied, there are mixed results regarding how these two distinct systems are functionally lateralised in neurotypical individuals from the general population.

Frontal-temporal regions within the left cerebral hemisphere have been implicated in processing verbal components of speech. When listening to speech, incoming auditory information is received in the primary auditory cortex and subsequently transferred to Wernicke’s area. Commonly specialised to the left temporal lobe, Wernicke’s area, plays a central role in semantic processing, where meaning from individual words in the auditory stream are pieced together (for a review, see Friederici, 2012). In the course of understanding the statement, the words can be subvocally rehearsed and the syntactic structure processed, with activity in the left inferior frontal region subserving phonological accesses to verbal knowledge.
stores (for reviews, see Price, 2012 Vigneau et al., 2006). Consistent with the notion that frontal-temporal networks are specialised in the left hemisphere, auditory word (animal name) identification recruits greater blood flow to frontal and temporal regions in the left than the right hemisphere, relative to a non-word (beep tone) identification task (Binder et al., 1997). Similarly, studies increasing the verbal (lexical, syntactic, semantic) complexity of statements have documented heightened responses in frontal and temporal activity in left-side compared to right-side homologous regions (Just, Carpenter, Keller, Eddy, & Thulborn, 1996; Keller, Carpenter, & Just, 2001; Prat, Keller, & Just, 2007).

Neuroimaging support for an internal capacity to represent auditory content visuospatially is evidenced by heightened cortical responses in a network of frontal, parietal and occipital regions. Participants instructed to mentally visualise a list of words (D'Esposito et al., 1997; Kosslyn, Thompson, Klm, & Alpert, 1995), listen to highly-imaginable nouns (Mellet, Tzourio, Denis, & Mazoyer, 1998), solve metaphors (Bottini et al., 1994) and follow auditory instructions to construct a target image (Mellet, Tzourio, Denis, & Mazoyer, 1996) show relative increases in blood flow in the dorsomedial prefrontal cortex, inferior parietal and angular regions. The absence of activity in (inferior) frontal and temporal regions suggests the possibility that people rely considerably less on language when solving auditory statements conveying spatial descriptions or conducive to imagery. Like mental imagery, visual perception of physical stimuli activates the frontal-parietal-occipital network, which could relate to shared neural mechanisms supporting visuospatial attention and the generation and manipulation of visual images in mind (Borst & Kosslyn, 2008).

Considerable overlap between networks subserving visual perception and auditory comprehension supports the idea that spoken words are mentally transformed into visuospatial representations, where listeners might visualise images (symbol, shape, landmark) or manipulate spatial relationships in the processes of disambiguating oral descriptions (Bergen et al., 2007; Verhoeven & Perfetti, 2008).

Within the context of auditory comprehension, research investigations on cerebral laterality of visuospatial functions have produced inconsistent results. Some studies have documented the typical pattern of visuospatial dominance marked either by greater activity in the right hemisphere frontal-parietal-occipital regions (Bottini et al., 1994; Kosslyn et al., 1995; Mellet et al., 1998), or weakened left hemisphere frontal-temporal language activity during auditory comprehension of
visuospatial instructions (Mellet et al., 1996). Conversely, other studies have found more pronounced activity in the left hemisphere (D’Esposito et al., 1997; Just et al., 2004b) or even bilateral activity (Binder, Westbury, McKiernan, Possing, & Medler, 2005). Possible explanations for this discrepancy include heterogeneity in the auditory stimuli (single words versus statements) and differences in statistical methods for quantifying the degree of laterality (for a review, see Bradshaw, Bishop, & Woodhead, 2017).

Further compounding this problem is the fact that there is individual variability in cerebral development of language and visuospatial laterality. Whitehouse and Bishop (2009), using fTCD, assessed hemispheric specialisation in neurotypical adults (n = 75) by administering word generation (verbal fluency) and visual short-term memory tasks to localise cerebral hemispheres dominant for language and visuospatial functions, respectively. While more than half the participants showed typical lateralisation (left-side language, right-side visuospatial functions; 53.30%), the remaining sample exhibited a departure from this characteristic pattern. Interestingly, around 34.70% of participants had language and visuospatial functions lateralised within the same hemisphere, with 12.00% showing bilateral representation of one function. Similar findings have also reported in other studies involving children and adults the general population, with estimates of atypical cerebral lateralisation ranging from 23.00% to 50.00% (Flöel et al., 2001; Flöel, Buyx, Breitenstein, Lohmann, & Knecht, 2005; Groen, Whitehouse, Badcock, & Bishop, 2012).

Thus it is reasonable to expect that individual variability in cerebral lateralisation could add ‘noise’ to neuroimaging studies, which often interpret asymmetric activity in the left and right hemispheres as reflecting greater engagement in language or visuospatial processing. These interpretations do not hold true for neurotypical individuals who exhibit atypical cerebral organisation (i.e. reversed, same-side, or bilateral representation of either language or visuospatial functions). One implication is that when addressing questions about language and visuospatial cognitive processes, researchers must first appropriately identify the hemisphere(s) servicing language and visuospatial functions, before using hemispheric activation to infer how these two functions operate to support cognitive task performance.
Using fTCD imaging, the current experiment examined language and visuospatial cerebral laterality in an unselected sample of adults, with the primary aim of using this information to evaluate relative recruitment of language and visuospatial processes during auditory comprehension of verbal, visual and ambiguous statements. The fTCD technique was used to monitor changes in blood flow to the middle cerebral artery (MCA), which is the main artery supply to the left and right cerebral hemispheres. By comparing differences in blood flow to the left and right MCAs, fTCD provides a measure of the strength and directionality of cerebral lateralisation which is quantified by a laterality index (LI) (Deppe, Ringelstein, & Knecht, 2004; Lonhmann, Ringlesetin, & Knecht, 2006).

The approach in this experiment involved two-stages. First, fTCD imaging was used to assess the pattern of language and visuospatial lateralisation for each participant. This was achieved by administering ‘gold standard’ laterality assessment measures, specifically the word generation and visual short-term memory tasks, previously shown to reliably localise language and visuospatial hemispheric functions (Bishop et al., 2009; Whitehouse et al., 2009). Most participants were predicted to show the typical pattern of lateralisation, with a smaller proportion expected to exhibit atypical patterns. Second, fTCD imaging was combined with the sentence verification task to explore whether participants enlist greater activity in their language cerebral hemisphere or their visuospatial cerebral hemisphere during auditory comprehension of verbal, visual and ambiguous verbal-visual statements.

It was hypothesized that most participants would recruit dominant activity in their language cerebral hemisphere during verification of verbal statements and show dominant activity in their visuospatial cerebral hemisphere for the visual statements. As for the ambiguous verification statements, it was predicted that approximately half the sample would favour use of their language cerebral hemisphere, whereas, the other half would favour their visuospatial cerebral hemisphere.
Experiment 3

4.1 Methods

Participants

Twenty-five undergraduate students ($M_{age} = 20.44$ years, $SD = 4.74$ years) from the University of Western Australia participated in this study. There were 18 females and 7 males. All participants were fluent in English and reported no history of any psychiatric, neurodevelopmental or significant medical condition. Handedness was assessed using the 4-item short form of the Edinburgh Handedness Inventory (range = -100 to 100) (Veale, 2014), where scores -60 and below denoted left-handedness, while scores 60 and above indicated right-handedness. Participants with scores in between the -60 and 60 cut-offs were classified as ambidextrous. There were 21 right-handed (16 females, 5 males) and 3 left-handed (2 females, 1 male) participants and 1 ambidextrous male.

Apparatus

The fTCD device (DWL Multidop T2; DWL Elektronische Systeme, Singen, Germany), consisted of two 2MHz transducer probes on a flexible headset. Each probe was covered with ultrasound gel and placed on the temporal skull windows on each side of the head. The two probes on the fTCD headset were then positioned to measure changes in the blood flow velocity through the left and right MCAs. Blood flow signals for the MCA were identified by a characteristic (low whooshing) sound as well as visual pattern (Bishop, Badcock, & Holt, 2010) monitored from the Multi-dop computer. Responses in the left and right MCAs were recorded while participants completed the three experimental tasks.

The word generation, visual short-term memory and sentence verification tasks were all programmed using Presentation Software (Neurobehavioural Systems) and were presented on a computer. The Presentation Software sent marker pulses to the fTCD to denote the beginning of each epoch, for the three experimental tasks. Responses for the sentence verification task were made on a keyboard connected to the computer.
**Laterisation Tasks**

The word generation task (Bishop et al., 2009) was used to isolate the dominant cerebral hemisphere for language functions. In this task, participants were instructed to think of as many different words beginning with a target letter presented on the computer screen. At the beginning of each trial, participants were cued with a beep tone, and following a 5 s period, a letter from the alphabet was presented on screen for a 15 s period during which participants engaged in covert word generation. After the thinking period, participants were told to say aloud all the words that they had generated, over a duration of 5 s. This was followed by a 35 s baseline rest period. A timeline of the word generation task can be seen in Figure 3.1 (top panel). Participants completed 23 test trials (all letters of the alphabet, except Q, X and Z). The total number of generated words was recorded for each participant. Repetition errors or intrusion errors were not counted.

The visual short-term memory task (Whitehouse et al., 2009) was administered to identify the dominant cerebral hemisphere for visuospatial functions. Each trial involved the presentation of a visual array of 17 white and 5 red circles, scattered across a black background. Participants were told to memorise the locations of the red circles. At the start of each trial, participants were cued with a tone and after 5 s the array of circles appeared on the screen for 5 s. Following this, participants viewed a blank screen for a 10 s retention period, and then another array of circles (17 white and 5 red) appeared on the screen for 5 s. On half of the 20 trials, the spatial location of one red and one white circle was swapped in this test array compared to the initial array, and on the other half, the locations of the red (and white) circles were identical across the two arrays. Participants were required to indicate if the positions of the red circles were the same or different compared to the initial circle array, by respectively raising their left or right index finger. Each trial ended with a 35 s baseline rest period. A timeline of the visual short-term memory task can be seen in Figure 3.1 (bottom panel). Accuracy data was recorded.
Word generation task

<table>
<thead>
<tr>
<th>“Clear mind”</th>
<th>Generate words</th>
<th>Say words</th>
<th>Baseline</th>
</tr>
</thead>
<tbody>
<tr>
<td>Time (s)</td>
<td>5</td>
<td>20</td>
<td>25</td>
</tr>
</tbody>
</table>

LI, 8-18 s

Visual short-term memory task

<table>
<thead>
<tr>
<th>“Clear mind”</th>
<th>Circles appear</th>
<th>Blank screen</th>
<th>Circles appear</th>
<th>Baseline</th>
</tr>
</thead>
<tbody>
<tr>
<td>Time (s)</td>
<td>5</td>
<td>20</td>
<td>26</td>
<td>46</td>
</tr>
</tbody>
</table>

LI, 22-32 s

Figure 3.1. Timeline for the word generation and visual short-term memory tasks. For each task, mean LI was calculated where peak blood flow differences in the language and visuospatial cerebral hemispheres occurred. The time points for which LIs were computed were based on Bishop et al. (2009) for the word generation task and Whitehouse et al. (2009) for the visual short-term memory task.

Sentence Verification task

Each trial of the sentence verification task had four phases, depicted in Figure 3.2. At the start of each trial, participants were cued by a beep tone, during a preparatory period where the words “clear mind” appeared on the screen for 5 s. This was followed by the auditory statement presentation phase, during which participants listened to a statement while they viewed a blank screen. After the statement was presented, true and false response options were presented on the computer screen to cue participants to verify the statement. Participants made their responses on a keyboard using their left index finger for “true” responses and their right index finger for “false” responses by pressing the shift keys on the left and right sides, respectively. There was no time limit to make a response. After a response was made, the trial ended with a 15 s baseline period, during which the word “rest” appeared on the screen.

The sentence verification task contained 6 practice (2 verbal, 2 visual, 2 ambiguous) trials and 84 test (28 verbal, 28 visual and 28 ambiguous) trials (see Appendix A). Given that a smaller number of test trials were administered
compared to Chapter 3, checks were conducted to confirm that all three statement conditions were balanced on sentence length, $F(2, 81) = .16, p = .86, d = .06$, and recording length, $F(2, 81) = 2.32, p = .10, d = .12$. The number of true and false trials for each statement condition was also balanced to ensure that blood flow changes associated with left and right finger motor responses would cancel out.

<table>
<thead>
<tr>
<th>Cue tone</th>
<th>Auditory statement presentation</th>
<th>True/false</th>
<th>Baseline</th>
</tr>
</thead>
<tbody>
<tr>
<td>“Clear mind”</td>
<td>~9-12</td>
<td>~11-15</td>
<td>~30</td>
</tr>
<tr>
<td>Time (s)</td>
<td>5</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

*Figure 3.2.* Timeline for the auditory sentence verification task. Comprehension was estimated to occur 11 to 15 s from the start of the trial. Mean LIs for the verbal, visual and ambiguous statements were calculated 7 to 17 s following the trial onset, where peak blood flow differences in the language and visuospatial cerebral hemispheres occurred.

Trials for verbal, visual and ambiguous statements were interleaved, with order of the three statement types (6 possible permutations) assigned approximately equally across the sample. For each participant, accuracy and median RT data were computed (only on correct trials) for each statement condition. RTs were recorded from the end of presentation of each auditory statement. Where individual participant RT data fell above or below two standard deviations from their mean of median RTs, these trials were excluded from the fTCD analyses.

**Procedure**

All participants completed the sentence verification task first, followed by the two lateralisation tasks. This order was used to ensure that performance of the latter two tasks did not influence strategy choice on the sentence verification task. The order of the word generation and the visual short-term memory task was counterbalanced across participants.
Data Analyses

The fTCD data were analysed offline using the dopOSCCI software (Badcock, Holt, Holden, & Bishop, 2012). Blood flow envelopes from the left and right probes were down-sampled to a rate of 100Hz. For each participant, epochs were corrected for heart rate cycle activity and were normalised to eliminate noise in the recordings (e.g. from movement). An artefact rejection procedure (± 40% of average cerebral blood flow velocity) was used to exclude epochs with unusually high or low levels of activity (Groen et al., 2012). Participants who had at least 70% of accepted epochs on all three tasks were included in the analyses.

Epoch lengths for the lateralisation tasks were selected based on previous research by Whitehouse and Bishop (2009). For both these tasks, the epochs were set to begin 12 s before the cuing tones, and to end at 30 s for the word generation task and 34 s for the visual short-term memory task. The period of interest for peak differences between the left-right MCA activity was set during the covert verbal fluency phase (8-18 s after the epoch onset) of the word generation task (Figure 3.1, top panel), and during the recognition phase (22-32 s after the epoch onset) of the visual short-term memory task (Figure 3.1, bottom panel).

For the sentence verification task, the epochs were set to begin 12 s before the cuing tone, so that the three tasks were comparable. Given that trials for the sentence verification task were self-paced, behavioural (accuracy and RT) data for the three statement conditions were preliminarily examined to determine the epoch length and the period of interest where maximum difference between the left and right MCA activation occurred.

For each participant, LI values were calculated for the two lateralisation tasks as well as the verbal, visual and ambiguous verbal-visual statements. This was done by subtracting MCA blood flow between the left and right hemispheres and subsequently averaging the cerebral blood flow ‘difference’ function over a 2 s window centred on the period of interest. The LI quantifies the degree of cerebral lateralisation, with more extreme values indicating greater lateralisation. For each participant’s LI, a 95% confidence interval was also computed to determine if the LI value differed significantly from zero. Where confidence intervals of the LI overlapped with zero, participants were categorised as having bilateral activation. Positive LIs which significantly differed from zero were classified as left-side lateralisation, while negative LIs that significantly differed from zero were deemed
right-side lateralisation. In this way, LI values from the word generation and visual short-term memory tasks were used to classify participants based on whether they showed the typical (left language, right visuospatial), reversed (right language, left visuospatial), same-side (both functions in left hemisphere, both functions in right hemisphere) or bilateral lateralisation.

For the sentence verification task, LIs for the verbal, visual and ambiguous statements were individually examined with reference to whether the participant primarily enlisted activity in their language or visuospatial hemisphere. Since it is not possible to distinguish whether language or visuospatial hemispheric processes were preferentially recruited in subsets of participants with bilateral organisation or same-side lateralisation for both functions, these individuals were excluded from the sentence verification LI analyses.

For those participants with typical cerebral lateralisation, positive LI values on the sentence verification task denote greater (left) language cerebral activity, while negative values reflect greater (right) visuospatial cerebral activity. Conversely, for individuals with the reversed lateralisation, positive LIs on the sentence verification task indicated greater (left) visuospatial cerebral activity, while negative values indicate greater (right) language cerebral activity. Where LI values for any of the three statement types overlapped with zero, participants were deemed to recruit a bilateral pattern of activation for the appropriate statement condition. For each statement condition, a ‘difference’ function was also computed, by subtracting mean blood flow between the language and visuospatial hemispheres. Temporal characteristics for the verbal, visual and ambiguous verification statements were also analysed by running intraclass correlations (Koo & Li, 2016) on the cerebral blood flow difference functions, over the period of interest, to compare the trajectory of language-visuospatial activity.

4.2 Results

\textit{fTCD Data Checks}

Preliminary analyses on the quality of the fTCD data revealed that all participants had at least 70% of acceptable epochs on the word generation ($M = 88.87\%, SD = 5.90$), visual short-term memory ($M = 91.20\%, SD = 3.32$) and sentence verification ($M = 97.86\%, SD = 5.74$) tasks. Split-half reliability was calculated over the odd- and even-numbered epochs, for each task, and were
acceptable for the word generation ($r = .73$) and the visual short-term memory task ($r = .71$). The verbal ($r = .83$) visual ($r = .72$) and ambiguous ($r = .76$) verification statements were also deemed to have acceptable split-half reliability. Imaging and behavioural (accuracy and RT) data for all three experimental tasks were screened for normality using Normal P and Q-plots, with univariate outliers curtailed, as described in the previous chapters. Relationships between all variables were approximately linear. Parametric assumptions of normality were confirmed by findings of non-significant Kolmogorov Smirnov statistics for all variables ($p > .05$) (Field, 2009).

Cerebral Lateralisation

Average left and right MCA activation plots for the word generation and visual short-term memory tasks for the entire sample are depicted in Figure 3.3. The mean LI for the word generation ($M = 1.77, SD = 2.37$) was positive and differed significantly from zero, $t(24) = 3.72, p < .05, d = .74$. In contrast, the mean visual short-term memory LI was negative, differing significantly from zero, $t(24) = -7.34, p < .05, d = 1.47$. These results indicate that on a group level, the word generation and visual short-term memory tasks primarily localised activation in the left and right cerebral hemispheres, respectively.
Word generation task

Visual short-term memory task

*Figure 3.3. Average activation plots for the word generation (top panel) and visual short-term memory (bottom panel) tasks. Cerebral blood flow velocity changes are presented for the left (blue) and right (red) MCAs. The difference function (black dotted line) depicts activity for the left- subtract right-MCA, where positive values indicate greater left hemispheric activity and negative values represent greater right hemispheric activity. Mean LIs for the two lateralisation tasks were calculated during the period of interest.*
To further examine the distribution of language and visuospatial cerebral lateralisation in the sample, LI values (including ± 95% confidence intervals) for the word generation and visual short-term memory tasks were plotted for each participant in Figure 3.4. A majority of participants ($n = 18, 72.00\%$) exhibited typical cerebral lateralisation, with dominant left-hemisphere activity during the word generation task and dominant right-side activity during the visual short-term memory task (Figure 3.4, bottom left quadrant). The remaining participants showed atypical cerebral lateralisation. Two participants (8%) exhibited the reversed pattern, with right-side language and left-side visuospatial cerebral activity (Figure 3.4, top right quadrant). There were four participants (16.00%) with same-side lateralisation for both language and visuospatial functions (in the right hemisphere) (Figure 3.4, bottom right quadrant). One participant (4.00%) showed bilateral activation during the word generation task (see Figure 3.4, where the confidence interval intercepts the vertical cut-off) and right-side dominance for the visual short-term memory task.

*Figure 3.4.* Scatter plots of language and visuospatial LIs (and 95% confidence intervals) for the word generation and visual short-term memory tasks. Participants for whom error bars overlapped with zero were characterised as having bilateral activation for the appropriate cognitive function.
Sentence Verification fTCD Epoch Parameters

Epoch parameters for the sentence verification task were estimated by assessing accuracy and RT data for the verbal, visual and ambiguous statements, using two one-way ANOVAs. All three sets of statements were equivalent on difficulty level, \( F(2, 72) = 1.65, p = .20, d = .20 \), and completion time, \( F(2, 72) = 2.41, p = .10, d = .25 \). Consequently, for each participant, overall average RT was computed across the three statement conditions \((M = 2.93 \text{ s}, SD = 1.40 \text{ s})\), and the lower- and upper-bounds of the SDs were used to estimate the phase that captured most of the responses. Using this approach, the true/false response phase was estimated to occur around 11 to 15 s from the epoch onset, with each epoch estimated to run for 30 s (see Figure 3.2).

Average language-visuospatial activation functions for the verbal, visual and ambiguous statements were then to identify the period of interest for which peak differences in language and visuospatial cerebral activity occurred. Inspection of Figure 3.5 revealed that the language-visuospatial difference function commonly peaked 7 to 17 s from the epoch onset across the three statement conditions. This was used as the referent point for which sentence verification LIs were computed.

Cognitive Preferences during Verification of Auditorily Presented Statements

In examining how the sample approached the auditory comprehension, only data from participants with language and visuospatial cerebral functions lateralised to separate hemispheres (18 typical lateralisation, 2 reversed lateralisation) were analysed on the verification task. For this analysis, the directionality of hemispheric blood flow responses for the typical and the reversed lateralised groups were taken into consideration, specifically focusing on whether participants were primarily utilising their language or visuospatial hemisphere to process content during auditory comprehension.

The shape of language-visuospatial blood flow difference functions for the verbal, visual and ambiguous statements were compared over the 7 to 17 s peak period of interest. Intraclass correlations revealed a moderate fit, mean ICC = .73, CI = .06 to .90, \( p < .05 \), indicating similar blood flow trajectories of language-visuospatial cerebral activity across the three statement types (see Figure 3.5).
Figure 3.5. Average activation plots during auditory verification of verbal (left panel), visual (middle panel) and ambiguous (right panel) statements. Mean MCA blood flow to the language (blue) and visuospatial (red) hemispheres, and the difference function of language subtract visuospatial activity (black dotted line) are depicted only for participants with these cerebral functions lateralised to separate hemispheres (18 typical lateralised, 2 reversed lateralised). Mean LIs for the verbal, visual and ambiguous statements were calculated over the period of interest.
The magnitude and direction of sentence verification LIs were assessed for participant groups with the typical and the reversed pattern of cerebral lateralisation. For the typical lateralised group, mean LIs for the verbal ($M = 1.48$, $SD = 1.87$), visual ($M = 1.97$, $SD = 2.05$) and ambiguous statements ($M = 1.07$, $SD = 1.92$) were all positive and differed significantly from zero (smallest $t = 2.36$, $p = .03$, $d = 2.38$) (Figure 3.6, top panel). The strength of the LIs were no different across the three statement conditions, $F(2,51) = .97$, $p = .39$, $d = .19$. These results suggest relatively greater language than visuospatial activation (i.e. more left than right hemisphere activation) during auditory statement verification in the typical lateralised group.

For the reversed lateralised group, mean LIs for the verbal ($M = 3.20$, $SD = .49$), visual ($M = 2.82$, $SD = 1.32$) and ambiguous ($M = 4.19$, $SD = .13$) statements were all significantly positive and were comparable across the three statement conditions, $F(2,3) = 1.51$, $p = .35$, $d = .12$ (Figure 3.6, bottom panel). Given that these participants had the reversed pattern of lateralisation, positive LIs indicate greater use of their visuospatial than language (i.e. more left hemisphere than right hemisphere) activation during auditory verification performance.
Figure 3.6. Mean LIs (and 95% confidence intervals) for the auditory verbal, visual and ambiguous verification statements, for participants with typical (top panel) and the reversed lateralisation (bottom panel). The LIs are presented with regard to the dominant cerebral hemisphere activated during each statement condition. For the typical lateralised group, positive LIs indicate greater language activation, while negative LIs indicate greater visuospatial activation. For the reversed lateralised group, positive LIs indicate greater visuospatial activation and negative LIs denote greater language activation. Bilateral activation was deemed for the statement condition if the confidence interval overlapped with zero.
Figure 3.6 also shows that most participants with typical lateralisation showed dominant blood flow to their language cerebral hemisphere across the three statement conditions (verbal = 72.22% of participants, visual = 77.78%, ambiguous = 77.78%). Conversely, in the reversed lateralised group, both participants (100%) showed significantly dominant activation in their visuospatial cerebral activation for the three statement conditions. There was no indication of differences between participants in the typical lateralised and the reversed lateralised group, when both accuracy and RTs for the three statement conditions were compared (smallest $U = 6.00$, $Z = -1.51$, $p > .05$).

4.3 Discussion

The aim of Experiment 3 was to establish the pattern of language and visuospatial cerebral lateralisation in neurotypical adults and then use this information to examine relative recruitment of verbal and visuospatial processes during auditory verification of verbal, visual and ambiguous statements. Within the recruited sample, most participants (72.00%) exhibited the typical pattern of cerebral organisation, with dominant left hemisphere activation on the language (word generation) task and dominant right hemisphere activation on the visuospatial (visual short-term memory) task. A smaller proportion of participants exhibited atypical lateralisation for language and visuospatial functions (16.00% same-side, 8.00% reversed organisation, 4.00% bilateral language functions). This breakdown of typical and atypical patterns of lateralisation falls within the range reported in other fTCD studies involving general population samples (Flöel et al., 2001; Flöel et al., 2005; Groen et al., 2012; Whitehouse & Bishop, 2009). Finding individual differences in cerebral lateralisation reinforces the idea that accounting for such variability would enhance neuroimaging studies examining the role of language and visuospatial functions to the performance of any cognitive task.

By assessing language and visuospatial cerebral organisation for each participant, it was predicted that verification of the verbal, visual and ambiguous verbal-visual statements would be differentiated by language and visuospatial processing demands, captured across the two hemispheres. The fTCD data summarised in Figure 3.6 indicates that this was not the case. Most participants with typical cerebral lateralisation showed dominant activity in their (left) language cerebral hemisphere during verification of all three statement types, verbal, visual
and ambiguous. Conversely, participants with the reversed lateralisation showed pronounced activation in their (left) visuospatial cerebral hemisphere across the three types of statements. These results are intriguing since favourable use of language or visuospatial processing strategies during auditory comprehension appeared to be differentiated based on the pattern of cerebral organisation, rather than statement content.

While it was predicted that the ambiguous statements could be solvable using language or visuospatial hemispheric processing, the directionality of cerebral organisation appeared to influence how people generally approached verification performance. Intriguingly, there was no indication of behavioural (accuracy/RT) differences between participants in the typical and the reversed lateralised groups across the verbal, visual and ambiguous verification statements. Put differently, pronounced engagement of language processing strategies in the typical lateralised group and dominant recruitment of visuospatial processing strategies in the reversed lateralised group did not seem to impact differences in verification performance. Given the small number of cases in the reversed lateralised group, further work is required to better understand how atypical cerebral organisation is linked to cognitive biases for visuospatial processing strategies.

In contrast with predictions, there were no differences in the strength and profile of hemispheric activity during auditory verification of verbal, visual and ambiguous statements, for participants in either the typical or reversed lateralised groups. The lack of differences in LIs across the verbal, visual and ambiguous conditions contrasts with other fMRI studies revealing clear hemispheric effects when auditory statements were increased on either verbal complexity (Keller et al., 2001; Prat et al., 2007) or on visuospatial demands (Bottini et al., 1994; Kosslyn et al., 1995; Mellet et al., 1998). For instance, Just et al. (1996) and Keller et al. (2001) found greater left hemisphere activation in language (inferior frontal, superior temporal) regions when participants solved statements with complex (lexical/syntactic) clauses (e.g. “The reporter that the senator attacked admitted the error”), compared to a simple statement condition (e.g. “The reporter attacked the senator and admitted the error”). Conversely, other studies have documented greater right hemisphere activation during tasks requiring listening to sequential spatial instructions to assemble a cube design (e.g. “right-down-down-back-back-back-up-up-back-back-right”) (Mellet et al., 1996) and evaluating the plausibility of
(imaginable) statements (e.g. “The old man had a head full of dead leaves”) (Bottini et al., 1994), relative to control conditions. There are two plausible explanations for our discrepant results.

Compared to the aforementioned studies, relatively longer statements (9 to 15 words) in our task might impose demands on phonological short-term and working memory stores associated with subvocal rehearsal, temporary storage and manipulation of spoken information (for reviews, see Baddeley, 2010; Caplan & Waters, 1999). This appeared to be more evident for the participants with typical lateralisation, who showed overriding activity in their language cerebral hemisphere across the three statement conditions, possibly reflecting increased demands on phonological encoding and/or manipulation of auditory information. This suggestion also seems to fit with results from Chapter 3 (Experiment 2), where dual-task articulatory suppression resulted in equivalent performance costs across the three statement conditions, where the verbal statements were not more adversely affected than the visual or the ambiguous statements.

It is possible that for long auditory statements, individuals (particularly those with typical cerebral lateralisation) might rely heavily on phonological language strategies to prevent information decay from short-term/working memory, irrespective of visuospatial content. However, this argument that longer auditory statements may favour verbal processing is not supported by consideration of the Just et al. (2004b) and Kana et al. (2006) studies. An analysis of their statement stimuli from the verification task revealed that the high-imagery statements generally contained significantly greater number of words than the low-imagery statements (Just et al. [2004b], $p = .003$; Kana et al. [2006], $p = .004$). Yet, enhanced visuospatial activation was evident for statements in the high-imagery versus low-imagery condition, for the neurotypical samples.

Another possibility is that failure to detect distinct hemispheric effects across the three statement types could be related to our fTCD verification task design. Referring to Figure 3.5, the baseline rest period seemed to contain residual cerebral activity from the experimental period, which can be seen 12 s before the epoch onset. Figure 3.5, also suggests that the preparatory ‘clear mind’ beep tone contributed to a slight increase in blood flow 5 s preceding the epoch onset. Consequently, the rest period of the verification task did not provide an adequate measure of baseline cerebral activity.
In the next chapter, these methodological issues were addressed by modifying epoch parameters of our verification task to ensure cerebral activity reached baseline levels during the rest period and also adapting the current auditory task to a reading format. If the auditory mode of presentation encouraged verbal encoding and representation across the three statement types, it was reasoned that a visual display of written statements could potentially ‘free up’ or reduce linguistic demands, especially for the visual and the ambiguous statements.
Chapter 5: Can a Reading Verification Task Provide Adequate Assessment of Cerebral Lateralisation and Thinking Style?
Introduction

The mental processes involved in reading have been extensively studied, and it has been argued that written information can be represented using two distinct cerebral networks underlying verbal processing, or alternatively, visuospatial processing to construct meaning (Binder et al., 2005; Sadoski & Paivio, 2004). During reading, language functions such as phonological, lexical and semantic processes can be used to subvocally rehearse words and link the sequence of words together to access meaning from verbal knowledge (Harm & Seidenberg, 2004; Perfetti & Stafura, 2014). When texts convey spatial descriptions or elicit vivid imagery, visuospatial functions provide an alternate route of processing, where visuospatial working memory can be used to form, maintain and access images from long-term memory to generate an image of written content (De Beni et al., 2005; Wooley, 2010).

Following on the idea that written content can influence whether verbal and visuospatial mental representations are drawn to extract meaning, the current experiment employed a visual presentation mode for the verification task that was previous administered auditorily in Chapter 4 (Experiment 3). Of central interest was whether adults from the general population would show a distinct profile of language and visuospatial hemispheric activity for the verbal, visual and ambiguous verification statements under this alternative mode of presentation. The reading sentence verification task administered in this study was designed to examine whether failure to find differential hemispheric effects across the three statement conditions in Chapter 4 was predominantly driven by verbal encoding due to the long auditory statement length.

With the visual mode of presentation, each statement from the reading verification task was displayed in printed form on a computer screen until a true/false response was made. In this experiment, the rest period of the reading verification task was also extended (from 15 s) to 22 s and the ‘clear mind’ preparatory phase removed to ensure cerebral blood flow remained at baseline levels prior to the epoch onset. These modifications were designed to provide better estimates of cerebral lateralisation during the reading verification task. If the visual mode of presentation is more amenable to capturing strategy differences across the three statement types, most participants are predicted to exhibit dominant activity in their language
hemisphere on the verbal statements, but show dominant visuospatial activity on the visual statements. It is also predicted that the ambiguous verification statements will predominantly be solved using the language hemisphere for some participants and the visuospatial hemisphere for other participants.

**Experiment 4**

5.1 **Method**

*Participants*

Participants were 25 undergraduate students (17 females, 8 males) from the University of Western Australia (\(M_{\text{age}} = 20.56\) years, \(SD = 4.03\) years), who did not self-report a history of neurodevelopmental or medical conditions. None of the participants had taken part in any of the earlier experiments. There were 22 right-handed (15 female, 7 male), 1 left-handed (female) and 2 ambidextrous (1 female, 1 male) individuals, as measured by the 4-item short version of the Edinburgh Handedness Inventory (Veale, 2014).

*Apparatus*

The apparatus used in the current study was the same as that described in Chapter 4, with the main difference being that the reading sentence verification task was programmed using Presentation Software (Neurobehavioural Systems).

*Task Design and Procedure*

The reading sentence verification task contained the same 6 practice trials and 84 test trials (28 verbal, 28 visual, 28 ambiguous) from Chapter 4, except the statements were presented in written format (size 14 font). The timeline for the reading sentence verification task is depicted in Figure 4.1. Each trial began with a beep tone, and immediately after, a statement was presented centrally on screen, along with true and false options beneath the statement. Participants were asked to verify the truth of each statement, using their left or right index finger to respectively, make true or false responses on a keyboard. Immediately after a response was made, the trial ended with a 22 s rest period, during which the word “rest” appeared on screen.
Trials for the verbal, visual and ambiguous verbal-visual statements were interleaved, as described in Chapter 4. Different to Chapter 4, RTs on the reading verification task were calculated from the onset of the statement presentation to when a true/false response was made. For each statement condition, accuracy (total correct out of 28) and median RTs (on correct trials) were calculated for each participant. All participants completed the reading sentence verification task first, followed by the two lateralisation (word generation and visual short-term memory) tasks, which were counterbalanced in order of presentation across the sample.

Data Analyses

The data analyses were identical to those reported for Chapter 4. Imaging and behavioural (accuracy and RT) data for all three experimental tasks were screened for normality using Normal P and Q-plots, with univariate outliers curtailed, as described in the previous chapters. Relationships between all variables were approximately linear. Parametric assumptions of normality were confirmed by findings of non-significant Kolmogorov Smirnov statistics for all variables ($p > .05$) (Field, 2009).

5.2 Results

fTCD Data Checks

All participants had a minimum of 70% of epochs with acceptable recordings, and mean rates of acceptable trials were high across the word generation ($M = 89.91\%, SD = 5.13\%$), visual short-term memory ($M = 88.60\%, SD = 6.21\%$)
and reading sentence verification \((M = 96.62\%, SD = 4.98\%)\) tasks. For each task, mean LIs were found to have reasonable odd-even split half reliability (smallest \(r = .71\)).

### Cerebral lateralisation

Scatter plots of individual mean LIs for the word generation and visual short-term memory tasks are shown in Figure 4.2. Similar to Chapter 4, most participants \((n = 17, 68.00\%)\) showed typical cerebral organisation, with language functions in the left hemisphere and visuospatial functions in the right hemisphere (Figure 4.2, bottom left quadrant). One participant \((4.00\%)\) exhibited the reversed pattern of lateralisation (Figure 4.2, top right quadrant). The remaining participants displayed same-side lateralisation for both tasks \((n = 5, 25\%)\) (Figure 4.2, top left and bottom right quadrants), or bilateral activity for one task \((n = 2, 8.00\%)\) (see Figure 4.2, where the confidence intervals intercept either the vertical or horizontal cut-off).

**Figure 4.2.** Scatter plots of language and visuospatial LIs (and 95% confidence intervals) for the word generation and visual short-term memory tasks. Bilateral activation was deemed where participant confidence intervals overlapped with zero.

### Reading Sentence Verification fTCD Epoch Parameters

Behavioural data for the reading sentence verification task were assessed to estimate the time period for comprehension during which participant made true/false judgments and to estimate the epoch length, for fTCD analyses. Using two one-way ANOVAs, accuracy and median RTs for the verbal, visual and ambiguous verbal-
visual statements were analysed, with Bonferroni adjusted post hoc t-tests ($\alpha = .017$) conducted where differences as a function of statement condition were found.

The analysis on accuracy data revealed a significant difference in difficulty level for the verbal ($M = 21.96, SD = 2.92$), visual ($M = 21.96, SD = 2.26$) and ambiguous ($M = 24.00, SD = 2.61$) statements, $F(2, 72) = 5.08, p < .05, r = .35$. However, post-hoc tests were all non-significant (smallest $p = .02$). Analyses comparing RT data confirmed that the verbal ($M = 8.22$ s, $SD = 1.86$ s), visual ($M = 9.39$ s, $SD = 2.69$ s) and ambiguous ($M = 7.94$ s, $SD = 2.51$ s) statements had roughly similar completion times, $F(2, 72) = 2.63, p = .08, r = .26$.

Since behavioural data did not indicate substantial differences across the three statement types, the same epoch parameters were entered into dopOSCCI for analysing fTCD data for all three statement conditions. For each participant, overall average RT was calculated across the three statement conditions ($M = 8.52$s, $SD = 2.43$ s), with standard deviations of the lower- and upper-bounds used to approximate the time period during which comprehension occurred (i.e. 6.09 to 10.95 s). The epoch length for the reading sentence verification task was estimated to end 33 s after the trial onset (see Figure 4.1).

The period of interest for the reading sentence verification task was defined 3-13 s from the epoch onset, based on inspection of the language-visuospatial difference functions for the verbal, visual and ambiguous statements. This peak period of interest appeared to overlap with the comprehension phase during which participants made true/false responses.

**Cognitive Preferences during Verification of Visually Presented Statements**

Cognitive preferences on the reading sentence verification task were examined only for participants for whom language and visuospatial functions were lateralised to separate hemispheres (17 typical lateralised, 1 reversed). Figure 4.3 shows the mean MCA activity to language and visuospatial hemispheres, and the difference cerebral blood flow functions (language minus visuospatial activity). Intraclass correlations conducted on the language-visuospatial difference functions, over the period of interest revealed a moderate fit, $mean \ ICC = .70, CI = .09$ to $.87$, $p < .05$, indicating similar patterns of blood flow changes to the language and visuospatial cerebral hemispheres, across the three statement conditions.
To identify the dominant cerebral hemisphere (language or visuospatial) activated on the reading sentence verification task, LIs for the three statement conditions were assessed only for participants with typical and the reversed pattern of cerebral lateralisation.
Figure 4.3. Average activation plots during reading verification of verbal (left panel), visual (middle panel) and ambiguous (right panel) statements. Mean MCA activity in the language (blue) and the visuospatial (red) hemisphere, and cerebral blood flow difference between the language and visuospatial hemispheres (black dotted line) were plotted only for participants with these cerebral functions lateralised in different hemispheres (17 typical lateralised, 1 reversed lateralised).
Figure 4.4. Mean LIs (and 95% confidence intervals) for the verbal, visual and ambiguous statements from the reading verification task, for participants in the typical (top panel) and the reversed (bottom panel) lateralised groups. In the typical lateralised group, positive LIs indicate greater language activation while negative LIs indicate greater visuospatial activation. For the only participant in the reversed lateralised group, positive LIs indicate greater visuospatial activation while negative LIs indicate greater language activation. Where the 95% confidence interval overlapped with zero, participants were deemed to have bilateral activation.
For the typical lateralised group, mean LIs for the verbal ($M = 3.58, SD = 2.56$), visual ($M = 3.61, SD = 1.64$) and ambiguous verbal-visual ($M = 2.27, SD = 1.91$) statements were all significantly positive (smallest $t = 4.90, p < .05$, $d = 1.19$), and, were similar in magnitude across the three statement types, $F(2,48) = 2.56, p = .09, d = .31$ (Figure 4.4, top panel). In the only participant with reversed lateralisation, mean LIs for the verbal ($M = -1.90$), visual ($M = -2.54$) and ambiguous ($M = -2.14$) statements were all negative, and were quantitatively similar across the three statement types (Figure 4.4, bottom panel).

As seen in Figure 4.4, most participants with typical cerebral lateralisation exhibited greater blood flow to their language rather than visuospatial cerebral hemisphere across all three statement conditions (verbal = 94.12%, visual = 100.00%, ambiguous = 82.36% of participants). Similarly, the only participant with the reversed lateralisation (Figure 4.4, bottom panel) exhibited greater cerebral activity in the language relative to visuospatial hemisphere during reading verification of verbal, visual and ambiguous statements.

5.3 Discussion

By extending the rest period for the verification task and removing the ‘clear mind’ preparatory phase, cerebral activity was successfully maintained at baseline levels prior to the epoch onset (see Figure 4.3), reflecting an improvement in our fTCD task design from Chapter 4 (Experiment 3). In contrast with predictions, task modifications to a reading format did not influence the pattern of results. Among the 68.00% of participants with language and visuospatial functions localised in different cerebral hemispheres, a majority showed dominant but similar activity in their language hemisphere across the verbal, visual and ambiguous statements (see Figure 4.4), similar to Chapter 4.

Although the written format was intended to reduce demands on phonological verbal processing of long auditory statements, reading verification of visual statements was not marked by enhanced visuospatial (or reduced language) hemispheric activity, relative to verbal statements. Furthermore, the set of ambiguous statements were found to be predominantly solved using language hemispheric activation, challenging the notion that these statements are equally amenable to verbalising and visualising processing, as found using self-report strategy ratings in Chapter 2 (Experiment 1). Where participants with the reversed (atypical) pattern of
cerebral lateralisation favoured dominant recruitment of visuospatial hemisphere processing in *Chapter 4 (Experiment 3)*, the only participant with reversed lateralisation in this study preferentially recruited language hemisphere processing during across all three statement types. The single case in the reversed lateralised group makes it difficult to comment on whether the visual format of the reading task encouraged greater use of language processing solutions.

The lack of differences in the strength and directionality of LIs for the verbal, visual and ambiguous verification statements, and the highly correlated MCA language-visuospatial cerebral blood flow trajectories, are outcomes consistent with the fTCD results from *Chapter 4*. These results suggest the possibility that comprehension of verbal, visual and ambiguous statements might draw more heavily on shared linguistic processing mechanisms (Meyer, Spray, Fairlie, & Uomini, 2014; Uomini & Meyer, 2013), than had been initially expected. Using fMRI, studies have identified some degree of overlap in cerebral responses during reading of verbal statements associated with verb interactions (e.g. “the scientist spoke to the student”) and visual statements conveying position, motion or colour information (e.g. “The white feather was under the tree”) (Anderson et al., 2016; Huth, Nishimoto, Vu, & Gallant, 2012). Common cerebral responses were identified in sensory regions (e.g. anterior visual cortex, superior fontal gyrus) for the verbal and visual statements. It is plausible that verbal statements are processed visuospatially to some degree (e.g. picturing a scientist talking to a student), even if people do not report the use of such processes. While this explanation potentially accounts for the lack of statement effects in visuospatial activity, it does not fully explain why our verbal, visual and ambiguous verification statements overlapped substantially in language activation in this study.

Nevertheless, in the Kana et al. (2006) study, there is reason to speculate that sentence verification of low- and high-imagery statements should produce a different pattern of hemispheric activation, particularly in neurotypical individuals. More specifically, elevated activity was observed in several right-hemisphere (superior parietal, precentral sulcus, interior temporal) regions supporting visuospatial functions during comprehension of statements in the high-imagery condition, when compared to the low-imagery condition. A greater rightward bias in hemispheric activity could be interpreted as increased reliance on visuospatial processing strategies in the neurotypical individuals on statements conveying visual imagery.
One possibility is that limited spatial resolution of fTCD (Deppe et al., 2000; Jansen et al., 2004) might not permit measurement of subtle, regional differences in cerebral activity associated with completing verbal, visual and ambiguous statements, leading to a lack of laterality effects across the three statement types.

Another possibility is that individuals from the general population might exhibit limited variability in how they actually approach reading comprehension, even though they might subjectively report pronounced use of visualising strategies, particularly on visual verification statements (in Chapter 2, Experiment 1). In comparison, if individuals selected for high levels of autistic-like traits show enhanced visuospatial abilities (as found in Chapter 3, Experiment 2), they might be more reliant on visuospatial processes during sentence comprehension than that reported in the current experiment and in Chapter 4.

In the next chapter, fTCD imaging was used to examine whether individuals selected for high levels of autistic traits favour visuospatial representation of sentence information relative to those with low levels of autistic traits, as predicted by the TiP account of autism. If the TiP account is supported, group differences in hemispheric mediation are expected, where the high autistic trait sample should favour greater recruitment of visuospatial than verbal cerebral processing relative to the low autistic trait sample, across the three statement types.
Chapter 6: Functional Transcranial Doppler Assessment of Cerebral Laterality and Thinking Style in Adults with Autistic-Like Traits
Introduction

Advances in functional neuroimaging have allowed researchers to examine mental processing strategies that underlie how individuals on the autism spectrum approach cognitive tasks within the TiP framework. Using neuroimaging techniques such as fMRI, studies have demonstrated that, where neurotypical adults show a pronounced network of activation in frontal-temporal (e.g. inferior frontal, superior temporal) areas during a range of verbal tasks, activation and synchronisation of these language networks is considerably reduced in autistic individuals (Gaffrey et al., 2007; Gervais et al., 2004; Harris et al., 2006; Just et al., 2004a; Kleinhans, Müller, Cohen, & Courchesne, 2008, Williams et al., 2013). In comparison, autistic individuals show stronger activation in parietal and occipital regions (e.g. superior parietal, extrastriate cortex) relative to their neurotypical counterparts during visuospatial task performance (Damarla et al., 2010; Keehn et al., 2008; Manjaly et al., 2007; Ring et al., 1999; Silk et al., 2006; Soulières et al., 2009).

Competing cognitive theories of autism have often interpreted over activation in the visuospatial network to reflect enhanced detailed-oriented processing (Frith & Happé 1994) or superior low-level perception (Mottron, Dawson, Soulières, Hubert, & Burack, 2006), however, these theories do not sufficiently explain why under activation in the language network is prominent in ASC. As described previously in this thesis, the TiP account assumes that people on the autism spectrum show a cognitive bias towards visuospatial processing and away from verbal processing. Within the TiP framework of autism, diminished language activation is understood to arise from spontaneous, preferential recruitment of visualising processing strategies (leading to pronounced visuospatial activation) on cognitive tasks, even though verbal-based tasks might be more effectively solved using verbalising strategies (Kunda & Goel, 2011). In having a discrepant profile of stronger visuospatial than verbal abilities, autistic individuals may also become more reliant on visualising over verbalising processing strategies, potentially explaining the imbalance between over participation of visuospatial regions and under activation in language regions.

While the conceptual boundaries between cognitive preferences and abilities have not been explicitly defined within the TiP framework, one important extension is to postulate that ambiguous test measures can potentially identify the nature of verbal-visual thinking biases in autism. Using ambiguous tasks, of which verbal or
visuospatial processing strategies work equally well for generating task solutions, two fMRI studies have examined how autistic and neurotypical adults rehearse and update strings of letters (Koshino et al., 2005) and faces (Koshino et al., 2008) in working memory. Letter stimuli in the Koshino et al. (2005) paper were ambiguous because the information could be processed phonologically using language, or encoded orthographically for letter shape using visuospatial processing. Similarly, face stimuli from the Koshino et al. (2008) paper could be rehearsed using verbal descriptors (e.g. elderly, bald) or remembered using visuospatial cues (e.g. shape, size) relating to facial features.

In the Koshino et al. (2005, 2008) studies, the autistic adults were found to display regional as well as hemispheric differences in the profile of cerebral activity during working memory performance. Relative to their neurotypical peers, the ASC group showed lower activation in left hemisphere frontal (e.g. inferior frontal, dorsolateral) regions, coupled with greater right hemisphere parietal (e.g. lateral premotor, superior parietal) activation. These results were interpreted by Koshino et al. (2005, 2008) as reflecting a tendency for autistic individuals to favour (parietal) visuospatial processing modalities when rehearsing ambiguous information in working memory, whereas, the neurotypical controls engaged (frontal) language processing. However, the TiP framework does not provide an explanation for why autistic individuals often exhibit differences in the distribution of cerebral activity in the left and right hemispheres, relative to their neurotypical counterparts.

Although language skills are most commonly lateralised in the left hemisphere of the brain, with visuospatial skills more likely dominant within the right hemisphere (Price, 2012; Thiebaut de Schotten et al., 2011; Whitehouse & Bishop, 2009), there is accumulating functional evidence for differences in hemispheric division in ASC (for reviews, Herringshaw et al., 2016; Preslar, Kushner, Marino & Pearce, 2014). For example, during sentence processing tasks (mainly examining language functions), autistic adults show reduced cerebral blood flow to the left hemisphere in frontal and temporal regions, relative to neurotypical comparison groups (Gervais et al., 2004; Just et al., 2004a; Müller et al., 1998). Diverging from the typical pattern of left-side language functions, studies have also documented preferential recruitment of the (reversed) right-side frontal-temporal regions (Boddaert et al., 2003; Redcay & Courchesne, 2008) or even a more bilateral distribution of language activity (Wang, Lee, Sigman, & Dapretto, 2006) in ASC.
Weak or atypical (reversed, bilateral) lateralisation in ASC could indicate the possibility of atypical language organisation, or the use of compensatory maladaptive processing strategies. However, other studies have failed to find any evidence of atypical language lateralisation in ASC (Gage, Siegel, & Roberts, 2003; Whitehouse & Bishop, 2008). Variable findings could reflect confounding issues with comorbid conditions in the autistic participants, which could, in part, influence the development of language cerebral dominance (Preslar et al., 2014).

Interpretations on the directionality of visuospatial functions in autism are also complicated by the possibility of atypical cerebral organisation. In a meta-analysis (Samson, Mottron, Soulières, & Zeffiro, 2012) examining visuospatial functional networks, autistic individuals were found to exhibit elevated activity in the right hemisphere parietal and temporal regions relative to neurotypical controls on a range of visual processing (e.g. object, face perception, reading3) tasks. Finding a greater rightward bias in cerebral activation in the autistic sample could reflect a more extreme development of visuospatial lateralisation in the expected (right) hemisphere. Interestingly, when between-group comparisons were confined to reading tasks, the autistic sample showed a divergent pattern of laterality, marked by higher activation in the right hemisphere, whereas, the neurotypical control group showed greater activity in their left hemisphere. Given mixed results on language laterality in ASC, the findings by Samson et al. (2012) could reflect one of two possibilities: (1) atypical language laterality in ASC, where individuals preferentially engage in right hemisphere language processing during reading, or, (2) typical language and visuospatial laterality in ASC, with preferential engagement in right hemisphere visuospatial processing during reading.

In the current experiment, fTCD imaging was utilised to clarify issues on language and visuospatial cerebral laterality and to investigate the TiP account of autism in a sample of adults from the general population with elevated but subclinical levels of autistic-like traits. As noted previously in the thesis, individuals who report high levels of autistic traits on the AQ questionnaire have been reported

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3 In the meta-analysis by Samson et al. (2012), studies examining reading were included due to the visual modality of statement presentation. However, in this thesis I argue that reading is an ambiguous verbal-visual task. Group differences in distribution of hemispheric activity found in Samson et al. (2012) potentially lend support to the idea of enhanced (right-side) visuospatial processing in the autistic group, but greater (left-side) linguistic processing in their neurotypical counterparts.
to display profiles of performance on behavioural and neuroimaging activity similar to people with clinically diagnosed ASC (Nummenmaa et al., 2012; Von dem Hagen et al., 2011). To capitalise on benefits of accessing larger samples and avoiding issues with comorbid diagnoses in ASC (Landry & Chouinard, 2016), participants selected for low versus high AQ scores were recruited to investigate cerebral laterality for language and visuospatial functions and also test for differences in strategy consistent with the TiP account.

Given variable findings on the pattern of cerebral lateralisation in ASC, fTCD was used to localise the cerebral hemisphere(s) specialised for language and visuospatial functions among the low and high autistic traits samples. Similar to Chapters 4 and 5, the gold standard word generation (Bishop et al., 2009) and visual short-term memory (Whitehouse et al., 2009) tasks were used to compare the strength and directionality of language and visuospatial laterality for the two AQ groups. Of central interest was whether the proportion of participants with the typical pattern of lateralisation in the high AQ group differed from the proportion in the low AQ group, or if group differences were evident in strength of laterality for either one of these (language or visuospatial) functions. Following Chapter 3, the cognitive profile of verbal and visuospatial abilities were also assessed for the low and high autistic trait samples using standardised Wechsler measures (WAIS-IV Vocabulary, Visual Puzzles). Under the TiP framework, individuals with high levels of autistic traits were predicted to outperform their low autistic trait counterparts on measures of visuospatial abilities, but underperform on measures of verbal abilities.

By characterising the pattern of cerebral lateralisation for individuals in the low and high autistic trait groups, fTCD was then used to determine the cerebral hemisphere (language, visuospatial) preferentially activated during reading verification of verbal, visual and ambiguous verbal-visual statements. Previous neuroimaging studies in ASC have generally documented increased cerebral participation of parietal-occipital visuospatial regions (Just et al., 2004a; Kana et al., 2006) as well as showing more pronounced right hemisphere bias in cerebral activity during sentence processing (Mason, Williams, Kana, Minshew, & Just, 2008; Müller et al., 1999; Samson et al., 2012; Takeuchi et al., 2004; Wang et al., 2006), understood to reflect a visual style of thinking. Based on this research and the TiP account, participants with high levels of autistic traits were predicted to show greater activation in their visuospatial (than language) cerebral
hemisphere relative those with low autistic traits across all three statement conditions, with most pronounced differences observed on the ambiguous statements.

**Experiment 5**

### 6.1 Method

*Participants*

Participants were selected from a screening exercise, in which 1061 undergraduate students (\(M_{\text{age}} = 20.56\) years, \(SD = 4.03\) years) from the University of Western Australia completed the AQ to fulfill part of their course requirement. Individuals who scored in the bottom (AQ score < 95) and the top (AQ score > 125) quintiles of the AQ distribution were invited to complete further testing, as in Chapter 3. There were 26 participants in the low AQ group and 24 participants in the high AQ group, who were matched on age, gender distribution and on handedness, as assessed by the 4-item short form of the Edinburgh Handedness Inventory (Veale, 2014) (see Table 5.1). All participants were fluent in English, and reported no history of any neurodevelopmental, psychiatric or medical condition.

**Table 5.1. Participant characteristics (means, with standard deviations presented in parentheses).**

<table>
<thead>
<tr>
<th></th>
<th>Low AQ  ((n = 26))</th>
<th>High AQ  ((n = 24))</th>
<th>Group comparison statistics</th>
</tr>
</thead>
<tbody>
<tr>
<td>Gender (female: male)</td>
<td>18:8</td>
<td>13:11</td>
<td>(\chi^2(1) = 1.20, p = .27, \Omega = .15)</td>
</tr>
<tr>
<td>Age (years)</td>
<td>20.00 (3.66)</td>
<td>19.25 (1.36)</td>
<td>(t(48) = .95, p = .35, d = .27)</td>
</tr>
<tr>
<td>AQ score</td>
<td>82.96 (4.95)</td>
<td>131.92 (4.90)</td>
<td>(t(48) = 35.11, p &lt; .05, d = 10.13)</td>
</tr>
<tr>
<td>Handedness</td>
<td>3: 2: 21</td>
<td>1: 2: 21</td>
<td>(\chi^2(2) = .92, p = .63, \Omega = .14)</td>
</tr>
</tbody>
</table>

**Verbal abilities**

- WAIS-IV Vocabulary: 12.23 (1.14) vs. 10.96 (3.07), \(t(48) = 1.91, p = .07, d = .71\)
- Word generation (no. words): 104.42 (13.17) vs. 87.04 (14.93), \(t(48) = 4.37, p < .05, d = 1.26\)

**Visuospatial abilities**

- WAIS-IV Visual Puzzles: 11.73 (2.34) vs. 11.42 (2.17), \(t(48) = .49, p = .63, d = .14\)
- Visual short-term memory: 17.81 (1.72) vs. 17.75 (1.70), \(t(48) = .12, p = .91, d = .03\)
Apparatus

The fTCD equipment was set up as described in Chapter 5. Recordings of blood flow activity to the left and right MCAs were measured through the temporal bone windows during the three experimental tasks.

Experimental Tasks and Procedure

The three experimental tasks were identical to those described in Chapter 5. All participants completed the reading sentence verification task, followed by the word generation and visual short-term memory tasks, which were counterbalanced in order of presentation within the low and high AQ groups. Participants then completed the WAIS-IV Vocabulary and Visual Puzzles subtests (Wechsler, 2008), described in detail in Chapter 3.

Data Analyses

The fTCD data were analysed the same way as in Chapter 5. Parametric assumptions of normality were confirmed for imaging and behavioural (accuracy and RT) data for all three experimental tasks. All participants had at least 70% of epochs with suitable recordings across the three tasks, and were included in the analyses. For each task, split-half reliability of the LIs were computed for the two AQ groups, by correlating blood flow velocity over the odd- and even-numbered trials. Split half reliability was acceptable for the word generation (low AQ $\alpha = .87$, high AQ $\alpha = .75$), visual short-term memory (low AQ $\alpha = .77$, high AQ $\alpha = .74$) and the reading sentence verification task (low AQ $\alpha = .82$, high AQ $\alpha = .80$).

6.2 Results

Verbal and Visuospatial Abilities

Independent sample t-tests were conducted to assess whether participants with low and high levels of autistic traits showed behavioural differences in their pattern of performances on the verbal (WAIS-IV Vocabulary, word generation) and visuospatial assessment measures (WAIS-IV Visual Puzzles, visual short-term memory). These results are summarised in Table 5.1.

There were no significant group differences in visuospatial abilities on the WAIS-IV Visual Puzzles subtest or on the visual short-term memory task. With regard to the verbal ability measures, a group difference in word generation
performance was observed, where participants in the high AQ group produced significantly fewer words compared to the low AQ group (see Table 5.1). There was also a non-significant trend towards poorer verbal abilities in participants with high levels of autistic traits on the WAIS-IV Vocabulary subtest, relative to their low autistic trait counterparts.

*Reading Sentence Verification: Behavioural Results*

Behavioural data from the reading sentence verification task were assessed using 2 (AQ group) x 3 (statement conditions) ANOVAs, with analyses conducted separately for accuracy and RT data (see Table 5.2 for descriptive statistics). Overall, these analyses did not reveal group differences in verification performance across the three sets of statements. None of the main effects of AQ group and interaction effects involving AQ group and statement condition were significant for the accuracy (largest $F(1, 48) = 1.97, p = .17, \eta^2_p = .04$) and RT (largest $F(2, 96) = .77, p = .47, \eta^2_p = .02$) analyses. However, significant main effects of statement condition were evident for the accuracy ($F(2, 96) = 8.31, p < .05, \eta^2_p = .15$) and RT analyses ($F(2, 96) = 26.84, p < .05, \eta^2_p = .36$). Bonferroni post hoc ($\alpha = .017$) tests indicated that participants with low and high autistic traits commonly completed the ambiguous statements faster and more accurately, compared to the verbal and the visual statements.

Table 5.2. *Summary statistics on the reading sentence verification task for participants with low and high AQ scores (standard deviations presented in parentheses).*

<table>
<thead>
<tr>
<th></th>
<th>Low AQ ($n = 26$)</th>
<th>High AQ ($n = 24$)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Mean accuracy (out of 28)</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Verbal</td>
<td>23.08 (2.51)</td>
<td>22.38 (2.79)</td>
</tr>
<tr>
<td>Visual</td>
<td>22.15 (2.56)</td>
<td>21.96 (2.61)</td>
</tr>
<tr>
<td>Ambiguous</td>
<td>24.42 (2.10)</td>
<td>23.41 (2.22)</td>
</tr>
<tr>
<td><strong>Median RT (s)</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Verbal</td>
<td>8.55 (1.84)</td>
<td>8.82 (1.80)</td>
</tr>
<tr>
<td>Visual</td>
<td>9.20 (1.88)</td>
<td>9.83 (2.08)</td>
</tr>
<tr>
<td>Ambiguous</td>
<td>7.95 (1.36)</td>
<td>8.11 (1.84)</td>
</tr>
</tbody>
</table>
Language and visuospatial cerebral lateralisation

Average left and right MCA activation plots and the difference (left hemisphere subtract right hemisphere) plots for the word generation and visual short-term memory tasks, are depicted in Figure 5.1, for the low and the high AQ groups. Intraclass correlation analyses conducted on the difference cerebral blood flow functions revealed similar time courses in the trajectory of activity for participants with low and high levels of autistic traits during word generation (mean ICC = .98, CI = .95 to .96, p < .05) and visual short-term memory (mean ICC = .53, CI = .15 to .83, p < .05), over the period of interest. Figure 5.1 also indicates that on a group level, the two AQ samples generally showed the typical pattern of activity with greater blood flow to the left (than right) hemisphere during word generation and greater activity in the right (than left) hemisphere for visual short-term memory.

Group differences in the strength of language and visuospatial lateralisation were assessed by comparing mean LIs for the word generation and visual short-term memory tasks (see Figures 5.1 and 5.2). The difference between low (M = 2.68, SD = 2.20) and high (M = 2.60, SD = 2.25) AQ groups on the word generation LI was not significant, t(48) = .13, p = .90, d = .04. However, for the visual short-term memory task, the high AQ (M = -1.95, SD = 2.57) group was found to a significantly less extreme mean LI, relative to the low AQ (M = -3.28, SD = 1.93) group, t(48) = 2.08, p < .05, d = .60. This can be observed in Figure 5.1 and also in Figure 5.2 (bottom left panel), where the high AQ group showed a smaller peak in blood flow to their right cerebral hemisphere relative to their left hemisphere during the period of interest, relative to the low AQ group.

A series of Pearson correlation coefficients were conducted to examine whether there was a relationship between the strength of cerebral laterality and behavioural performance on the verbal (word generation total words produced, WAIS-IV Vocabulary) and visuospatial measures (visual short-term memory total correct, WAIS-IV Visual Puzzles) tasks. However, none of these correlations were significant for participants in the low (largest r = -.25, p = .23) and the high (largest r = -.09, p = .67) autistic trait samples, even when data were collapsed for the two groups (largest r = .04, p = .80).
Figure 5.1. Average cerebral blood flow velocity changes to the left (blue) and right (red) MCAs during word generation and visual short-term memory task performance, for participants with low (left panel) and high (right panel) AQ scores. The difference function (black dotted line) depicts left MCA subtract right MCA activity, where positive values indicate greater left hemispheric activity, while negative values represent greater right hemispheric activity. The period of interest for the word generation and visual short-term memory tasks were previously defined by Whitehouse and Bishop (2009) and used as referent points for which the trajectory of cerebral blood flow difference functions and the LIs were compared between the low and high autistic trait samples.
Individual mean LIs for the word generation and visual short-term memory tasks were plotted to identify the pattern and distribution of language and visuospatial cerebral laterality for the low and high autistic trait groups. Figure 5.2 shows that the higher (i.e. less negative) mean LI for the visual short-term memory task in the high AQ group reflects less right-side lateralisation for visuospatial functions relative to the low AQ group.4

In the low autistic trait sample, most participants (n = 22, 84.62%) showed typical lateralisation of cerebral functions, with greater left hemispheric activity during word generation, and greater right hemispheric activity during visual short-term memory (Figure 5.2, left panel, bottom left quadrant). In comparison, slightly over half the participants (n = 15, 62.50%) in the high autistic trait sample displayed the typical left-lateralised activity for word generation and right-lateralised activity for visual short-term memory (Figure 5.2, right panel, bottom left quadrant).

Atypical cerebral lateralisation was found in 4 participants in the low AQ group (3 same-side for both functions, 1 bilateral visuospatial function) and in 9 participants in the high AQ group (6 same-side for both functions, 3 bilateral visuospatial function). However, Fisher’s Exact test did not yield a significant difference in the frequency of typical and atypical cerebral lateralisation between the groups with low and high levels of autistic traits, p = .11, φ = .25.

4Although it is possible that participants with low AQ scores showed augmented or more pronounced right lateralisation on the visual short-term memory task than those with high AQ scores, this was not the case. The mean visual short-term memory LI for each of the low and high autistic trait groups were compared with the corresponding mean for general population samples (by collapsing data from participants recruited from Chapters 4 and 5). There was no evidence of a reliable difference in mean visual short-term memory LI for the low AQ group and the general population group, t(74) = .12, p = .90, d = .03. However, there was a non-significant trend towards a less pronounced (i.e. less negative) visual short-term memory LI in the high AQ group, relative to the general population sample, t(72) = 1.85, p = .07, d = .44.
**Figure 5.2.** Distribution of language and visuospatial cerebral lateralisation, for participants with low (left panel) and high (right panel) AQ scores on the word generation and visual short-term memory tasks, as measured by fTCD. Positive LI values reflect greater left hemisphere activity, while negative values indicate greater right hemisphere activity. Error bars represent 95% confidence intervals. Error bars which overlap with zero denote bilateral activation for the appropriate cognitive function.
Figure 5.3. Mean MCA blood flow changes to the language (blue) and visuospatial (red) hemispheres, for participants with low (left panel) and high (right panel) AQ scores during the reading verification task. The difference function (black dotted line) denotes differences in activity between the language and visuospatial hemispheres. The period of interest for the reading verification task was determined in Chapter 5 and was used to compare the trajectory of language-visuospatial hemispheric activity and statement LIs between the two AQ groups.
Cognitive Preferences during Reading Verification Performance

To evaluate the extent to which individuals with low and high levels autistic traits enlisted language or visuospatial hemispheric activation during sentence verification, only participants for whom language and visuospatial cerebral functions were laterised to separate hemispheres were included (low AQ \( n = 22 \) participants, high AQ \( n = 15 \)). Mean activation plots for the verbal, visual and ambiguous statements from the reading sentence verification task are depicted in Figure 5.3, for the two AQ groups.

Figure 5.3 shows that participants in the high and low AQ groups commonly showed greater activation in their language over visuospatial cerebral hemisphere, across the three statement conditions. Intraclass correlations also revealed significant consistency in the trajectory of language-visuospatial cerebral activity for the high and low AQ groups across the verbal (\( \text{mean ICC} = .97, \text{CI} = .80 \text{ to } .99, p < .05 \)), visual (\( \text{mean ICC} = .87, \text{CI} = -.10 \text{ to } .96, p < .05 \)) and ambiguous statements (\( \text{mean ICC} = .55, \text{CI} = -.22 \text{ to } .81, p < .05 \)) (see Figure 5.3).

Individual LIs for the reading sentence verification task were then subjected to a 2 (AQ group) x 3 (statement condition) ANOVA to assess the possibility that subtle group differences in style of processing might be captured by finding a significant main effect of AQ group and/or a significant AQ group x statement condition interaction. However, this analysis yielded only a significant main effect of statement condition, \( F(2, 70) = 17.91, p < .05, \eta^2_p = .34 \). Bonferroni adjusted post hoc (\( \alpha = .017 \)) tests revealed that the low and high AQ samples commonly showed less activity in their language relative to visuospatial hemisphere when verifying content in the ambiguous statements (Figure 5.3, bottom panels), compared to the verbal (Figure 5.3, top panels) and the visual (Figure 5.3, middle panels) statements.

Using the verification statement LIs, participants were categorised as using their language or visuospatial hemisphere during comprehension (see Figure 5.4). In the low AQ group, most participants exhibited greater blood flow to their language than visuospatial cerebral hemisphere during the verbal \( (n = 19, 86.36\%) \), visual \( (n = 20, 90.90\%) \) and ambiguous \( (n = 18, 81.82\%) \) statements (Figure 5.4, top panel). Similarly, for the high AQ group, most participants showed greater language (than visuospatial) cerebral activity across the verbal \( (n = 14, 93.33\%) \), visual \( (n = 14, 93.33\%) \) and ambiguous \( (n = 12, 80.00\%) \) statements.
Figure 5.4. Mean reading sentence verification LIs (and 95% confidence intervals) during the verbal, visual and ambiguous statement conditions, for the subset of participants with low (top panel) and high (bottom panel) AQ scores who had language and visuospatial functions lateralised to separate hemispheres. LIs for each statement condition are presented in terms of the dominant cerebral hemisphere (language, visuospatial) activated. Bilateral activation was denoted when the confidence interval overlapped with zero.
**Associations between cognitive abilities and strategy preferences on ambiguous statements**

The relationship between cognitive profile and strategy preferences on the ambiguous statements was explored by correlating WAIS-IV scaled scores on the verbal (Vocabulary) and visuospatial (Visual Puzzles) ability measures with LIs for the ambiguous statement condition. No significant correlations were found between degree of hemispheric activation on the ambiguous statements and verbal or visuospatial abilities, for the low and high AQ groups (all $p$s > .05, see Table 5.3).

**Table 5.3. Pearson correlations between Wechsler verbal (Vocabulary) and visuospatial (Visual Puzzle) abilities and laterality indices (LI) for the ambiguous statements, for the low and high AQ groups. Correlation analyses were only conducted for participants with language and visuospatial functions lateralised to separate hemispheres. All correlations had a $p$ value above .05.**

<table>
<thead>
<tr>
<th></th>
<th>Low AQ ($n = 22$)</th>
<th>High AQ ($n = 15$)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Verbal abilities</td>
<td>Visuospatial abilities</td>
</tr>
<tr>
<td>Ambiguous LI</td>
<td>.04</td>
<td>-.27</td>
</tr>
<tr>
<td></td>
<td>.24</td>
<td>-.11</td>
</tr>
</tbody>
</table>

**Associations between neural correlates of reading verification performance with language and visuospatial laterality**

Given the lack of AQ group differences in sentence verification LIs, the LI each statement condition was correlated with LIs on the word generation and visual short-term memory tasks to examine how hemispheric processing on each statement type related to cerebral laterality. These analyses were conducted for the low and high AQ groups collapsed, and were only on those participants with language and visuospatial functions lateralised to separate hemispheres.

For the word generation task, language LIs were significantly positively associated with LIs for the visual statement condition and the ambiguous statement condition. There was also a non-significant trend towards stronger language LIs and being associated with larger LIs for the verbal statement condition. None of the correlations involving the visual short-term memory task were significant.
Table 5.5. Pearson correlations between laterality indices (LI) on the sentence verification task with gold standard language (word generation) and visuospatial (visual short-term memory) measures, collapsed for the low and high AQ groups.

<table>
<thead>
<tr>
<th></th>
<th>Gold standard laterality measures</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Language LI</td>
</tr>
<tr>
<td>Verbal statement LI</td>
<td>.31</td>
</tr>
<tr>
<td>Visual statement LI</td>
<td>.33*</td>
</tr>
<tr>
<td>Ambiguous statement LI</td>
<td>.56*</td>
</tr>
</tbody>
</table>

*p < .05, two-tailed.

6.3 Discussion

By accounting for individual variability in cerebral lateralisation, Experiment 5 then examined the profile of language and visuospatial hemisphere activation associated with reading comprehension of verbal, visual and ambiguous statements in adults with low versus high levels of autistic-like traits under the TiP account.

Using fTCD imaging, most participants in the high autistic trait sample were found to exhibit typical hemispheric division, with language production specialised in the left hemisphere and visual short-term memory functions focused in the right hemisphere. Rates of typical cerebral lateralisation did not differ among the high (62.50%) and low (84.62%) AQ groups, and fell close to the range reported in large studies involving general population samples (50.00 to 77.00%) (Flöel et al., 2001; Flöel et al., 2005; Groen et al., 2012; Whitehouse & Bishop, 2009), while also consistent with results from Chapters 4 and 5 (68.00 to 72.00%). Our results contrast with other studies which have reported atypical lateralisation in autistic people relative to neurotypical control comparisons, particularly in the domain of language (Boddaert et al., 2003; Gervais et al., 2004; Just et al., 2004a; Müller et al., 1998; Redcay & Courchesne, 2008; Wang et al., 2006). Among the two fMRI studies using verbal fluency tasks similar to that administered in the current experiment, both have documented a departure from typical left-side language specialisation in ASC. Kleinhans et al. (2008) showed dominant right hemisphere frontal-temporal (inferior frontal gyrus, inferior temporal gyrus, middle temporal area, superior temporal gyrus, insular cortex) activity in autistic individuals, whereas Kenworthy et al. (2013) found weakened left hemisphere responses in the inferior frontal gyrus in this group.

Discrepant findings of typical language lateralisation in the high AQ sample might be explained by recruitment of individuals selected for high levels of autistic
traits, as opposed to a sample with clinically diagnosed ASC. It is plausible that autistic individuals who lie on the more extreme end of the spectrum could show a more pronounced departure from left hemisphere language specialisation than subclinical individuals with milder autistic traits. Atypical language lateralisation has also been linked to other clinical conditions where language skills are affected (e.g. developmental language disorder, specific learning disability with reading impairments) (Illingworth & Bishop, 2009; Whitehouse & Bishop, 2008; for review, see Bishop, 2013). As such, it remains possible that comorbid language impairment might be more prevalent in autistic individuals, or high language proficiency of our recruited undergraduate high autistic trait sample, potentially account for typical language lateralisation.

Intriguingly, while the high autistic trait sample performed poorer on one measure of verbal (word generation) abilities and also showed a non-significant trend towards weaker vocabulary skills than their low autism trait counterparts, there were no group differences in the direction or strength of language laterality. One possible explanation for why atypical language lateralisation was not more common in the high AQ group is that verbal abilities were comparatively weaker than the low AQ group, but not within the clinically impaired range. This suggestion fits with findings of typical left hemisphere language lateralisation in autistic individuals with better or intact verbal abilities, and conversely, a reduction or reversal of left hemisphere bias in subgroups of autistic individuals with more severe language impairment (Anderson et al., 2010; De Fosse et al, 2004; Floris et al., 2016). There might be a threshold, beyond which maladaptive language impairments in ASC begin to be associated with atypical language laterality.

On a group-level, participants with high levels of autistic traits showed weaker right hemisphere lateralisation than those with low autistic traits on the visual short-term memory task. This is in direct contrast to meta-analysis results from Samson et al. (2012), which documented augmented right hemisphere participation of parietal and temporal regions in autistic individuals compared to neurotypical individuals during visuospatial task performance. In the Samson et al. (2012) paper, the largest between-group differences were found in the right fusiform gyrus, subserving object and face processing functions. Contrasting results could reflect the fact that the visual short-term memory task administered in this study does not directly assess object or face processing, but instead, requires visuospatial attention
and memory processes to temporarily encode and retrieve spatial locations. Supporting this argument in attributing the present results to the nature of the visuospatial task, other studies of visual attention have provided evidence of a reduced right hemisphere asymmetry in autistic adults (Dundas, Best, Minshew, & Strauss, 2012) as well as (non-clinical) adults high levels of autistic traits (English, Maybery, & Visser, 2015, 2017; English, Kitching, Maybery, & Visser, 2018); which is the same pattern reported in the current study. Recent work by English and colleagues, for instance, demonstrated that while adults with low AQ scores attend better to information presented to their left (than right) visual field (likely a consequence of right hemisphere visuospatial specialisation), this leftward attention bias was significantly reduced for participants with high AQ scores (English et al., 2015, 2017).

More direct evidence of attenuated right hemisphere activity in individuals with high levels of autistic traits comes from a study by English et al. (2018), which used transcranial direct current stimulation in combination with a visual attention (grey scales) task. They found that excitatory (anodal) stimulation applied to the right posterior parietal cortex lead to a pronounced leftward shift in visual attention in the high AQ group, to a level comparable with attention in the low AQ group during the (no-stimulation sham) baseline condition. English et al. (2018) proposed that underactivity in the right-hemisphere posterior parietal cortex might underlie atypical (i.e. less leftward) visual attention processing in individuals with high levels of autistic traits, relative to those with low autistic traits. Given the limited spatial resolution of fTCD, it is unclear whether the reduced right posterior parietal activity found in the English et al. (2018) study corresponds to less pronounced rightward visuospatial lateralisation in our recruited high AQ sample. Another possibility is that weaker right-lateralised activation in participants with high levels of autistic traits could result from recruiting a different network of brain activity to the low autistic trait sample during visual short-term memory. Further investigation, ideally with fMRI, is warranted.

While the degree of right hemisphere visuospatial lateralisation was considerably weaker for the high autistic trait sample, this was not associated with better (or worse) performance on the two visuospatial assessment measures (visual short-term memory accuracy, Wechsler Visual Puzzles scores), compared to their low autistic trait counterparts. Furthermore, correlations between the behavioural
measures of visuospatial abilities and fTCD measures of visual short-term memory LI were all non-significant for the low and high AQ groups. In other words, the strength of visuospatial lateralisation did not relate to how well participants performed the visuospatial tasks. A similar lack of association between visuospatial task performance (e.g. visual short-term memory, visual attention) and strength of visuospatial lateralisation was found in other fTCD studies involving adults (Rosch, Bishop, & Badcock, 2012) and children (Groen et al., 2012) selected from the general population. Conversely, using fMRI, Everts et al. (2009) showed positive correlations between strength of visuospatial laterality and better visual (Rey Search) performance for children as well as adults. By administering the visual short-term memory task with fMRI, it would be possible to distinguish whether null associations between behavioural performance and visuospatial laterality were potentially influenced by poor spatial resolution of fTCD.

In examining the TiP framework, participants with high and low levels of autistic traits were compared on their profile of verbal and visuospatial abilities, with fTCD also used to evaluate cognitive biases for language or visuospatial hemispheric processing during reading verification performance. If cognitive biases are altered in individuals on the autism spectrum, the TiP account can be used to predict greater activation of visuospatial than language hemispheric processing in the high AQ group, especially on the ambiguous statement condition, relative to the low AQ group. Additionally, if cognitive abilities play an important role within the TiP framework, participants with high levels of autistic traits were expected to show weaker verbal abilities and superior visuospatial abilities relative to their low autistic trait counterparts.

Contrary to predictions, most participants in the high AQ group showed dominant activation in their language cerebral hemisphere on the ambiguous statements, as well as the verbal and visual statements, suggesting substantial engagement in verbal semantic processing to assimilate meaning (see Figure 5.4). These results conflict with TiP predictions of visual thinking and contrast with fMRI findings from Kana et al. (2006), in that the autistic sample exhibited pronounced visuospatial cerebral participation of parietal-occipital regions (e.g. intraparietal sulcus, superior parietal, cuneus, precuneus, lingual gyrus) during verification of high- as well as low-imagery statements. In comparison, the neurotypical sample from the Kana et al. (2006) paper showed greater cerebral activity in several
right hemisphere regions (superior parietal, precentral sulcus, interior temporal) during verification of high-imagery relative to low-imagery statements. While less pronounced right hemispheric responses in the neurotypical group during verbal statement verification could reflect reduced reliance on visuospatial processing, a laterality index was not quantified using fMRI. Nevertheless, using fTCD the expected difference in laterality for the visual relative to the verbal statements was not observed in our low autistic-trait comparison sample.

Challenging assumptions of visual thinking biases in the TiP account, the profile of activation on the ambiguous verbal-visual statements suggest preferential recruitment of language over visuospatial hemispheric activity in participants with high levels of autistic traits. The pattern of fTCD results on the ambiguous statements in our high autistic trait sample contrasts with fMRI findings showing elevated right hemisphere visuospatial processing in autistic individuals during ambiguous verbal-visual tasks involving working memory, relative to neurotypical individuals (Koshino et al., 2005, 2008). In addition to finding considerable overlap in the degree of lateralisation on the ambiguous verification statements, the two AQ sample displayed a significantly smaller (but positive) LI for the ambiguous statements relative to the set of verbal and the visual statements. These results suggest that individuals in the high and low autistic trait groups commonly engaged in linguistic processing to verify content from verbal and visual statements, but to lesser degree on the ambiguous statements.

With regard to the profile of cognitive abilities, finding weak verbal abilities in our high autistic trait sample is an outcome consistent with the TiP account. Verbal weaknesses in the high AQ group were evidenced by significantly poorer fluency on the word generation task, and also a trend towards poorer Wechsler Vocabulary scores, in comparison the low AQ group. Intriguingly, despite showing comparatively weaker verbal abilities, individuals with high levels of autistic traits seemed to rely heavily on language processing when solving all three statement types. Correlations between participants’ verbal and visuospatial abilities and the strength of (language-visuospatial) cerebral activation (i.e. LI) on the ambiguous statements were all non-significant, for both the low and high AQ groups. These results suggest that weak verbal abilities in our high autistic trait sample did not impede the degree to which they engaged in language hemispheric processing during reading comprehension.
The results from this experiment lend support to the idea that cognitive abilities might function independently from verbal-visual thinking biases in individuals with low and high levels of autistic traits, within the TiP framework. In comparison, the dual-task results from Chapter 3 (Experiment 2) showed cross-modality effects, where participants in the high AQ sample with stronger visuospatial abilities were more susceptible to performance costs in the verbal domain (i.e., when verbal processing was blocked via articulatory suppression). Given mixed findings and methodological differences between fTCD and dual-task approaches, further work is necessary to clarify the relationship between cognitive abilities and cognitive preferences from a TiP standpoint.

One limitation of the current experiment was that the sentence manipulation failed to yield hemispheric differences in visuospatial laterality, particularly for the visual (and ambiguous) statements, which were designed to be open to visuospatial processing. Finding significantly positive correlations between the LIs for the visual and the ambiguous statements with the word generation task LI, challenges the idea that these statements require visuospatial processing, and instead suggest the possibility that these statements primarily demand linguistic processing. Additionally, results of a non-significant (but trending) association between the verbal statement LI and the strength of language lateralisation assessed with the word generation task pose questions regarding the construct validity of verbal verification statements. fTCD measurements of MCA blood flow activity might fail to reliably capture subtle differences in hemispheric variability across the sentence types and/or detect visuospatial activation differences between the two AQ groups, particularly in occipital-parietal regions where differences have been reported between autistic and neurotypical comparisons in Kana et al. (2006).

Anatomically, cortical coverage of the MCA branches laterally towards the frontal and temporal lobes, with the artery supplying parietal and occipital regions to a lesser degree (see Table 1, Badcock & Groen, 2017). Restricted MCA perfusion to parietal-occipital brain regions could explain why fTCD might fail to capture greater activity in participants’ visuospatial than language hemisphere for the visual or ambiguous verbal-visual statements, despite subjective reports and dual-task spatial tapping interference indicating these statements are open to visualising strategies (as found in Chapters 2 and 3). Poor spatial resolution is a limitation of fTCD, as it provides information regarding differences in the left and right hemisphere.
processing based only on MCA cortical territory. Consequently, if our low and high AQ samples show differences in cerebral processing activity falling outside cortical boundaries of the MCA, fTCD might not sufficiently detect this.

In the next chapter, fMRI was used to further characterise functional organisation for language and visuospatial cerebral networks and to examine the TiP framework in adults differing in levels of autistic-like traits. It was reasoned that if fTCD is not sensitive enough to detect subtle hemispheric or regional differences in language and visuospatial cerebral activity among individuals with low versus high levels of autistic traits, then high spatial resolution of fMRI should.
Chapter 7: Functional Magnetic Resonance Assessment of Cerebral Laterality andThinking Style in Adults with Autistic-like Traits
Introduction

One key advantage of fMRI over fTCD is its high spatial resolution, enabling localisation of neural activity within specific regions of the brain. The fMRI technique detects changes in brain metabolism by measuring BOLD signals, providing an indication of cerebral blood flow and oxygen uptake in the brain during neural activity. Compared to fTCD, sophisticated fMRI analyses permit researchers to construct functional maps of cerebral regions activated throughout the whole brain and further clarify how certain regions of interest, based on previous literature, vary in activity across experimental conditions or differ between groups (Somers et al., 2011; Poldrack, 2007). Capitalising on these advantages, the current experiment utilised fMRI to identify functional organisation for language and visuospatial cerebral networks and to examine the TiP account of ASC in adults with low and high levels of autistic-like traits.

A majority of fMRI studies have provided evidence for altered language and visuospatial processing in ASC. Within the language domain, diminished frontal-temporal activity in the inferior frontal gyrus, middle frontal gyrus and superior temporal gyrus has been commonly reported in autistic individuals (Gaffrey et al., 2007; Gervais et al., 2004; Harris et al., 2006). Additionally, visuospatial (extrastriate) cerebral regions show atypical participation in ASC during verbal task performance (e.g. verification of low imagery statements, word categorisation) (Gaffrey et al., 2007; Kana et al., 2006), with a recent functional connectivity study suggesting over-connectivity between visuospatial networks and regions supporting language in autistic people (Shen et al., 2012).

In comparison, during visuospatial task performance, autistic individuals show more pronounced activity in parietal-occipital regions including the superior parietal, inferior parietal, precuneus, middle occipital, extrastriate and fusiform gyrus regions, relative to their neurotypical counterparts (Damarla et al., 2010; Keehn et al., 2008; Samson et al., 2012; Silk et al., 2006). Even on ambiguous (e.g. working memory, fluid reasoning) tasks where neurotypical individuals show a widespread network of frontal-temporal language activity, autistic individuals have been distinguished by pronounced recruitment of parietal-occipital areas servicing visuospatial functions to perform the same task (Koshino et al., 2005, 2008; Sahyoun et al., 2009). This pattern of over-activation in parietal-occipital
visuospatial regions and under-activation in frontal-temporal language regions, corresponds with superior behavioural performance on visuospatial than verbal assessment measures in ASC, and is consistent with the TiP account.

As discussed previously, assessing language and visuospatial functions within the TiP framework is not straightforward, given functional evidence suggesting atypical distribution of cerebral activity within the left and right hemispheres in people on the autism spectrum, including those with high autistic levels of traits. For instance, in Chapter 6 (Experiment 5), participants scoring high on the AQ exhibited reduced rightward lateralisation for visual short-term memory relative to their low AQ scoring counterparts. Rather than finding stronger right hemisphere visuospatial lateralisation in the high AQ group based on TiP predictions of enhanced visuospatial information processing, English et al. (2018) proposed that underactivity in the right hemisphere parietal cortex could represent atypical visual attention processing in this sample (from attending less to the left visual field). Regarding the directionality of language specialisation in ASC, meta-analyses have not arrived to firm conclusions on whether the frontal-temporal language network is typically lateralised but shows under-recruitment (Preslar et al., 2014; Sperdin & Schaer, 2016), or if the language network is atypically lateralised in the opposite (right) hemisphere (Herringshaw et al., 2016). If frontal-temporal and parietal-occipital regions are functionally organised differently in people on the autism spectrum, localisation of language and visuospatial networks is necessary, before discerning how these two distinct systems function within the TiP account.

In this experiment, the word generation and visual short-term memory tasks were administered in conjunction with fMRI to identify specific loci of language and visuospatial networks in undergraduate adults selected for low versus high autistic trait levels. It is well established that most people from the general population show a greater network of left-lateralised activity in frontal-temporal (inferior frontal gyrus, middle frontal gyrus, insular cortex, anterior cingulate, thalamus, anterior cerebellum, precuneus, caudate, claustrum and the putamen) regions during word generation (Wagner, Sebastian, Lieb, Tüscher, & Tadić, 2014), and greater right-lateralised activity in frontal-parietal-occipital (superior frontal, inferior parietal, superior parietal, extrastriate) regions for visual short-term memory (Croizé et al., 2004; Thomason et al., 2008).
Different to Chapter 6, language and visuospatial lateralisation was assessed by comparing activation in predefined regions of interest (ROIs) directly associated with word generation and visual short-term memory task performance for the two participants groups. Here, laterality analyses focused on examining BOLD signals in the frontal-temporal language ROIs and also for the frontal-parietal-occipital visuospatial ROIs, comparing activation between left- and right-hemisphere homologous regions. Of central interest was whether the profile of activation for the high AQ group in these language ROIs and visuospatial ROIs would show divergence from typical left-lateralised language and right-lateralised visuospatial functions, relative to the low AQ group. Where group differences in activity were identified on the ROI analyses, further analyses were conducted to examine how neural differences impacted behavioural performance on the word generation and visual short-term memory tasks.

Following identification of the pattern of language and visuospatial functions, fMRI was used to assess the extent to which participants with low and high levels of autistic traits recruited language and visuospatial processing during reading sentence verification, under the TiP account. During reading, the verbal semantic system facilitates access to word knowledge stores to verify meaning, whereas the visuospatial system provides access to visual imagery and spatial relationships described in text to decipher content (Binder et al., 2005; Sadoski, & Paivio, 2004). Candidate regions in the verbal semantic network lie in frontal-temporal areas, and include the inferior frontal gyrus (orbital part) and superior temporal gyrus (see Figure 5, Binder et al., 2009). Regions that form the visuospatial network are located in frontal-parietal-occipital areas, involving the dorsomedial prefrontal cortex, inferior parietal gyrus, angular gyrus and posterior cingulate (see Figure 6, Binder et al., 2009).

By accounting for the pattern of cerebral lateralisation on an individual level, BOLD responses in the verbal semantic ROIs and visuospatial ROIs associated with reading were examined, across the verbal, visual and ambiguous verification statements. However, if a sizable number of the sample (particularly those in the high autistic trait sample) show language and visuospatial functions located primarily in the same hemisphere (i.e. not permitting us to deduce the nature processing modality), between-group differences in the level of activation within verbal semantic ROIs and visuospatial ROIs will be examined.
Using a similar paradigm to that used in this thesis, Kana et al. (2006) documented heightened activation in parietal-occipital regions underlying visuospatial processing, coupled with reduced inferior frontal activity associated with verbal semantic processing in the autistic sample, for the low- and high-imagery statements. Similarly, in the course of sentence comprehension, autistic individuals have been found to show either a reduced leftward asymmetry in frontal-temporal activity, or greater right hemisphere activity in parietal-occipital regions (Mason et al., 2008; Müller et al., 1999; Takeuchi et al., 2004; Wang et al., 2006). If cerebral laterality is altered in the same way as ASC, participants in the high autistic trait sample are expected to show differential modulation of left- and right-hemisphere processing in language ROIs and visuospatial ROIs during sentence processing, relative to their low autistic trait counterparts. Based on the TiP account, the high AQ group was predicted to show superior activation in parietal-occipital regions of the visuospatial network and reduced activation in frontal-temporal regions of the verbal semantic network, across the verbal, visual and ambiguous statements. Where group differences in language ROIs and visuospatial ROIs were identified, further analyses were conducted to explore how neural differences in sentence processing related to the profile of verbal and visuospatial abilities, for the low and high autistic trait samples.

The word generation, visual short-term memory and reading sentence verification tasks were adapted for fMRI scanning and modified slightly from Chapter 6. For each task, the baseline control condition was modified to appropriately match the experimental conditions for low-level processing, motor (button press) output and block duration (see Figures 6.1 and 6.2). This was done to ensure that by subtracting out BOLD responses during the baseline condition from BOLD responses for the corresponding experimental condition(s), a robust measure of the critical functional regions associated with task performance would be revealed (Stark & Squire, 2001). Exploratory ‘whole-brain’ analyses were conducted to verify if the three fMRI experimental tasks elicited brain activation in areas consistent with previous literature, before conducting the ROI analyses where cerebral activation differences between low and high autistic trait samples were compared.
Experiment 6

7.1 Method

Participants

A total of 1191 undergraduate students from the University of Western Australia completed the AQ in a mass screening exercise to fulfill part of their course requirement. As in Experiments 2 and 5, individuals who scored in the bottom (AQ score < 95) and the top (AQ score > 125) quintiles of the AQ distribution were invited to participate in the major phase of testing. There were 17 participants in the low AQ group and 16 in the high AQ group who participated in this study. The two AQ groups were balanced on age, gender distribution, and on handedness distribution using the 4-item Edinburgh Handedness Inventory (Veale, 2014) (see Table 6.1). All participants were English speaking, and reported no history of any psychiatric, neurological or neurodevelopmental diagnosis.

Table 6.1. Participant characteristics (means, with standard deviations presented in parentheses).

<table>
<thead>
<tr>
<th></th>
<th>Low AQ</th>
<th>High AQ</th>
<th>Group comparison statistics</th>
</tr>
</thead>
<tbody>
<tr>
<td>Gender (female: male)</td>
<td>8:9</td>
<td>8:8</td>
<td>(\chi^2(1) = .03, p = .86, \phi &lt; .05)</td>
</tr>
<tr>
<td>Age (years)</td>
<td>22.53 (3.84)</td>
<td>23.00 (6.13)</td>
<td>(t(31) = .27, p = .79, d = .10)</td>
</tr>
<tr>
<td>AQ score</td>
<td>86.00 (6.71)</td>
<td>135.13 (7.34)</td>
<td>(t(31) = 20.09, p &lt; .05, d = 7.22)</td>
</tr>
<tr>
<td>Handedness</td>
<td>1: 1: 15</td>
<td>1: 0: 15</td>
<td>(\chi^2(2) = 1.42, p = .49, \phi = .04)</td>
</tr>
</tbody>
</table>

Verbal abilities

<table>
<thead>
<tr>
<th></th>
<th>Low AQ</th>
<th>High AQ</th>
<th>Group comparison statistics</th>
</tr>
</thead>
<tbody>
<tr>
<td>WAIS-IV Vocabulary</td>
<td>11.83 (1.93)</td>
<td>12.19 (2.32)</td>
<td>(t(31) = .48, p = .63, d = .17)</td>
</tr>
<tr>
<td>Word generation (no. words)</td>
<td>26.94 (6.19)</td>
<td>23.75 (3.94)</td>
<td>(t(31) = 1.75, p = .09, d = .63)</td>
</tr>
</tbody>
</table>

Visuospatial abilities

<table>
<thead>
<tr>
<th></th>
<th>Low AQ</th>
<th>High AQ</th>
<th>Group comparison statistics</th>
</tr>
</thead>
<tbody>
<tr>
<td>WAIS-IV Visual Puzzles</td>
<td>10.71 (2.05)</td>
<td>12.06 (2.49)</td>
<td>(t(31) = 1.71, p = .10, d = .61)</td>
</tr>
<tr>
<td>Visual memory (out of 26)</td>
<td>21.29 (3.70)</td>
<td>22.76 (2.21)</td>
<td>(t(31) = 1.37, p = .18, d = .49)</td>
</tr>
<tr>
<td>Attention baseline (out of 26)</td>
<td>24.42 (1.66)</td>
<td>23.88 (1.82)</td>
<td>(t(31) = .89, p = .38, d = .32)</td>
</tr>
</tbody>
</table>

General Procedure

All participants attended a practice session, scheduled prior to their fMRI testing session. During the practice session, they completed a metal safety checklist to rule out contraindications for fMRI scanning. They also completed the 4-item Edinburgh Handedness Inventory (Veale, 2014), the WAIS-IV Vocabulary and Visual Puzzles subtests (Wechsler, 2008) and practice versions of the word
generation, visual short-term memory and reading sentence verification task. The three practice tasks were completed on a laptop computer, while participants concurrently listened to audio recordings of fMRI scanner sounds through their headphones to familiarise them with the noise that would be experienced inside the scanner during task performance. The fMRI testing session was conducted at the Radiology Department of the Sir Charles Gairdner Hospital in Perth, Western Australia. All participants completed the reading sentence verification task first, with the order of the word generation and visual short-term memory tasks counterbalanced within each AQ group. None of the practice stimuli were administered in the fMRI testing session.

**Experimental Tasks**

All three experimental tasks were adapted for fMRI block design testing (see Figures 6.1 and 6.2). The fMRI block design involved presenting task trials in a series of “on” (experimental conditions) and “off” (baseline) periods (Amaro & Barker, 2006), so that BOLD signals associated with cognitive task performance could be estimated by subtraction and then compared between the two AQ groups. All three tasks were presented using a rear projection to a mirror system mounted on a scanner head coil worn by participants. The tasks were controlled by Presentation Software (Neurobehavioral Systems) and were synchronised with trigger pulses from the fMRI scanner.

The word generation task contained a think-word condition and baseline fixation condition interleaved in order of presentation, with 8 blocks per condition. On each block of the think-word condition, participants were visually presented with two target letters (size 200 Times New Roman font), one letter at a time, for 11.25 s each (see Figure 6.1). They were asked to try their best to silently and continuously generate as many different words beginning with the letter viewed on screen (test items = A, C, F, H, I, K, L, M, N, P, R, S, T, V, W, Y). During the baseline block, participants viewed a fixation cross on screen for 22.50 s and were given instructions to clear their minds and relax, so as to restrict the amount of self-thought/subvocal speech production. Test stimuli (font type and size) for each condition were presented in size 200 Times New Roman font in order to match the experimental and baseline conditions on perceptual factors. Test stimuli (font type and size) for each condition were presented in size 200 Times New Roman font in order to match the
experimental and baseline conditions on perceptual factors. In this way, block-subtractions between the experimental and baseline conditions were designed to capture subvocal word generation. Due to concerns of pronounced head movement artefacts associated with speech output (for a review, see Fiez, 2001), participants were not required to report aloud the words that were generated during the think-word condition in the fMRI scanner. Instead, an out of scanner estimate of word generation performance was obtained during the practice session, during which participants completed six practice items for which they reported words aloud (practice items = B, E, O, J, P and V). Covert versions of the word generation task have been found to produce leftward lateralised patterns of fMRI BOLD responses (Häberling, Steinemann, & Corballis, 2006).

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<tr>
<th>+</th>
<th>F</th>
<th>A</th>
<th>+</th>
<th>C</th>
<th>E</th>
<th>+</th>
<th>L</th>
<th>R</th>
</tr>
</thead>
<tbody>
<tr>
<td>Duration (s)</td>
<td>22.50</td>
<td>11.25</td>
<td>11.25</td>
<td>22.50</td>
<td>11.25</td>
<td>11.25</td>
<td>22.50</td>
<td>11.25</td>
</tr>
</tbody>
</table>

Figure 6.1. Schematic representation of the word generation fMRI block design.

The visual short-term memory task was similar to that described in Chapter 6, but also incorporated a baseline visual attention condition, for comparison with the experimental visual memory condition. The experimental and baseline conditions were designed to be matched on perceptual and motor response factors, but differ on visual short-term memory load (see Figure 6.2, top panel). In both conditions, participants were required to remember spatial locations of an initial array of circles (17 white, 5 red, circles 90 pixels in diameter), and after a delay period, decide if a second circle array was the same or different to the first array. As illustrated in Figure 6.2, the delay (retention) period for the visual memory condition (5.00 s) was manipulated to be longer than the delay for the attention baseline condition (.10 s). It was expected that during the attention baseline condition, participants would be able to detect whether there was a change from the first to the second test display with minimal demand on memory processes. For each condition, participants were cued to make a same/different judgement using a two-button box (same: left thumb, different: right thumb) when they saw a black border appear on screen. When no
response was provided within a 4.00 s time window, the trial was scored incorrect and the next trial was administered.

Participants completed 13 blocks of each condition, with the visual memory and baseline attention conditions interleaved. Each block contained two trials from the same condition. To ensure that the durations of trials for the two conditions were approximately matched, the display time for the second array of circles in the baseline attention condition was adjusted to appear for 4.90 s (immediately after the .10 s retention period), before a true/false button press response could be made (see Figure 6.2, top panel). Performance accuracy (out of 26) for each condition was computed in the fMRI scanner for each participant.

The reading sentence verification task contained sets of verbal, visual and ambiguous verbal-visual statements, and also incorporated a false-font baseline condition to control for perceptual input and eye movements associated with reading (see Figure 6.2, bottom panel). During each of the three statement conditions, a sentence appeared on screen one word at a time (every .40 s), from left to right, until the complete sentence was administered (range = 3.60 to 6.00 s). Although below the average adult reading speed (Rayner, Slattery, & Bélange, 2010), the .40 s stimulus presentation rate was selected to ensure that all participants were able to sufficiently read the statement as the words appeared on screen. Immediately after the statement was administered, a true and false display appeared on screen to cue participants to verify the content. Half of the statements in each statement condition were true, while the other half were false. Participants made their responses on a two-button response box (true = left thumb, false = right thumb). If a true/false response was not made 5.00 s after the complete statement was presented on screen, the trial was deemed incorrect, and the next trial commenced.

In the false-font baseline condition, participants viewed a series of hashtags (1 to 4 strings in length) on screen, one string at a time (every .40 s), from left to right. They were instructed to use their eyes to track the hashtags as it appeared on screen to simulate eye movement associated with reading. The number of hashtag strings in the baseline blocks varied depending on the average number of words from the statements in the preceding experimental blocks. This was done to ensure that the baseline and experimental conditions were matched on low-level visual character processing.
Figure 6.2. Schematic representation of the visual short-term memory task (top panel) and the reading sentence verification task (bottom panel). For each task, the baseline control condition was designed to match the experimental condition on motor response output, low-level processing demands and block duration.
To match the duration of the baseline condition with the experimental conditions, the duration of the final hashtag presentation phase was individually adjusted based on each participant’s averaged RT on the (preceding) experimental blocks. After this variable lag period, the words “left” and “right” appeared below the false-font hashtags to cue a button press response. On half the trials the “left” option was underlined, and on the remaining half, the “right” option was underlined. Using the two-button response box, participants made a button press corresponding to the underlined word.

The three statement conditions and the false-font hashtag baseline condition were presented in a pseudorandomised order, with 8 blocks each. In each block, three trials from the same condition were administered. Participants completed 24 test trials for each statement condition (for stimuli, see Appendix A) and 24 baseline trials. In-scanner performance accuracy and median RTs were computed separately for each statement. Different to Chapter 6 (Experiment 5) where RTs were calculated immediately after the trial onset, median RTs were calculated after all the words within the statement had appeared on screen.

Image Acquisition and Preprocessing

The fMRI images were acquired using a 3T Philips Magnetic Resonance scanner, while participants wore an 8-channel head coil lined with foam-padding inserts to limit head movement artefacts. Prior to completing the three experimental tasks, a T1-weighted high resolution anatomical image was collected for each participant (379 seconds, 175 slices, 1 mm x 1 mm x 1 mm). Functional images for the word generation, visual short-term memory and reading sentence verification task were collected using a single shot echo planar imaging sequence (repetition time = 3s, echo time = 30 ms, flip angle = 90°), with 32 slices to ensure whole brain coverage (slice thickness = 4.0 mm, interslice gap = .4mm, inplane resolution = 1.31 mm x 1.31 mm).

To allow for T1 equilibrium effects, two dummy scans were administered immediately before the onset of each task. The total scan time was fixed for the word generation task (6 minutes), but varied for the visual short-term memory (range = 9.63 to 10.39 minutes) and sentence verification (range = 9.74 to 15.00 minutes) tasks, as these tasks required button-press responses. However, the overall mean scan time for the low (M = 28.63 minutes, SD = 1.15, range = 27.15 to 31.13
minutes) and the high (\(M = 28.45\) minutes, \(SD = 1.36\), range = 25.53 to 31.13 minutes) AQ groups was approximately equivalent, \(t(31) = .41, p = .68, d = .15\).

Data preprocessing was conducted for all three experimental tasks using the Statistical Parametric Mapping software (SPM 12; Wellcome Trust Centre for Neuroimaging, London, UK, http://www.fil.ion.ucl.ac.uk/spm/software/). For each task, the functional images were corrected for slice timing using the middle (i.e. 16\(^{th}\)) anatomical slice as a reference slice. In-scanner motion for each participant was then examined. Where participants displayed more than 1mm of gradual movement in the transitional plane in the fMRI scanner, their data were not analysed for the appropriate task. Using the (< 1mm) motion criterion, imaging data from one male participant from the low AQ group was excluded for the visual short-term memory task, leaving a sample size of 16 in the low AQ group and 16 in the high AQ group for this task. All participants were included in the imaging analyses for the word generation and the reading sentence verification task.

Motion correction was then applied by realigning each participant’s in-scanner time series movement to the first acquired functional image using a cubic b-spline interpolation procedure (Freire, Roche, & Mangin, 2002). For each participant, the mean functional image was co-registered to their T1 anatomical scan using the Unified Segmentation algorithm (Ashburner & Friston, 2005). Functional and T1 anatomical scans were then resampled to 2 x 2 x 4 mm voxels and spatially normalized to an EPI template in Montreal Neurological Institute (MNI) space. Lastly, the functional scans were spatially smoothed using a 5 x 5 x 8 mm (full width half maximum) Gaussian filter.

**Behavioural Analyses**

Data for each AQ group were screened for normality, as described in the previous chapters. All parametric assumptions of normality were confirmed. Group differences on the verbal (WAIS-IV Vocabulary, word generation) and visuospatial (WAIS-IV Visual Puzzles, visual short-term memory) assessment measures were tested using a series of independent samples t-tests. For the sentence verification task, a 2 x 3 ANOVA was used to compare AQ group differences in behavioural performance across the verbal, visual and ambiguous statement conditions.
Whole Brain Analyses

For each of the three tasks, the preprocessed functional images were subjected to a first-level (within-subject) analysis. Contrast images for each participant were estimated using box-car functions to model the experimental versus baseline condition, for the word generation (think-word > fixation), visual short-term memory (visual memory > attention baseline) and the reading sentence verification task (each of the three statement conditions > false-font baseline). For the sentence verification task, six higher-order first-level contrasts (i.e. verbal > visual, verbal > ambiguous, visual > verbal, visual > ambiguous, ambiguous > verbal and ambiguous > visual) were also created to identify subtle differences in activation across the three statement conditions. When estimating the first-level model, in-scanner movement regressors for each participant were also included. The first-level contrasts were performed using the general linear model to fit BOLD responses at each voxel and were convolved with a canonical haemodynamic response function using a 128s high-pass filter.

In the second-level analyses, the main effects of each experimental task were assessed using an exploratory whole brain analysis, collapsed for the low and high autistic trait samples. This provided a way of examining activation signal maps for each task and checking whether our fMRI tasks were assessing the purported verbal or visuospatial constructs. Main task effects were estimated by applying single-sample t-tests to the contrast images created for the word generation (i.e. think-word > baseline) and the visual short-term memory (i.e. visual memory > attention baseline) tasks. For the reading sentence verification task, main effects of each sentence condition were assessed using a series of one-sample t-tests on contrasts for the verbal statements > false-font baseline, visual statements > false-font baseline, and ambiguous statements > false-font baseline contrasts, and also for the six higher-order contrasts. For each task, the main effects were estimated at a Family Wise Error (FWE) correction rate of $p < .05$, with an extent threshold set to a cluster size ($K_E$) of $> 10$ contiguous voxels per cluster to minimize the possibility of detecting false-positive activations which could have occurred by chance (Lieberman & Cunningham, 2009).
Region of Interest Analyses

Between-group (AQ) effects were assessed on predefined ROIs for each task. The ROIs for the word generation task were brain areas involved with verbal (phonemic) fluency, including the inferior frontal gyrus, middle frontal gyrus, insular cortex, anterior cingulate, thalamus, anterior cerebellum, precuneus, caudate, claustrum and the putamen (Wagner et al., 2014). The ROIs for the visual short-term memory task were the superior frontal gyrus, inferior parietal gyrus, superior parietal gyrus and the precuneus, which support memory retention of visuospatial information (Rottschy et al., 2012). ROIs for the visual short-term memory task were also extended to include the extrastriate cortex and fusiform gyrus, since previous ASC studies have reported atypical occipital activity associated with use of visuospatial imagery (e.g. Ring et al., 1999; Samson et al., 2012).

For the word generation and visual short-term memory tasks, activation in homologous ROIs in the left and right cerebral hemispheres was examined in the between-group analyses. This was done to assess the possibility that individuals with high levels of autistic traits might show hemispheric differences in the recruitment of language and visuospatial functions, and to also compare the pattern of cerebral lateralisation between the two AQ groups.

For the reading sentence verification task, ROIs implicated with verbal semantic processing and visuospatial processing were selected based on Binder et al (2009). The language ROIs included the inferior frontal gyrus (orbital part) and the superior temporal gyrus, while the visuospatial ROIs comprised of the inferior parietal gyrus, angular gyrus, dorsomedial prefrontal cortex, posterior cingulate, extrastriate cortex and fusiform gyrus. Analyses for the language ROIs and visuospatial ROIs for the reading sentence verification task were conducted bilaterally, in homologous regions within the left- and right-hemispheres. This was done to assess whether the low and high autistic trait samples would show activation differences in any of the language and visuospatial ROIs, and to also evaluate the possibility of group differences in cerebral lateralisation during reading.

The level of activation within each ROI was examined using anatomically defined masks built in the Wake Forest University Pickatlas (version 3.0.5) toolbox (Maldjian, Laurienti, Kraft, & Burdette, 2003) in SPM12. The between-group ROI analyses were performed first at a FWE correction level of $p < .05$. If no between-group differences were identified at the corrected level, the ROI analyses were then
performed at an uncorrected level (for fMRI analyses guidelines, see Poldrack et al., 2008). An uncorrected threshold level of \( p < .001 \) was selected to appropriately balance between Type I and Type II error rates (Lieberman & Cunningham, 2009). Using an extent cluster threshold of \( K_E > 10 \) contiguous voxels within each ROI, the mean beta fit (percent signal change) values were extracted and analysed in SPSS using two-sample t-tests or ANOVAs (where appropriate) to tease apart AQ group effects.

**Laterality Analyses**

For each participant, the strength and direction of language and visuospatial cerebral lateralisation was computed from first-level contrasts for the word generation (think-word > fixation) and the visual short-term memory (visual memory > attention baseline) tasks. Using the Wake Forest University Pickatlas (version 3.0.5) toolbox, a combined mask containing all ROIs for the word generation task and a combined mask of all ROIs for the visual short-term memory task were built. For each task, the combined ROI mask included anatomical boundaries of homologous regions in the left and right hemispheres, to specifically examine cerebral lateralisation in predefined areas directly linked with cognitive performance.

A laterality index was then calculated for each participant for each of the word generation and visual short-term memory tasks using the LI-toolbox (Wilke & Lidzba, 2007). This was done based on the formula \( LI = 100 \times ((L-R)/(L+R)) \), where L and R refer to clusters of activation in the left and right cerebral hemispheres, respectively, within anatomical boundaries of the combined ROI mask. The LI-toolbox estimates LI values based on a bootstrap algorithm by generating 10000 indices across different statistical thresholds to produce a reliable measure of laterality (Bradshaw et al., 2017). For each task, the LI-toolbox (Wilke & Lidzba, 2007) computed an overall weighted bootstrapped measure of laterality, ranging from -1 to 1. Participants with LI values smaller than -.2 were categorised as having right hemisphere lateralisation, while LI values greater than .2 were categorised as having left hemisphere lateralisation. Bilateral lateralisation was denoted for the appropriate cognitive function when the LI fell in between the -.2 and .2 cut-offs (Badcock, Bishop, Hardiman, Barry, & Watkins, 2012).
7.2 Results

Behavioural Results

Table 6.1 presents behavioural results on the verbal and visuospatial assessment measures for the low and the high AQ groups. Independent samples t-tests found no significant difference between groups on all measures, although there were weak trends favouring better WAIS-IV Visual Puzzles scores, and poorer word generation task performance in participants with high levels of autistic traits.

Mean accuracy and median RT data for the reading sentence verification task are presented in Table 6.2 for the low and high AQ groups. The only significant effect which emerged from the 2 (AQ group) x 3 (statement condition) ANOVA conducted for each performance measure was a main effect of statement condition on RTs ($F(2, 62) = 56.79, p < .05, \eta_p^2 = .65$), in which participants completed the ambiguous statements faster compared to the verbal and the visual statements (Bonferroni pair-wise $\alpha < .017$). Neither of the group main effects nor the AQ group x statement condition interactions were significant when analyses were conducted on the accuracy (largest $F(2, 62) = .57, p = .57, \eta_p^2 = .02$) and RT (largest $F(2, 62) = 1.57, p = .22, \eta_p^2 = .05$) data.

Table 6.2. Summary statistics for participants with low and high AQ scores on the reading sentence verification task (standard deviations presented in parentheses).

<table>
<thead>
<tr>
<th></th>
<th>Low AQ (n =17)</th>
<th>High AQ (n =16)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Mean accuracy (out of 24)</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Verbal</td>
<td>19.76 (2.28)</td>
<td>19.47 (2.27)</td>
</tr>
<tr>
<td>Visual</td>
<td>19.35 (1.93)</td>
<td>20.00 (2.56)</td>
</tr>
<tr>
<td>Ambiguous</td>
<td>19.24 (1.68)</td>
<td>19.88 (1.45)</td>
</tr>
<tr>
<td><strong>Median RT (s)</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Verbal</td>
<td>2.35 (1.05)</td>
<td>2.38 (.92)</td>
</tr>
<tr>
<td>Visual</td>
<td>2.89 (.86)</td>
<td>2.56 (.89)</td>
</tr>
<tr>
<td>Ambiguous</td>
<td>1.17 (.49)</td>
<td>1.34 (.74)</td>
</tr>
</tbody>
</table>

Whole Brain Analysis: Areas Associated with Word Generation and Visual Short-term Memory

The whole brain analyses focused on identifying whether brain regions specialised for language processing were generally activated during word generation, and if visuospatial cerebral areas were primarily activated during visual short-term memory, with imaging data collapsed across the two autistic trait groups. Brain
regions (and coordinates) that were significantly activated during the think-word > fixation contrast for the word generation task and the visual memory > attention baseline contrast for the visual short-term memory task are summarised, respectively, in Tables 6.3 and 6.4.

Word generation (think-word > fixation) performance was marked by significant activation in frontal areas including the precentral gyrus and supplemental motor areas, with activation extending into the left inferior frontal gyrus (triangularis) and the left superior frontal gyrus. There was also significant activation in temporal cortex, particularly in the left fusiform gyrus which spanned to the left inferior temporal gyrus, with clusters of activity in subcortical (left hippocampus, right insular, left anterior cingulate) and motor (left caudate, right cerebellum) areas. Referring to Table 6.3, the cluster size ($K_E$) generally suggests greater cerebral activation in the left- than right-hemisphere during the think-word condition relative to the fixation condition.

During the visual short-term memory task (visual memory > attention baseline), participants exhibited significant activation in the left inferior parietal gyrus, which extended to the superior parietal gyrus and postcentral gyrus. Significant activation was also found in the left insular, left middle occipital gyrus and left precentral gyrus, with a bilateral pattern of activity in the superior frontal gyrus. Although $K_E$ values suggest relatively larger activation clusters in the left hemisphere than the right hemisphere during the visual short-term memory task (see Table 6.4), a visuospatial network of frontal-parietal-occipital regions was identified.
Table 6.3. **Whole brain analyses showing areas significantly activated during word generation, collapsed for participants with low and the high AQ scores (FWE, \( p < .05, K_E > 10 \) voxels).**

<table>
<thead>
<tr>
<th>Cluster ((K_E))</th>
<th>MNI coordinates</th>
<th>Brodmann area</th>
<th>Statistics</th>
</tr>
</thead>
<tbody>
<tr>
<td>(x)</td>
<td>(y)</td>
<td>(z)</td>
<td></td>
</tr>
<tr>
<td><strong>Think-word &gt; Fixation baseline</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Left hemisphere</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Precentral gyrus</td>
<td>1403</td>
<td>-46</td>
<td>4</td>
</tr>
<tr>
<td>Fusiform gyrus</td>
<td>810</td>
<td>-38</td>
<td>-44</td>
</tr>
<tr>
<td>Supplementary motor area</td>
<td>689</td>
<td>0</td>
<td>6</td>
</tr>
<tr>
<td>Caudate</td>
<td>186</td>
<td>-18</td>
<td>0</td>
</tr>
<tr>
<td>Superior parietal gyrus</td>
<td>87</td>
<td>-24</td>
<td>-64</td>
</tr>
<tr>
<td>Inferior parietal gyrus</td>
<td>48</td>
<td>-46</td>
<td>-38</td>
</tr>
<tr>
<td>Hippocampus</td>
<td>44</td>
<td>-10</td>
<td>-16</td>
</tr>
<tr>
<td>Superior frontal gyrus</td>
<td>20</td>
<td>-26</td>
<td>-6</td>
</tr>
<tr>
<td>Anterior cingulate gyrus</td>
<td>14</td>
<td>-2</td>
<td>0</td>
</tr>
<tr>
<td><strong>Right hemisphere</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Cerebellum (6)</td>
<td>765</td>
<td>26</td>
<td>-62</td>
</tr>
<tr>
<td>Cerebellum (8)</td>
<td>97</td>
<td>28</td>
<td>-68</td>
</tr>
<tr>
<td>Superior occipital gyrus</td>
<td>44</td>
<td>24</td>
<td>-94</td>
</tr>
<tr>
<td>Insular</td>
<td>43</td>
<td>42</td>
<td>18</td>
</tr>
<tr>
<td>Vermis (4,5)</td>
<td>14</td>
<td>2</td>
<td>-50</td>
</tr>
</tbody>
</table>

Table 6.4. **Whole brain analyses showing significant areas activated during visual short-term memory, collapsed for participants with low and high AQ scores (FWE, \( p < .05, K_E > 10 \) voxels).**

<table>
<thead>
<tr>
<th>Cluster ((K_E))</th>
<th>MNI coordinates</th>
<th>Brodmann area</th>
<th>Statistics</th>
</tr>
</thead>
<tbody>
<tr>
<td>(x)</td>
<td>(y)</td>
<td>(z)</td>
<td></td>
</tr>
<tr>
<td><strong>Visual memory &gt; Attention baseline</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Left hemisphere</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Inferior parietal gyrus</td>
<td>327</td>
<td>-40</td>
<td>-42</td>
</tr>
<tr>
<td>Superior frontal gyrus</td>
<td>222</td>
<td>-22</td>
<td>0</td>
</tr>
<tr>
<td>Superior frontal gyrus (medial part)</td>
<td>195</td>
<td>-1</td>
<td>20</td>
</tr>
<tr>
<td>Insular</td>
<td>72</td>
<td>-32</td>
<td>22</td>
</tr>
<tr>
<td>Precentral gyrus</td>
<td>37</td>
<td>-48</td>
<td>4</td>
</tr>
<tr>
<td>Middle occipital gyrus</td>
<td>28</td>
<td>-26</td>
<td>-70</td>
</tr>
<tr>
<td>Cerebellum (9)</td>
<td>23</td>
<td>-14</td>
<td>-54</td>
</tr>
<tr>
<td><strong>Right hemisphere</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Superior frontal gyrus</td>
<td>153</td>
<td>22</td>
<td>-4</td>
</tr>
<tr>
<td>Postcentral gyrus</td>
<td>77</td>
<td>48</td>
<td>-30</td>
</tr>
</tbody>
</table>
Region of Interest Analysis: AQ group differences in Word Generation and Visual Short-term Memory

A series of independent-samples t-tests were then conducted to compare differences in brain activation for participants with low and high levels of autistic traits in each of the predefined ROIs, for the word generation and visual short-term memory tasks. The ROI analysis for the visual short-term memory task failed to demonstrate differences in cerebral activity between the low and high AQ groups, across all visuospatial ROIs (superior frontal gyrus, inferior parietal gyrus, superior parietal gyrus, precuneus, extrastriate cortex, fusiform gyrus) in the left and right hemispheres. For the word generation task, two language ROIs revealed significant between-group effects, where participants with high levels of autistic traits showed greater activation in the right insular cortex and the right putamen, compared to those with low autistic traits (uncorrected $p < .001$, $K_E > 10$, see Table 6.5, Figures 6.3 and 6.4).

Table 6.5. Regions of interest analyses yielding significant AQ group differences during word generation (think-word > fixation) task performance (uncorrected, $p < .001$, $K_E > 10$ voxels).

<table>
<thead>
<tr>
<th>Cluster</th>
<th>MNI coordinates</th>
<th>Brodmann area</th>
<th>Statistics</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>$x$ $y$ $z$</td>
<td></td>
<td></td>
</tr>
<tr>
<td>High &gt; Low AQ group</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Right insular</td>
<td>25 40 -6 -2</td>
<td>13</td>
<td>4.21</td>
</tr>
<tr>
<td>Right putamen</td>
<td>17 36 -6 2</td>
<td>49</td>
<td>3.44</td>
</tr>
</tbody>
</table>

Figure 6.3. Sagittal-transverse view (left image) and dorsal view (right image) showing significantly greater right insular (red) and right putamen (green) activation in the high AQ group relative to the low AQ group during word generation (think word > fixation baseline) task performance ($p < .001$, uncorrected, $K_E > 10$ voxels).
Given that behavioural trends on the word generation task indicated non-significant trend towards poorer performance in the high AQ group, associations between right hemisphere insular and putamen ROI activity with verbal fluency were further examined. Beta fit (percent signal change) values for the right insular ROI and the right putamen ROI were extracted for each participant, and tested for correlations with number of words produced on the word generation task outside the fMRI scanner.

None of the correlation analyses between behavioural performance and degree of activation in the right insular cortex (Figure 6.4, left panel) or the right putamen (Figure 6.4, right panel) were significant, for both the low AQ (largest \( r = .17, p = .51 \), right insular cortex) and high AQ (largest \( r = -.23, p = .90 \), right insular cortex) groups. Furthermore, Fischer-Z transformed comparisons of these correlation coefficients did not yield group differences in the strength of the relationship between behavioural task performance and signal changes in the right insular (\( z = 1.06, p = .29 \)) or right putamen (\( z = .10, p = .92 \)) ROIs.

Figure 6.4. Scatter plot and trend lines indicate non-significant relationships between behavioural performance on the word generation task and percent signal changes in the right insular (left panel) and right putamen (right panel) ROIs during the think-word > fixation contrast, for participants with low (white triangles) and high (grey circles) AQ scores.
Another possibility was that greater right hemisphere insular and putamen responses during word generation in the high AQ sample could reflect atypical language lateralisation, relative to their low AQ counterparts. Individual LIs for the word generation and visual short-term memory tasks were computed for participants in the two AQ groups based on the level of activation within the combined ROI mask, for each laterality task (which included homologous ROIs in the left and right cerebral hemispheres).

Overall, the two AQ groups did not differ significantly on mean LIs for the word generation ($t(31) = 1.05, p = .30, d = .38$) or visual short-term memory ($t(30) = .97, p = .34, d = .35$) tasks, indicating similarities in the direction and degree of language and visuospatial lateralisation. To further examine the possibility of group differences in the pattern of cerebral lateralisation, participant LIs for the word generation and the visual short-term memory tasks were plotted in Figure 6.5. Only a minority of participants in the low ($n = 3, 18.75\%$) and the high ($n = 5, 31.25\%$) AQ groups showed the typical pattern of cerebral lateralisation.

Looking at Figure 6.5 (left side of the .2 vertical cut-off) for each plot, most participants in the low ($n = 15, 93.75\%$) and high ($n = 16, 100\%$) AQ groups showed (typical) left hemisphere language lateralisation during the word generation task. However, the typical pattern of right hemisphere lateralisation for visual short-term memory was not found (Figure 6.5, below the -.2 horizontal cut-off). Most participants in the low ($n = 13, 81.25\%$) and high ($n = 11, 68.75\%$) AQ groups showed atypical visuospatial lateralisation, with these functions localised either bilaterally (Figure 6.5, middle left of each plot) or in the left hemisphere (Figure 6.5, top left for each plot). There was no indication of differences in the frequency of atypical lateralisation for visual short-term memory, for the low and high AQ groups, $\chi^2(1) = .13, p = .72, \theta = .06$. 

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\(150\)
Figure 6.5. Distribution of language and visuospatial cerebral lateralisation for participants with low (left panel) and high (right panel) AQ scores during word generation and visual short-term memory, assessed using fMRI. For the word generation task, language lateralisation was examined in frontal-temporal regions (inferior frontal gyrus, middle frontal gyrus, insular, anterior cingulate, thalamus, anterior cerebellum, precuneus, caudate, claustrum and putamen) supporting verbal fluency (Wagner et al., 2014). For the visual short-term memory task, visuospatial lateralisation was examined in frontal-parietal-occipital regions (superior frontal gyrus, inferior parietal gyrus, superior parietal gyrus, precuneus, extrastriate cortex and fusiform gyrus) subserving mental imagery, spatial encoding and temporary maintenance of information in memory (Ring et al., 1999; Rottschy et al., 2012; Samson et al., 2012). An anatomical mask encompassing homologous ROIs in the left and right hemisphere were constructed for each task using the Wake Forest University Pickatlas (version 3.0.5) toolbox (Maldjian et al., 2003). Participant LIs were calculated using the LI-toolbox (Wilke & Lidzba, 2007). LI values greater than .2 reflected left hemisphere lateralisation while LI values smaller than -.2 indicated right hemisphere lateralisation. Bilateral specialisation was denoted for the appropriate cognitive function where LI values fell in between the -.2 and +.2 cut-offs.
Whole Brain Analysis: Areas Associated with Reading Sentence Verification

The analyses then turned to the reading sentence verification task first to evaluate whether the verbal, visual and ambiguous verbal-visual statements generally differed in language and visuospatial cerebral processing demands. Whole-brain analyses were conducted with data collapsed across the two AQ groups, and the main effects of each statement condition contrasted against the false-font baseline condition. Table 6.6 summarises the brain regions (and coordinates) significantly activated during reading verification of the verbal, visual and ambiguous statements, relative to the false-font baseline. All three statement conditions showed some overlap in a network of regions in the inferior frontal gyrus (opercular part), inferior parietal gyrus, middle occipital gyrus, cerebellum (7b) and pallidum. However, Table 6.6 also shows a number of regional differences in cerebral activation across the three statement types.

Table 6.6. Brain areas significantly activated during the reading sentence verification task (statement condition > baseline), collapsed for participants with low and high AQ scores (FWE, p < .05, KE > 10 voxels).

<table>
<thead>
<tr>
<th>Cluster (Kz)</th>
<th>MNI coordinates</th>
<th>Brodmann area</th>
<th>Statistics</th>
</tr>
</thead>
<tbody>
<tr>
<td>x</td>
<td>y</td>
<td>z</td>
<td></td>
</tr>
<tr>
<td><strong>Verbal statements &gt; False-font baseline</strong></td>
<td></td>
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<tr>
<td><strong>Left hemisphere</strong></td>
<td></td>
<td></td>
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</tr>
<tr>
<td>Middle occipital gyrus*</td>
<td>4586</td>
<td>-26</td>
<td>-90</td>
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<tr>
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<tr>
<td>Middle temporal gyrus</td>
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<td>-26</td>
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<tr>
<td>Superior parietal gyrus</td>
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<td>-26</td>
<td>-56</td>
</tr>
<tr>
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<td>23</td>
<td>-6</td>
<td>-28</td>
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<tr>
<td>Cerebellum (10)</td>
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<td>-22</td>
<td>-42</td>
</tr>
<tr>
<td>Cerebellum (7b)*</td>
<td>21</td>
<td>-34</td>
<td>-68</td>
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<tr>
<td><strong>Right hemisphere</strong></td>
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<tr>
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<td>Inferior frontal (orbital part)*</td>
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<td>26</td>
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<td>23</td>
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<td>-56</td>
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<tr>
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<td>15</td>
<td>12</td>
<td>6</td>
</tr>
<tr>
<td>Hippocampus</td>
<td>13</td>
<td>26</td>
<td>-34</td>
</tr>
<tr>
<td>Cerebellum (10)</td>
<td>12</td>
<td>22</td>
<td>-42</td>
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<td>Clustering</td>
<td>Cluster (KE)</td>
<td>MNI coordinates</td>
<td>Brodmann area</td>
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<tr>
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<td>-------------</td>
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<td>---------------</td>
</tr>
<tr>
<td><strong>Visual statements &gt; False-font baseline</strong></td>
<td></td>
<td></td>
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<tr>
<td><strong>Left hemisphere</strong></td>
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<td>-54</td>
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<td>Precentral gyrus</td>
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<tr>
<td>Inferior parietal gyrus*</td>
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<td>-40</td>
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<tr>
<td>Supplementary motor area</td>
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<td>Cerebellum (7b)*</td>
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<td>-32</td>
<td>-70</td>
</tr>
<tr>
<td><strong>Right hemisphere</strong></td>
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</tr>
<tr>
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<td>Precentral gyrus</td>
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<td>48</td>
<td>10</td>
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<tr>
<td>Superior frontal gyrus</td>
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<td>28</td>
<td>0</td>
</tr>
<tr>
<td>Middle frontal gyrus</td>
<td>97</td>
<td>48</td>
<td>34</td>
</tr>
<tr>
<td>Precuneus</td>
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<td>12</td>
<td>-64</td>
</tr>
<tr>
<td>Inferior frontal (orbital part)*</td>
<td>34</td>
<td>32</td>
<td>28</td>
</tr>
<tr>
<td>Pallidum*</td>
<td>31</td>
<td>12</td>
<td>6</td>
</tr>
<tr>
<td>Cerebellum</td>
<td>28</td>
<td>22</td>
<td>-42</td>
</tr>
<tr>
<td>Hippocampus</td>
<td>11</td>
<td>28</td>
<td>-34</td>
</tr>
<tr>
<td><strong>Ambiguous statements &gt; False-font baseline</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Left hemisphere</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Middle occipital gyrus*</td>
<td>5158</td>
<td>-26</td>
<td>-90</td>
</tr>
<tr>
<td>Precentral gyrus</td>
<td>1450</td>
<td>-46</td>
<td>6</td>
</tr>
<tr>
<td>Inferior parietal gyrus*</td>
<td>1051</td>
<td>-40</td>
<td>-42</td>
</tr>
<tr>
<td>Supplementary motor area</td>
<td>661</td>
<td>-2</td>
<td>4</td>
</tr>
<tr>
<td>Middle temporal gyrus</td>
<td>122</td>
<td>-60</td>
<td>-28</td>
</tr>
<tr>
<td>Caudate</td>
<td>96</td>
<td>-16</td>
<td>-4</td>
</tr>
<tr>
<td>Cerebellum (7b)*</td>
<td>51</td>
<td>-32</td>
<td>-68</td>
</tr>
<tr>
<td>Cerebellum (9)</td>
<td>25</td>
<td>-20</td>
<td>-40</td>
</tr>
<tr>
<td>Thalamus</td>
<td>15</td>
<td>-4</td>
<td>-30</td>
</tr>
<tr>
<td><strong>Right hemisphere</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Superior occipital gyrus</td>
<td>546</td>
<td>30</td>
<td>-66</td>
</tr>
<tr>
<td>Inferior frontal (opercular part)</td>
<td>419</td>
<td>46</td>
<td>12</td>
</tr>
<tr>
<td>Superior frontal gyrus</td>
<td>81</td>
<td>30</td>
<td>0</td>
</tr>
<tr>
<td>Inferior frontal (orbital part)*</td>
<td>61</td>
<td>34</td>
<td>26</td>
</tr>
<tr>
<td>Pallidum*</td>
<td>50</td>
<td>12</td>
<td>6</td>
</tr>
<tr>
<td>Caudate</td>
<td>27</td>
<td>16</td>
<td>0</td>
</tr>
</tbody>
</table>

* Indicates shared brain regions significantly activated across the verbal, visual and ambiguous statements.
Higher-order contrasts were conducted to evaluate the main effects across the three statement conditions, and confirmed a number of differences in activated brain regions and coordinates, summarised in Table 6.7, Table 6.8 (and also in Appendix B, Table B.1). In particular, when compared to the verbal statement condition, the visual statements and the ambiguous statements commonly elicited significantly greater activation in the left inferior parietal gyrus, left precuneus and left and right superior frontal gyrus; areas implicated in visuospatial processing (see Table 6.7 and Figure 6.6). Sentence verification of the verbal statements was associated with greater activity core language areas relative to the other statement types. More specifically, the verbal statements showed larger left inferior frontal gyrus (orbital part) regions compared to the visual statements, and a larger cluster of activity in the superior temporal gyrus, compared to the ambiguous verbal-visual statements (see Table 6.8 and Figure 6.7).

Figure 6.6. Main effects for the visual > verbal statement condition (red; FWE, \( p < .05 \)) and the ambiguous > verbal statement condition (green; FWE, \( p < .05 \)), collapsed for the entire sample. These regions represented are listed in Table 6.7.

Figure 6.7. Main effects for the verbal > visual statement condition (red; FWE, \( p < .05 \)) and the verbal > ambiguous condition (green; FWE, \( p < .05 \)), collapsed for the entire sample. These regions are listed in Table 6.8.
Table 6.7. Higher-order contrasts showing brain areas with greater activity during the visual and the ambiguous statements relative to the verbal statement condition, collapsed for participants with low and high AQ scores (FWE, $p < .05$, $K_E > 10$ voxels).

<table>
<thead>
<tr>
<th>Cluster (KE)</th>
<th>MNI coordinates</th>
<th>Brodmann area</th>
<th>Statistics</th>
</tr>
</thead>
<tbody>
<tr>
<td>x</td>
<td>y</td>
<td>z</td>
<td></td>
</tr>
</tbody>
</table>

**Visual > Verbal statements**

**Left hemisphere**
- Inferior parietal gyrus: 747, -50, -34, 46, 40, 7.57
- Precuneus: 733, -10, -72, 58, 7, 7.16
- Superior frontal gyrus: 466, -22, 6, 62, 6, 7.61
- Inferior temporal gyrus: 234, -54, -60, -6, 37, 7.27
- Precentral gyrus: 86, -50, 4, 26, 44, 6.35
- Calcarine fissure: 80, -12, -62, 18, 18, 6.01
- Inferior frontal (triangular part): 64, -40, 32, 18, 46, 6.28
- Parahippocampus: 38, -30, -42, -10, -, 6.35
- Cerebellum (6): 25, -22, -68, -26, -, 6.81
- Cerebellum (9): 14, -10, -54, -54, -, 5.89

**Right hemisphere**
- Supramarginal gyrus: 387, 44, -36, 42, 40, 6.53
- Superior frontal gyrus: 225, 28, 4, 58, 6, 6.91
- Angular gyrus: 221, 42, -74, 38, 39, 7.26
- Inferior temporal gyrus: 153, 52, -52, -14, 37, 7.26
- Precuneus: 117, 14, -58, 22, 23, 6.60
- Inferior frontal (opercular part): 114, 52, 8, 22, 44, 7.61
- Cerebellum (6): 102, 34, -46, -38, -, 7.53
- Inferior frontal (triangular part): 52, 48, 36, 14, 46, 5.93
- Fusiform gyrus: 51, 32, -36, -14, 36, 5.98
- Cerebellum (6): 48, 22, -66, -26, -, 6.03
- Cerebellum (9): 35, 12, -56, -50, -, 6.15

**Ambiguous > Verbal statements**

**Left hemisphere**
- Inferior parietal gyrus: 490, -36, -42, 46, 7, 7.18
- Precuneus: 340, -8, -70, 58, 7, 6.90
- Middle occipital gyrus: 176, -50, -72, -2, 19, 6.28
- Superior frontal gyrus: 173, -24, -2, 58, 6, 6.44
- Middle cingulate gyrus: 40, -8, 16, 38, 32, 5.33
- Precentral gyrus: 26, -48, 4, 26, 44, 5.77
- Supplementary motor area: 25, -6, -6, 62, 6, 5.65
- Cerebellum (6): 24, -30, -50, -34, -, 5.25

**Right hemisphere**
- Middle occipital gyrus: 1029, 36, -74, 38, 39, 7.14
- Inferior temporal gyrus: 407, 52, -50, -14, 37, 6.64
- Superior frontal gyrus: 167, 26, 8, 58, 6, 6.44
- Inferior frontal (opercular part): 128, 50, 8, 22, 44, 6.90
- Middle cingulate gyrus: 122, 6, -36, 42, 31, 6.04
- Middle frontal gyrus: 30, 34, 32, 42, 9, 6.35
Table 6.8. Higher-order contrasts showing brain areas with greater activity during the verbal statements relative to the visual and ambiguous statement conditions, collapsed for participants with low and high AQ scores (FWE, $p < .05$, $K_E > 10$ voxels).

<table>
<thead>
<tr>
<th>Cluster $(K_E)$</th>
<th>MNI coordinates</th>
<th>Brodmann area</th>
<th>Statistics $Z$</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Verbal &gt; Visual statements</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Left hemisphere</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Inferior frontal (orbital part)</td>
<td>766</td>
<td>-48 22 -6 47</td>
<td>7.21</td>
</tr>
<tr>
<td>Inferior occipital gyrus</td>
<td>517</td>
<td>-18 -96 -6 18</td>
<td>7.10</td>
</tr>
<tr>
<td>Posterior cingulate gyrus</td>
<td>13</td>
<td>-10 -52 30 23</td>
<td>5.27</td>
</tr>
<tr>
<td><strong>Right hemisphere</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Calcarine fissure</td>
<td>704</td>
<td>14 -88 -2 17</td>
<td>7.08</td>
</tr>
<tr>
<td>Middle temporal gyrus</td>
<td>201</td>
<td>46 -34 -2 21</td>
<td>6.07</td>
</tr>
<tr>
<td>Inferior frontal (triangular part)</td>
<td>86</td>
<td>50 24 -2 47</td>
<td>6.68</td>
</tr>
<tr>
<td>Middle temporal pole</td>
<td>35</td>
<td>50 12 -26 38</td>
<td>6.56</td>
</tr>
<tr>
<td>Cerebellum (crus 1)</td>
<td>47</td>
<td>32 -80 -34 -</td>
<td>6.04</td>
</tr>
<tr>
<td>Middle cingulate gyrus</td>
<td>14</td>
<td>2 -20 34 23</td>
<td>6.90</td>
</tr>
<tr>
<td><strong>Verbal &gt; Ambiguous statements</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Left hemisphere</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Superior temporal gyrus</td>
<td>649</td>
<td>-58 -2 -14 22</td>
<td>7.24</td>
</tr>
<tr>
<td>Calcarine fissure</td>
<td>439</td>
<td>-10 -88 -2 18</td>
<td>7.27</td>
</tr>
<tr>
<td>Inferior temporal gyrus</td>
<td>57</td>
<td>-42 -6 -38 20</td>
<td>6.06</td>
</tr>
<tr>
<td><strong>Right hemisphere</strong></td>
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</tr>
<tr>
<td>Cerebellum (crus 2)</td>
<td>158</td>
<td>22 -80 -38 -</td>
<td>6.73</td>
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<tr>
<td>Lingual gyrus</td>
<td>45</td>
<td>10 -80 -2 18</td>
<td>5.38</td>
</tr>
<tr>
<td>Calcarine fissure</td>
<td>17</td>
<td>14 -92 10 17</td>
<td>5.12</td>
</tr>
</tbody>
</table>

**Region of Interest Analyses: AQ Group Differences in Reading Verification**

Due to a large number of participants with left hemisphere language and bilateral visuospatial functions, it was not possible to deduce the function preferentially activated during the reading task with reference to their lateralisaton pattern (as previously done in Chapter 6). To examine AQ group differences in language and visuospatial activity across the three sets of statements a series of 2 x 3 ANOVAs were conducted on each ROI, with beta fit (percent signal change) values extracted from participants. A significant main effect of statement condition was found across all of the language ROIs and the visuospatial ROIs (see Table 6.9).
Table 6.9. Region of interest ANOVA analysis summarising significant main effects of statement condition and the follow-up pair-wise comparisons for the reading sentence verification task (uncorrected, $p < .001$, $K_E > 10$ voxels).

<table>
<thead>
<tr>
<th>Cluster $(K_E)$</th>
<th>MNI coordinates $(x, y, z)$</th>
<th>Brodmann area</th>
<th>Significance tests comparing beta fit signals</th>
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</thead>
<tbody>
<tr>
<td>Language ROIs</td>
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<tr>
<td>Left inferior frontal (orbital part)</td>
<td>264 -48 24 -6 47</td>
<td>47</td>
<td>74.83 Verbal &gt; Visual = Ambiguous</td>
</tr>
<tr>
<td>Right inferior frontal (orbital part)</td>
<td>60 52 30 -6 47</td>
<td>47</td>
<td>19.39 Verbal &gt; Visual = Ambiguous</td>
</tr>
<tr>
<td>Left superior temporal gyrus</td>
<td>131 -58 -2 -14 22</td>
<td>22</td>
<td>51.63 Verbal &gt; Ambiguous &gt; Visual</td>
</tr>
<tr>
<td>Right superior temporal gyrus</td>
<td>541 52 -40 18 22</td>
<td>22</td>
<td>32.39 Ambiguous &gt; Verbal &gt; Visual</td>
</tr>
<tr>
<td>Visuospatial ROIs</td>
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<td></td>
<td></td>
</tr>
<tr>
<td>Left angular gyrus</td>
<td>106 -38 -78 30 39</td>
<td>39</td>
<td>89.20 Visual &gt; Ambiguous &gt; Verbal</td>
</tr>
<tr>
<td>Right angular gyrus</td>
<td>75 35 -76 30 39</td>
<td>39</td>
<td>74.52 Visual &gt; Ambiguous &gt; Verbal</td>
</tr>
<tr>
<td>Left dorsomedial prefrontal cortex</td>
<td>1168 -22 4 62 6</td>
<td>6</td>
<td>111.84 Visual &gt; Ambiguous &gt; Verbal</td>
</tr>
<tr>
<td>Right dorsomedial prefrontal cortex</td>
<td>1422 26 10 50 6</td>
<td>6</td>
<td>65.09 Visual = Ambiguous &gt; Verbal</td>
</tr>
<tr>
<td>Left extrastriate cortex</td>
<td>128 -34 -80 34 39</td>
<td>39</td>
<td>106.07 Visual &gt; Ambiguous &gt; Verbal</td>
</tr>
<tr>
<td>Right extrastriate cortex</td>
<td>55 42 -74 38 39</td>
<td>39</td>
<td>98.50 Visual &gt; Ambiguous &gt; Verbal</td>
</tr>
<tr>
<td>Left fusiform gyrus</td>
<td>122 -30 -35 -14 36</td>
<td>36</td>
<td>80.40 Visual &gt; Ambiguous = Verbal</td>
</tr>
<tr>
<td>Right fusiform gyrus</td>
<td>433 34 -36 -14 36</td>
<td>36</td>
<td>55.86 Visual &gt; Ambiguous = Verbal</td>
</tr>
<tr>
<td>Left inferior parietal gyrus</td>
<td>888 -36 -40 46 40</td>
<td>40</td>
<td>116.27 Visual &gt; Ambiguous &gt; Verbal</td>
</tr>
<tr>
<td>Right inferior parietal gyrus</td>
<td>496 44 -36 46 40</td>
<td>40</td>
<td>89.82 Visual &gt; Ambiguous &gt; Verbal</td>
</tr>
<tr>
<td>Left posterior cingulate</td>
<td>160 -10 -59 14 23</td>
<td>23</td>
<td>51.96 Visual &gt; Ambiguous = Verbal</td>
</tr>
<tr>
<td>Right posterior cingulate</td>
<td>146 12 -58 18 23</td>
<td>23</td>
<td>72.08 Visual &gt; Ambiguous &gt; Verbal</td>
</tr>
</tbody>
</table>
Within the language ROIs, Bonferroni adjusted post-hoc analyses (α < .017) revealed significantly greater activity in the left and right inferior frontal gyrus (orbital part), and, the left superior temporal gyrus for verification of the verbal statements compared to verification of the visual and the ambiguous statements. The right superior temporal language ROI showed significantly greater activation for the ambiguous statements, relative to the verbal and the visual statements. In the visuospatial ROIs, the left and right angular gyrus, extrastriate cortex, fusiform gyrus, inferior parietal cortex, posterior cingulate and the left dorsomedial prefrontal cortex showed highest activation during the visual statements compared to the ambiguous and the verbal statements. The ambiguous statements showed relatively greater activity than the verbal statements across most of the visuospatial ROIs, except the left posterior cingulate.

None of the main effects of AQ group were significant across the language ROIs and visuospatial ROIs. However, an AQ group x statement condition interaction was found in the right dorsomedial prefrontal cortex; a visuospatial ROI (see Figure 6.8). Post-hoc t-tests indicated that while the high AQ group showed a slight increase in right dorsomedial prefrontal cortex activity during verification of the visual statements, the low AQ group showed deactivation. The opposite pattern of activity was observed for the ambiguous statements, where participants with high AQ scores showed deactivation in the right dorsomedial prefrontal cortex whereas, those with low AQ scores showed an increase in activity.

![Figure 6.8](image_url)

*Figure 6.8.* Mean percent change (beta fit) signals in the right dorsomedial prefrontal ROI during reading sentence verification, for participants with low and high AQ scores.
Associations between Right Dorsomedial Prefrontal Activity during Sentence Verification and Cognitive Profile

The relationship between right dorsomedial prefrontal activity during sentence verification and verbal-visuospatial ability profile was then examined for participants with low and high levels of autistic traits. Since the right dorsomedial prefrontal cortex is a visuospatial ROI, activity in this region during sentence verification performance should correlate more strongly with visuospatial abilities than language abilities. Beta fit (percent signal change) values were individually extracted from the right dorsomedial prefrontal cortex for each of the three statement conditions and were correlated with the WAIS-IV scores on the verbal (Vocabulary) and visuospatial (Visual Puzzles) assessments measures, for the two AQ groups (see Table 7.0). None of the correlations for the high AQ group were significant. However, for low AQ group, right dorsomedial prefrontal activation during the verbal statement condition was negatively associated with WAIS-IV Vocabulary scores, where participants with better verbal abilities showed less activation (or more deactivation) in the right dorsomedial prefrontal cortex.

Table 7.0. Pearson’s correlations between beta fit signals in the right dorsomedial prefrontal ROI during reading verification, with Wechsler verbal (Vocabulary) and visuospatial (Visual Puzzles) ability scores, for the low and high AQ groups.

<table>
<thead>
<tr>
<th></th>
<th>Low AQ (n =17)</th>
<th>High AQ (n =16)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Verbal abilities</td>
<td>Visuospatial abilities</td>
</tr>
<tr>
<td>Right dorsomedial prefrontal activity</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Verbal statements</td>
<td>-0.57*</td>
<td>-0.45</td>
</tr>
<tr>
<td>Visual statements</td>
<td>0.20</td>
<td>0.04</td>
</tr>
<tr>
<td>Ambiguous statements</td>
<td>-0.16</td>
<td>-0.32</td>
</tr>
</tbody>
</table>

*p < .05, two-tailed.

7.3 Discussion

Using fMRI, Experiment 6 examined the functional characteristics of frontal-temporal and frontal-parietal-occipital regions underlying language and visuospatial functions, in adults selected for low and high levels of autistic-like traits. We assessed whether cerebral networks for language and visuospatial functions in the high AQ group differed in organisation from the low AQ group, and if altered hemispheric or regional responses in these areas fitted with predictions of the
TiP account. Rates of atypical cerebral lateralisation were unexpectedly high compared to Chapter 6 (Experiment 5). Most participants with low (81.25%) and high (68.75%) levels of autistic traits were found to show (typical) left-lateralised activity for word generation but atypical bilateral activation for visual short-term memory. There was also limited support for superior visuospatial recruitment of parietal-occipital regions, or reduced language activation in frontal-temporal regions in the high AQ group during reading verification of verbal, visual and ambiguous statements, as was predicted under the TiP account. Instead, circumscribed differences in subcortical language (insular, putamen) and frontal visuospatial (dorsomedial prefrontal) activity were found in the right hemisphere of the high AQ sample. These fMRI results fit the idea that poor spatial resolution of fTCD in Chapter 6 is likely to have precluded detection of subtle, focal differences in language and visuospatial processing between individuals with low and high levels of autistic traits.

Unlike Chapter 6 (Experiment 5) where group differences in language activity were not found on the word generation task, the high autistic trait sample in the present study showed elevated responses in right hemisphere insular and putamen ROIs relative to those with low autistic traits. Located subcortically, the insular and putamen have neural projections closely connected to frontal-temporal regions (Ardila, Bernal, & Rosselli, 2014; Catani et al., 2012), and serve a central role in articulatory control of speech (Price, 2012). Articulatory control refers to the preparatory elements of internalised speech, where the insular and putamen are involved with verbal planning and coordination of motor programs, facilitating access to phonemic (word sound) rules during verbal fluency (Palmer et al., 2001).

Although heightened activation in right hemisphere insular and putamen ROIs could reflect more sophisticated verbal planning in the high AQ group, this is unlikely since they also displayed a behavioural trend towards poorer word generation relative to the low AQ group. Similar to the pattern of results found in this study, Kleinhans et al. (2008) reported greater right hemisphere insular cortex activity in autistic individuals which occurred in conjunction with behavioural difficulties with verbal fluency. Consequently, it is plausible that augmented right hemisphere insular responses could reflect increasing cognitive demands on articulatory speech plans when tasks are difficult or unfamiliar.
Finding stronger right putamen ROI activity in the high AQ sample opposes the direction and pattern of hemispheric responses in ASC, where weaker activity in the left putamen during verbal fluency has been associated with more severe repetitive behavioural symptoms (Kenworthy et al., 2013). Maladaptive behavioural symptoms in ASC are likely to be absent or less pronounced in our non-clinical sample with high levels of autistic traits and might explain the lack of group differences in left putamen ROI activity. This explanation does not, however, address why our recruited low and high autistic trait samples were differentiated on their profile of neural responses particularly in right hemisphere subcortical language regions.

Where atypical right hemisphere language activity has been documented in ASC, studies have generally compared the magnitude of group differences (e.g. Bodaert et al., 2003; Kleinhans et al., 2008; Takeuchi et al., 2004), without directly examining whether this stemmed from underlying differences in brain activation or deactivation in those regions. When beta fit percentage signal changes in the right insular (Figure 4, left panel) and right putamen (Figure 4, right panel) were further examined, these language ROIs were generally deactivated across two AQ groups, but were considerably less deactivated for participants with levels of high autistic traits. Challenging the notion that cerebral regions relevant for task performance should show an increase in activation relative to baseline, several regions within the frontal-temporal network have been found to show deactivation in neurotypical samples during language performance (Hutchinson et al., 1999; Moreno, Schiff, & Hirsch, 2015).

During verbal fluency, neural deactivation could arise from the redistribution of blood flow to neighbouring areas (known as the vascular steal effect) (Kannurpatti & Biswal, 2004), or result from inhibitory feedback systems in the frontal-temporal language network (Hutchinson et al., 1999). Intriguingly, the degree of deactivation in the right insular or right putamen ROIs during verbal fluency was not significantly correlated with outside scanner estimates of word generation task performance, for the low and the high AQ groups. One limitation is verbal fluency was not assessed during fMRI scanning due to concerns of in-scanner head movement artefacts associated with overt speech production. Consequently, it cannot be verified as to whether behavioural estimates of verbal fluency obtained during fMRI scanning
might have been more closely associated with right insular or right putamen deactivation, which differentiated the low and high autistic trait samples.

Another possibility is that null associations between behavioural performance on the word generation task and neural responses in the right insular or right putamen ROIs could arise if neural mechanisms underlying verbal fluency are not centrally regulated by ‘top-down’ processing. This suggestion appears to fit with findings by Wood, Saling, Abbott and Jackson (2001) showing reliable associations between degree of left inferior frontal gyrus activity and out-of-scanner estimates of verbal fluency in a general population sample, implicating a central regulatory role in frontal (rather than subcortical) language regions. Similarly, in a functional connectivity study (Fu et al., 2006) manipulating the complexity of verbal fluency, contrasts between a ‘difficult’ versus ‘easy’ fluency condition was associated with inhibitory responses in the middle frontal gyrus onto areas downstream of the language circuitry.

If frontal language areas exert similar suppressive effects on the insular and putamen cortex during verbal fluency, then less deactivation in the high AQ group might represent altered frontal connectivity associated with centrally regulating task difficulty when faced with increasing task demands requiring more cognitive effort. A functional connectivity study could provide more detailed information regarding the frontal-temporal language network underlying verbal fluency, specifically whether downstream circuits from the frontal cortex to the insular and putamen ROIs are differentially affected between individuals with low versus high levels of autistic traits.

Despite appearing to show less pronounced right insular and right putamen deactivation in the high autistic trait sample, the laterality analyses revealed typical left-language specialisation for most participants in the high (100.00%) and the low (93.75%) AQ groups (Figure 6.5). That is, local activation differences in the right putamen and right insular ROIs might not have been significant enough to differentiate the low and high AQ groups on language lateralisation, once pooled across the frontal-temporal language ROIs in the left and right hemispheres. Finding typical left-side language specialisation in our high autistic trait sample is consistent with Chapter 6 (see Figure 5.2), but contrasts with other fMRI studies implicating atypical functional lateralisation in multiple areas within the frontal-temporal language network of autistic individuals (Boddaert et al., 2003; Gervais et al., 2004;
Atypical language lateralisation is more commonly found in autistic individuals with more severe language impairments, suggesting that the development of hemispheric specialisation may, in part, influence language abilities (Anderson et al., 2010; De Fosse et al., 2004; Floris et al., 2016). Relative to individuals with a clinical diagnosis of ASC, the recruited sample of undergraduate students with high levels of autistic traits might have more subtle language weaknesses, possibly explaining the focal pattern of activation differences the frontal-temporal language network. One advantage of the present study is that bootstrapping methods were employed to calculate participant LIs across multiple threshold levels, whereas the two previous fMRI studies examining verbal fluency in ASC (Kenworthy et al., 2013; Kleinhans et al., 2008) used a single threshold level to extract cerebral activity in ROIs within the left and right hemispheres. The problem with single thresholding is that it does not permit data from individuals with subthreshold activity in the regions of interest to be analysed, resulting in exclusion of some autistic and neurotypical participants from the LI analyses. Given that the bootstrapping LI analyses are threshold-independent and relatively more resistant to outliers than single threshold methods (for a review, see Bradshaw et al., 2017), our findings of left-lateralised language in individuals with low and high levels of autistic traits are likely to be robust.

Contrary to predictions, the high autistic trait sample showed considerable overlap in frontal-parietal-occipital visuospatial activity with their low autistic trait counterparts during visual short-term memory performance. While studies have reported stronger activation in autistic individuals compared to neurotypical controls particularly in parietal-occipital regions (Manjaly et al., 2007; Ring et al., 1999; Samson et al., 2012), our ROI analyses did not differentiate the AQ groups on inferior parietal, superior parietal, fusiform or extrastriate activity during visuospatial task performance. Additionally, where the high autistic trait sample in Chapter 6 (Experiment 5) showed weakened right hemisphere lateralisation for visual short-term memory functions, this was not the case in the current experiment.

The frequency of atypical visuospatial lateralisation was unexpectedly elevated for the low and high AQ groups (68.75 to 81.25%) when compared to the previous fTCD experiments involving adults selected for autistic-like traits.
(7.69 to 25.00%) (in Chapter 6) as well as general population samples (8.00 to 16.00%) (in Chapters 4 and 5). Although poor spatial resolution of fTCD could explain discrepant results on visuospatial laterality, the language laterality results from this fMRI experiment is consistent with fTCD findings from Chapter 6 in that most of the low and high AQ samples showed typical lateralisation.

To further reconcile differences between the fMRI and fTCD results on visuospatial laterisation, follow-up fMRI laterality analyses using MCA cortical territory were conducted (see Appendix B, Figure B.1). However, these analyses continued to revealed bilateral organisation for visual short-term memory functions across a majority of participants in the low (87.50%) and high (87.50%) autistic trait samples. When taken together, these results point towards the significance of methodological differences between the designs of the visual short-term memory tasks used in the fMRI and fTCD studies.

In Chapter 6 (Experiment 5), the visual short-term memory task did not contain an attention baseline condition, making it difficult to distinguish whether weakened right visuospatial laterisation in the high autistic trait sample arises from differences in visual encoding, retention or recognition. In this study, the contrast between cerebral activation during the visual memory condition minus cerebral activation during the attention baseline condition was designed to examine cognitive processes underlying memory retention of the spatial array. However, if the attention baseline condition also required some degree of visuospatial encoding, retention and recognition processing (i.e. eliciting right-lateralised visuospatial activity), block-subtractions from the experimental condition could result in a more (symmetric) bilateral pattern of visuospatial activity.

Given that most studies assessing visual short-term memory have contrasted task-related activity with a fixation baseline condition (e.g. Song & Jiang, 2006; Todd & Marios, 2004), comparisons with our study are difficult to make. Future fMRI and fTCD research could incorporate a baseline rest condition, along with the visual memory and attention baseline conditions to examine how the magnitude and directionality of visuospatial lateralisation varies across these three conditions. It is also recommend that the proposed visual short-term memory task is piloted on a general population sample, before assessing the possibility of differences in visuospatial laterality between individuals selected for low and high levels of autistic traits.
The TiP account of autism was evaluated by comparing relative recruitment of cerebral regions in verbal semantic and visuospatial networks among participants with low and high levels of autistic traits during reading verification performance. Before discussing these results, one caveat was that failure to sufficiently localise participants’ dominant visuospatial cerebral hemisphere meant that it was not possible to account for individual variability in cerebral lateralisation in the current investigation of the TiP framework. Consequently, information processing biases in the low and high AQ groups on the verification task could not be examined on an individual-level (conducted in Experiment 5), as to whether each participant preferentially recruited neural processes in their language or visuospatial cerebral hemisphere. Instead, for low and high autistic trait samples, group-level differences in neural responses were examined by comparing levels of activity in frontal-temporal language ROIs and frontal-parietal-occipital visuospatial ROIs during verification of verbal, visual and ambiguous statements. The relative profile of verbal and visuospatial abilities in the low and high AQ groups were also examined to further assess the potential influence of these cognitive abilities in the TiP framework.

Representing a milder variation of the discrepant verbal-visuospatial profile observed in Chapters 3 and 6, the high autistic trait sample exhibited trends towards better visuospatial abilities on the Wechsler Visual Puzzle subtest and weaker verbal abilities on the word generation task. On the reading verification task, the low and high AQ samples recruited similar activity across the language ROIs, but showed a divergent pattern of responses in the right dorsomedial prefrontal ROI of the visuospatial network. Like Chapter 6, our fMRI results suggest that individuals with levels of high autistic traits can sufficiently recruit language to support reading comprehension, but also illustrate that they enlist visuospatial mental representations differently to their low autistic trait counterparts.

The interaction effect of group and statement condition for beta fit signals in the right-dorsomedial prefrontal cortex provides preliminary evidence for functional differences in the visuospatial network for individuals with high versus low autistic trait levels, as is expected within the TiP account of autism. The dorsomedial prefrontal cortex services spatial working memory and executive control functions, with right hemisphere prefrontal-parietal connections closely linked to flexible problem-solving of visuospatial information (Corbetta, Patel, & Shulman, 2008;
Thiebaut de Schotten et al., 2011; for reviews, see Corbetta & Shulman, 2002; Miller & Cohen, 2001). During reading, spatial working memory provides temporary storage and manipulation of visuospatial content and mental-imagery, while executive control processes help the reader to problem-solve and decode inferences from written text (for reviews, see Baddeley, 2010; Ferstl, Neumann, Bogler, & von Cramon, 2008). Event-related fMRI studies have also documented incremental changes in prefrontal activity (relative to a baseline control condition) in general population samples during visuospatial and executive function task performance (for a review, see Levy & Goldman-Rakic, 2000). This is relevant because it highlights that increased activation (rather than deactivation) of the dorsomedial prefrontal cortex is expected when tasks require visuospatial and executive control processing, helping to link the profile of beta fit signals with processing strategies among the two AQ groups.

Interestingly, despite showing comparable performance across the three statement conditions, AQ group differences in activation/deactivation profiles of the right dorsomedial prefrontal ROI were evident during verification of the visual and ambiguous statements, but not the verbal statements (see Figure 6.8). For the verbal statement condition, the two groups commonly exhibited deactivation of the right dorsomedial prefrontal cortex, possibly reflecting an absence of visuospatial and executive control processing, or alternatively, neural inhibition of visuospatial regions that are not central for processing verbal statements. Tenuously supporting the latter suggestion, during the verbal statement condition, negative correlations between right dorsomedial prefrontal activity and Wechsler Vocabulary scores for the low AQ group indicate that participants with better language abilities showed larger deactivation in the visuospatial ROI (see Table 7.0). The absence of such associations in the high AQ group potentially suggests disparate links between language abilities and prefrontal regulation (e.g. suppression) of visuospatial and/or executive processing during reading verification of verbal statements. However, given that these correlation analyses were not conducted based on a priori hypotheses, a functional connectivity study in a larger sample of individuals with low and high levels of autistic traits during the reading sentence verification task would be necessary to draw firm conclusions.

In comparison with the Kana et al. (2006) study where autistic individuals showed similar recruitment of parietal-occipital visuospatial areas during low-
imagery and high-imagery statements, the high autistic trait sample displayed a
different pattern of prefrontal responses on the verbal and visual statement
conditions. In Figure 6.8, when the visual statements were compared to the verbal
statements, the high AQ group showed a large increase in activation (from
deactivation) in the right dorsomedial prefrontal ROI, suggesting a shift towards
visuospatial processing, or alternatively, away from language processing.
Conversely, Figure 6.8 shows deactivation of the right dorsomedial prefrontal region
for the low AQ group indicating that they were perhaps less reliant on visuospatial
processing strategies to construct meaning from visual statements. Here, the profile
of right dorsomedial prefrontal responses lends support to the TiP account, where
individuals with high levels of autistic-like traits, who show trends towards stronger
visuospatial abilities, might be more likely to vividly visualise or spatially
manipulate content in visual statements. Alternatively, individuals with low levels of
autistic-like traits, who show trends towards stronger language abilities, might
depend less on visuospatial processing strategies when solving visual statements.

The notion of cognitive biases towards visual thinking in individuals with
high levels of autistic traits is, however, questioned by the fact that they did not also
show increased activation in the right dorsomedial prefrontal ROI during verification
of the ambiguous verbal-visual statements. Unlike the high AQ group, large
activation of the right dorsomedial prefrontal ROI was evident in the low AQ group
during the ambiguous statement condition suggesting relatively greater engagement
in visuospatial and/or executive control processing. In contrast with predictions of
the TiP account, the high AQ sample did not exhibit heightened activity in the
visuospatial network (dorsomedial prefrontal, inferior parietal, angular gyrus,
posterior cingulate, middle occipital, extrastriate, fusiform areas) or reduced verbal
semantic activity (inferior frontal gyrus, superior temporal areas) on the ambiguous
statements, relative to their low AQ counterparts. These results contrast with other
fMRI studies employing ambiguous tasks, where autistic individuals were
differentiated by showing over-recruitment in parietal-occipital (e.g. inferior parietal,
extrastriate cortex, fusiform) regions of the visuospatial network during working
memory (Koshino et al., 2005, 2008) and fluid reasoning (Sahyoun et al., 2009),
whereas neurotypical individuals favoured activation in the frontal-temporal
language network (e.g. inferior frontal, superior temporal).
The representational nature of our ambiguous statements could explain why we did not detect favorable use of visuospatial processing, or heightened responses in parietal-occipital regions in our high autistic trait sample, as commonly observed in ASC. For instance, in the ambiguous (working memory and fluid reasoning) tasks administered in previous ASC studies (Koshino et al., 2005, 2008; Sahyoun et al., 2009), physical representations such as those from face and shape sequences, might provide visual cues that encourage or facilitate visuospatial encoding and manipulation of features within the stimuli. By contrast, statement stimuli in the present study required participants to mentally construct meaning from ambiguous statements without such visuospatial cues.

Another consideration is that, unlike visuospatial tasks involving physical representations, reading comprehension requires at least some basic aspect of linguistic processing (e.g. word recognition), where readers mentally transform meaning into visuospatial images (De Beni et al., 2005). It is worth noting that when statements were highly loaded with visuospatial content, as in the case for the visual statements, that high AQ group showed a large increase in right dorsomedial prefrontal ROI activity (not seen in the low AQ group), indicative of visuospatial processing. Individuals with high levels of autistic traits might be ‘atypical’ in the sense that they engage more in visuospatial processing strategies (Happé & Frith, 1994; Mottron et al., 2006) on tasks that evoke visual-imagery (e.g. visual statements), but not on tasks where language processing strategies can be applied to generate solutions (e.g. verbal and ambiguous statements).

An alternative, but complementary view is that the recruited sample of undergraduate students with high levels of autistic traits have intact verbal abilities (as measured by the Wechsler Vocabulary subtest) which could enable them to access or utilise verbal semantic resources to facilitate reading comprehension. While under-activation of the frontal-temporal language network is commonly reported in the ASC literature, there is accumulating evidence that subsets of autistic individuals with preserved or better language skills show similar recruitment of frontal-temporal (inferior frontal, middle temporal, superior temporal) activity during sentence comprehension (Anderson et al., 2010) and passive listening (Lombardo et al., 2015). In this regard, the absence of between-group differences in language ROIs activity might reflect relative sparing of verbal semantic processing in our high autistic trait group during sentence comprehension.
A novel but important finding is that our verbal, visual and ambiguous statement stimuli were differentiated by degree of activation within the language ROIs and visuospatial ROIs, in the expected directions (see Table 6.9). Comparisons of the statement conditions revealed that verification of verbal statements produced greatest activity in most language ROIs, while the visual statements showed greatest activity across the visuospatial ROIs, in line with self-reported strategies obtained from an unselected sample (in Chapter 2, Experiment 1). These results are also in agreement with a previous fMRI study in general population undergraduate students which documented similar effects of statement condition during low- versus high-imagery statements (Just et al., 2004b), and add support for distinctions between the verbal semantic and visuospatial cerebral networks (Binder et al., 2009).

Furthermore, finding an intermediate level of activation across language ROIs and visuospatial ROIs during the ambiguous statement conditions strengthens suggestions that these statements are amenable to verbal semantic and visuospatial mental representations, even though the high AQ group did not favour visuospatial processing modalities.

To my knowledge, this is the first study to provide evidence for functional differences in verbal semantic and visuospatial networks in individuals with high levels of autistic traits, which could reflect increased cognitive effort or use of alternative strategies relative to their low autistic trait counterparts. As well as showing a trend towards poorer verbal fluency, the high AQ sample exhibited less deactivation in right hemisphere subcortical (insular and putamen) regions of the language network. Furthermore, group differences in right hemisphere dorsomedial prefrontal responses in the high AQ group likely reflected greater use of visuospatial and/or executive control processing during comprehension of visual statements, although they seemed to depend less on these strategies when verifying ambiguous statements. Most importantly, focal activation differences in two language (insular, putamen) regions and one visuospatial (dorsomedial prefrontal) region were not significant enough to differentiate samples with low and high levels of autistic traits on pattern of cerebral lateralisation, or on verbal-visual thinking preferences within the TiP framework. In the next chapter, the results from all six experiments contained in this thesis were summarised with implications of the findings also discussed.
Chapter 8: General Discussion
8.1 A Recap of the Aims of This Thesis

Proposed by Kunda and Goel (2011), the TiP account attributes uneven patterns of performance on verbal and visuospatial tasks in people on the autism spectrum to a strong cognitive bias towards visual thinking. The studies reported in this thesis were motivated by previous research on the TiP framework that revealed cortical differences between autistic and neurotypical comparison groups during sentence comprehension (Anderson et al., 2010; Eyler et al., 2012; Harris et al., 2006; Just et al., 2004a; Kana et al., 2006; Redcay & Courchesne, 2008; Takeuchi et al., 2004), and also by evidence linking atypical cerebral lateralisation to comparatively weaker verbal than visuospatial skills (Herringshaw et al., 2016; Preslar et al., 2014). The aim of this thesis was to address the TiP account of autism by developing understanding of the cognitive and neural mechanisms underpinning verbal and visuospatial skills in adults with high versus low levels of autistic-like traits. To achieve this broad aim, the research conducted for this thesis included developing a novel sentence verification task, and then using it to examine the role of cognitive abilities, cognitive biases and cerebral lateralisation within the TiP framework.

The six experimental studies included in this thesis can be broadly divided into two distinct arms. First, I attempted to develop three distinct sets of statements for a sentence verification task, where one set would predominantly invoke verbal processing, a second set would predominantly invoke visual processing, and the third set would predominantly invoke verbal processing for some participants and visual processing for others. These were labelled the verbal, visual and ambiguous statements. The aim in developing these sets of statements was to provide task conditions that might be conducive to identifying differences in the employment of verbal and visuospatial reasoning strategies between samples selected to differ in autistic traits. The second feature of my methodological approach was to use two tasks widely accepted in the neuroimaging literature as gold-standard instruments for ascertaining the direction and strength of lateralisation for language (the word generation task) and visuospatial function (the visual short-term memory task). By administering gold standard laterality measures with fTCD and fMRI, the results from this thesis provide new insights into the TiP framework and cerebral lateralisation in individuals with high versus low levels of autistic traits.
In this final chapter, the results from the task-development studies are summarised with reference to the utility of our sentence verification paradigm for assessing the TiP framework. This is followed by a more comprehensive discussion of the three empirical studies addressing the TiP framework in adults selected for low and high levels of autistic traits, as measured by the AQ. Five key findings relevant to verbal and visuospatial characteristics of the high AQ sample will be discussed, along with implications for the TiP account. This is followed by a discussion on methodological limitations and suggestions for future research.

8.2 Test-Development Studies: Establishing a New Task for Assessing the TiP Account of Autism

To establish whether cognition in people on the autism spectrum reflects a shift towards visual thinking, it is important to develop test measures that account for normal variability in verbalising and visualising test-tasking approaches. Individual differences in information processing style can influence the degree to which people within the general population spontaneously verbalise or visualise information to construct meaning during sentence comprehension (Mayer & Massa, 2003; Wyer et al., 2008). This means that the same statement can be processed differently by different people. Yet, previous investigations on the TiP account, including work by Kana et al. (2006), have assumed that participants within the neurotypical comparison group routinely solved low- and high-imagery verification statements using respectively, verbal and visuospatial processing strategies. The approach in this thesis was to (1) develop a novel sentence verification task by considering self-reported strategies, (2) assess task utility in localising language and visuospatial cerebral functions, and (3) examine whether the task could potentially identify individual differences in verbal-visual thinking.

Using a visualising-verbalising rating scale, Experiment 1 focused on identifying potential test stimuli for the novel sentence verification task by evaluating the degree to which young adults from the general population employed visualising or verbalising strategies. Robust statistical criteria were used to analyse and categorise the initial pool of 180 candidate statement stimuli according to whether the statements were verbal, visual or ambiguous verbal-visual in nature. Statements in the verbal category were rated to be completed predominantly using verbalising strategies, and consisted of word synonyms, double-negatives, verbal
analyses and word oddity statements. Statements in the visual category were rated to predominantly require visualising strategies, and included sentences conveying alphanumeric transformations, clock positions, map representations and telephone keypad information. Statements in the ambiguous verbal-visual category comprised of alphabet representations, syllogisms, mental arithmetic and verbal-visual oddity statements, rated to be approximately equally open to verbalising and visualising strategies. To my knowledge, this study is the first to use self-report methods to empirically identify sets of verbal and visual statements for potentially assessing language and visuospatial functions, and, ambiguous statements for evaluating the degree to which individuals favour verbal versus visual information processes.

The utility of the novel sentence verification task was examined in Experiments 3 and 4 in unselected adult samples, by using fTCD imaging to measure blood flow changes to language and visuospatial cerebral hemispheres via the left and right MCAs. By using gold standard (word generation, visual short-term memory) tasks to establish directionality of language and visuospatial cerebral lateralisation, it was predicted that the verbal and the visual statements would enlist dominant activation in respective language and visuospatial cerebral hemispheres. It was also predicted that the ambiguous statements would be solved by some participants using language hemispheric processing, with the remaining participants using visuospatial hemispheric processing.

Contrary to expectations, fTCD results from Experiments 3 and 4 indicated that the sentence verification task has limited utility in localising visuospatial hemispheric functions (see Figures 3.6 and 4.4) and failed to provide evidence of individual variability in information processing biases. Across all three statement conditions, most participants in Experiments 3 (auditory presentation format) showed dominant activation in their language cerebral hemisphere, while modifying the verification task to a reading format (in Experiment 4) did not impact the pattern of fTCD results. In Experiments 3 and 4, the trajectory of MCA blood flow and strength of LIs for each statement condition were highly correlated suggesting that the verbal, visual and ambiguous verification statements might share substantial linguistic demands (Meyer et al., 2014; Uomini & Meyer, 2013), more so than initially predicted. Another possibility was that poor spatial resolution of fTCD might restrict measurement of cerebral activity outside MCA cortical territory, particularly in parietal-occipital regions (Badcock & Groen, 2017). Given that frontal-parietal-
occipital regions of the visuospatial network are more strongly lateralised in the right hemisphere (Thiebaut de Schotten et al. 2011; Thomason et al., 2008), limited spatial resolution of fTCD potentially accounts for why the verbal, visual and ambiguous verification statements were not differentiated on visuospatial hemispheric processing.

Statement type effects for reading sentence verification were further examined in Experiment 6 using high spatial resolution fMRI. This allowed us to compare the degree of cerebral activation in predefined regions within the frontal-temporal language network and the frontal-parietal-occipital visuospatial network, across the three statement types. Consistent with self-report results from Experiment 1, sentence verification of verbal statements produced greatest activity across frontal-temporal ROIs in the language network, whereas statements from the visual condition recruited greatest activity across frontal-parietal-occipital ROIs in the visuospatial network (see Table 6.9). Given that the verbal and visual statements were initially selected based on subjective (visualising-verbalising) strategy ratings and were subsequently differentiated by degree of fMRI-measured activation within language and visuospatial networks, these findings add to establishing construct validity for our verbal and visual statements.

The fMRI results also confirmed that limited spatial resolution of fTCD in Experiments 3 and 4 might have prevented detection of subtle activation differences in language and visuospatial ROIs, which differentiate the verbal and visual statements. Verification of the ambiguous statements was marked by an intermediate level of activation across ROIs in the language and visuospatial networks (see Table 6.9), suggesting that the ambiguous statements draw on the two processing modalities, but each to a lesser extent than the verbal or the visual statements. While the ambiguous statements appear to have limited construct validity in assessing the degree to which individuals show cognitive biases towards verbal or visual thinking (discussed more in Section 8.5), fMRI findings extend the self-report pilot results by distinguishing the verbal, visual and ambiguous verbal-visual statements on relative language and visuospatial cerebral demands.
8.3 Autistic-trait Comparison Studies: Investigating Cognitive Abilities, Cognitive Biases and Cerebral Lateralisation within the TiP Framework

Three studies were conducted to examine the TiP account of autism in adults selected for low and high autistic trait levels, using a dual-task methodology (Experiment 2), as well as fTCD (Experiment 5) and fMRI (Experiment 6) neuroimaging. By combining behavioural and neuroimaging techniques, these studies sought to provide a robust empirical test of the TiP framework by examining whether the high autistic trait sample show verbal and visuospatial differences evident in their (1) cognitive abilities, (2) cognitive biases and (3) pattern of cerebral lateralisation, relative to their low autistic trait counterparts. In what follows, five critical findings from the behavioural and neuroimaging studies are summarised and discussed.

8.4 Broader Phenotypic Expression of Verbal and Visuospatial Abilities as a Function of Autistic Traits within the TiP Framework

A major obstacle in understanding the role of cognitive abilities in the TiP account concerns the fact that several studies have often recruited autistic and neurotypical comparison groups to be matched on both verbal and visuospatial abilities (Damarla et al., 2010; Harris et al., 2006; Just et al., 2004a; Russell-Smith et al., 2014; Soulières et al., 2009; Wallace et al., 2009; Williams et al., 2008, 2012, 2013). While this approach enables group comparisons of potential biases in verbal versus visual thinking, it does not permit assessment of whether the profile of superior visuospatial relative to verbal abilities associated with autism can influence how individuals on the spectrum might appraise cognitive tasks. Using an unconstrained approach, participants from Experiments 2, 5 and 6 were selected from the low and high extremes of the AQ distribution and assessed on well-established verbal (word generation, Wechsler Vocabulary) and visuospatial (visual short-term memory, Wechsler Visual Puzzles) measures. From a TiP standpoint, if visual thinking is prominent in high AQ samples, their cognitive profiles should favour stronger visuospatial abilities in comparison to weaker verbal abilities.

The results from this thesis provide support that cognitive strengths in visuospatial abilities and weaknesses in verbal abilities established in ASC
(Ankenman et al., 2014; Black et al., 2009; Dawson et al., 2007; Ehlers et al., 1997; Nader et al., 2015) also extend to individuals from the general population with high levels of autistic traits. Participants in the high AQ group exhibited significantly higher scores on the Wechsler Visual Puzzles subtest (Experiment 2) and produced fewer responses on the word generation task (Experiment 5) relative to their low AQ counterparts. Additionally, non-significant trends favoured slightly stronger visuospatial abilities on the Wechsler Visual Puzzles subtest in the high autistic trait group, but comparatively weaker language abilities on the word generation (Experiment 6) and the Wechsler Vocabulary (Experiment 5) measures, relative to low autistic trait group.

From a TiP standpoint, superior Wechsler Visual Puzzles scores in our high AQ samples are understood to stem from enhanced visual thinking, where individuals are more proficient in accessing and utilising visuospatial processing strategies, relative to their low AQ counterparts. These results are consistent with the body of literature demonstrating faster and more accurate visuospatial performance on the Embedded Figures Test (for meta-analysis, see Cribb et al., 2016), visual search (Almeida et al., 2013, 2014) and on the Wechsler Block Design subtest (Grinter et al., 2009; Stewart et al., 2009) in individuals scoring on the higher extreme of the AQ distribution. One notable difference is that visuospatial advantages reported in those studies have been conceptualised within the context of the weak central coherence theory of autism (Frith & Happé 1994), under which individuals with high levels of autistic traits are assumed to have a detail-focused processing style.

Under weak central coherence theory, detailed-focused processing facilitates attention to hidden shapes in the Embedded Figures Test and other visual search tasks, and is also helpful for segmenting target configurations within the Wechsler Block Design subtest. From a weak central coherence standpoint, superior visuospatial performance in our high AQ sample could arise from focusing on the figural components in the Wechsler Visual Puzzles subtest, where participants must correctly identify (3 of 6) fragmented pieces that create a target design. However, as well as requiring detail-focused processing, the Wechsler Visual Puzzles subtest involves integrative processing in the form of ‘pulling together’ in mind the chosen three pieces, and evaluating whether the resultant image matches the target design (McCrea & Robinson, 2011). Given that weak central coherence theory posits an
associated weakness in global integration in people on the autism spectrum, it does not neatly explain how our high AQ sample achieved better Wechsler Visual Puzzle scores relative to their low AQ counterparts. Importantly, the uneven profile of visuospatial strengths in our high autistic trait groups which occurred alongside verbal weaknesses, appears to fit better with TiP assumptions of an advantage in visual-based instead of verbal-based thinking (but see Section 8.5), than with weak central coherence theory.

Where one previous correlational study has shown associations between higher AQ scores and poorer performance on verbal matrices problems (Fugard et al., 2011), our results extend this evidence by showing poorer verbal fluency (Experiments 5 and 6) in high AQ groups relative to low AQ groups. Similarly, difficulties with verbal fluency have been reported in autistic samples (Kleinhans et al., 2008; Spek et al., 2009) and shown to be linked to broader difficulties in aspects of social communication (Bishop & Norbury, 2005) and repetitive symptomology (Turner, 1999). Given that the high (and low) autistic trait samples in this thesis were recruited based on extreme total scores on the AQ measure, this design was not conducive for testing how particular dimensions of autistic traits related to limited verbal fluency.

The results from this thesis provide preliminary evidence for a broader autism phenotype characterised by enhanced visuospatial relative to verbal abilities, and therefore build on the TiP account of autism. Given that only one verbal (Vocabulary) and one visuospatial (Visual Puzzles) Wechsler subtest was administered from the core subtests required to calculate verbal and visuospatial composite scores, the cognitive profile of low and high AQ groups cannot be interpreted with confidence. Significant AQ group differences were also not consistently documented across all of the administered verbal (e.g. Wechsler Vocabulary) and visuospatial (e.g. visual short-term memory) measures. Instead, group differences were most prominent on the Wechsler Visual Puzzles subtest and word generation task, both of which are timed tasks. These results raise the possibility that visuospatial strengths and verbal weaknesses in individuals with high levels of autistic traits might begin to emerge under conditions of speeded processing or at more advanced levels of task complexity (Minshew et al., 1997; Williams, Goldstein, & Minshew, 2006). Alternatively, in autism, some aspects of verbal skills might be more affected than others, while other aspects of visuospatial skill might
develop more or less proficiently. Further clarification of these possibilities can be achieved by administering a more comprehensive battery of verbal and visuospatial measures which have embedded timed versus untimed tasks, such as the Clinical Evaluation of Language Fundamentals (Wiig, Semel, & Secord, 2003) and the Cambridge Neuropsychological Test Automated Battery (Luciana, 2003). Importantly, the verbal and visuospatial profile of individuals with high levels of autistic traits is in line with the TiP account, and so the next section considers whether the high AQ sample also exhibit cognitive biases towards visual thinking.

8.5 Testing for Differences in Cognitive Biases in Verbal-Visual Thinking in Autistic Traits using Ambiguous Statements

The set of ambiguous statements from the verification task were used to evaluate the nature of verbal-visual cognitive biases in individuals with low versus high levels of autistic traits. Dual-task methods were employed in Experiment 2 to examine the extent to which comprehension of the ambiguous statements was contingent on verbal and visuospatial processing strategies. Using fTCD, Experiment 5 assessed cerebral blood flow activity to participant’s language and visuospatial hemispheres and computed an LI during ambiguous statement verification to identify the preferred modality of processing. The use of fMRI in Experiment 6 enabled detailed comparisons of cerebral activation in specific ROIs within frontal-temporal language and frontal-parietal-occipital visuospatial networks associated with solving the ambiguous statements. Based on the TiP account, it was predicted that the high AQ sample would preferentially engage visuospatial processing to verify ambiguous statements, whereas the low AQ sample would favour use of verbal processing strategies to solve these statements.

Our dual-task, fTCD and fMRI results provide converging evidence showing typical use of verbal processing in individuals with high levels of autistic traits to support sentence comprehension, challenging the TiP assumption that thinking is predominantly visually mediated in individuals on the autism spectrum (Hurlburt et al., 1994; Grandin, 2009; Selfe, 2011). Similar to their low AQ counterparts, participants in the high AQ sample showed pronounced accuracy costs on the ambiguous statements during concurrent articulatory suppression, suggesting common engagement of verbal processing when verifying ambiguous content.
fTCD analyses of ambiguous statement LIs also revealed that most of our recruited high AQ sample showed greater activation in their language than visuospatial cerebral hemisphere on the ambiguous statements. Furthermore, using fTCD, comparisons of blood flow trajectories for the low and high AQ groups were highly correlated on the set of ambiguous statements, suggesting the possibility that common language neural mechanisms (Meyer et al., 2014) were recruited in the course of comprehending the ambiguous content. These results were confirmed by fMRI. Overlapping patterns of language activation were found for the low and high autistic trait groups across the network of frontal-temporal ROIs (i.e. inferior frontal gyrus, superior temporal areas), in the left and right hemispheres, during ambiguous verification performance. Thus, the behavioural and neuroimaging results from Experiments 2, 5 and 6 show that individuals with high AQ scores can engage in verbal thinking, and, recruit language cerebral processing to the same extent as their low AQ counterparts to facilitate ambiguous statement verification.

In demonstrating that individuals with high levels of autistic traits show intact verbal thinking, it was also necessary to evaluate the TiP hypothesis of enhanced visual thinking biases associated with the autism spectrum. While the profile of visuospatial processing in the low and high AQ groups were not distinguished by dual-task spatial tapping (in Experiment 2) and fTCD, fMRI results revealed differences in frontally-mediated visuospatial activation on the ambiguous statements. In contrast with the TiP account, the high AQ sample was found to show less activation in the right dorsomedial prefrontal ROI of the visuospatial network, relative to the low AQ sample (see Figure 6.8). The right dorsomedial prefrontal cortex subserves visuospatial working memory functions during reading, indicating the possibility that participants in the low AQ group possibly engaged in visual imagery to store and manipulate ambiguous content, to a greater extent than the high AQ group. However, close associations between dorsomedial prefrontal activation and executive control processing (for reviews, see Corbetta & Shulman, 2002; Miller & Cohen, 2001) makes it difficult to determine the extent to which heightened activation in the low AQ group could, in part, stem from utilisation of executive functions (e.g. attentional control, problem-solving) to verify ambiguous statements.

Despite appearing to engage more in visuospatial/executive function strategies, the low AQ sample performed the ambiguous statements no better than the high AQ sample (in Experiment 6). In other words, neural differences in right
dorsomedial frontal activity were not associated with behavioural differences in how accurately or quickly participants in the low and high autistic trait groups performed the ambiguous statements. Additionally, when comparing activity in parietal-occipital regions of the visuospatial network (i.e. inferior parietal gyrus, angular gyrus, posterior cingulate and fusiform) the two AQ groups showed overlapping responses during ambiguous statement verification. Taken together, our fMRI results provide more support for common rather than distinct neural mechanisms underpinning visuospatial processing in individuals with low and high levels of autistic traits. Focal differences in right dorsomedial prefrontal activity are not sufficient, by itself, to indicate between-group differences in visual thinking biases, and possibly reflect subtle differences in visuospatial and/or executive strategies between the low and high AQ samples.

The results from this thesis indicate that similar to their low AQ counterparts, individuals with high AQ scores are capable of using both visual thinking and verbal thinking to support sentence comprehension. While autistic individuals might subjectively perceive themselves as being visual thinkers (Grandin, 2009; Hurlburt et al., 1994; Selfe, 2011), it is plausible that people on the autism spectrum have at least some access to verbal mental representations (Williams et al., 2012; Winsler et al., 2007). Further clarification of this can be achieved by combining our sentence verification task with self-report measures of test-taking approaches including the verbalising-visualising scale used in Experiment 1, as well as subjective questionnaire measures assessing thinking style. Such a study could involve comparisons between groups with clinically diagnosed ASC and neurotypical controls, or non-clinical groups differing in milder autistic trait levels, to provide an in-depth understanding of how personal accounts of thinking style might map onto test-taking approaches on the verification task.

As recommended by Kunda and Goel (2011), this thesis sought to develop a behavioural measure probing the extent to which individuals prefer verbal or visuospatial information processing when solving ambiguous verbal-visual statements. However, despite efforts to construct and pilot the ambiguous verification statements to be amenable to verbalising and visualising strategies, the high and low AQ groups were differentiated only on subtle aspects of executive functions and/or visuospatial processing. In contrast, while not using ambiguous statements in their sentence verification task, Kana et al. (2006) reported elevated
fMRI visuospatial responses in their autistic sample relative to their neurotypical sample. Arguably, group differences in visual thinking biases might be more pronounced in extreme samples, that is, when comparing clinically diagnosed ASC and neurotypical groups, rather than non-clinical groups differing in milder autistic trait levels (discussed more in Section 8.6).

Having said this, while our ambiguous verification statements were designed to be equally open to verbal and visuospatial processing modalities, the possibility that these statements lacked sensitivity in teasing apart individual differences in verbal-visual thinking styles cannot be ruled out (see Experiment 3, Figure 3.6, Experiment 4, Figure 4.4). Differences in the cognitive demands between our sentence verification task and the executive function tasks employed in the previous TiP investigations provide an appealing explanation for why the ambiguous statements failed to differentiate the low and high AQ samples on preferred processing strategies. Where the sentence verification task was designed to assess listening/reading comprehension, executive function tasks such as tower planning (Wallace et al., 2009; Williams et al., 2012, Experiment 2; Holland & Low, 2010, Experiment 3), mathematical/card set-shifting (Whitehouse et al., 2006, Experiment 3; Holland & Low, 2010, Experiments 1 & 2; Russell-Smith et al., 2014), working memory (Koshino et al., 2005; Koshino et al., 2008) and matrices reasoning (Sahyoun et al., 2009) commonly require maintenance of complex rules during problem solving. Such “rule-based” executive function tasks are understood to depend, to some extent, on verbal thinking via inner speech to regulate performance (e.g. in monitoring/revising disc moves to create a tower configuration, sorting cards by shape but not colour, or responding if a stimulus appeared n-back in a sequence) (Joseph, Steele, Meyer, & Tager-Flusberg, 2005; Russell, Jarrold, & Hood, 1999).

While the TiP framework conceptualises restricted verbal thinking to span across all cognitive domains, Williams et al. (2012) proposes that people on the autism spectrum are capable of verbal meditation on cognitive tasks that impose little demand on executive functions. The fundamental assumption made by Williams et al. (2012) is that inner speech is not globally impaired in ASC, with autistic individuals spontaneously engaging in articulatory rehearsal on short-term memory tasks (evidenced by significant dual-task articulatory suppression interference), but failing to recruit verbal processing to support executive function performance (evidenced by a lack of dual-task articulatory suppression interference).
If our sentence task is less dependent on “rule-based” aspects of executive function, leaving high AQ samples able to draw on verbal short memory (or without resorting to visuospatial compensatory strategies) to support comprehension, the ambiguous statements might not be ideal in distinguishing high and low AQ groups on visuospatial strategy preferences. Nevertheless, in light of finding fMRI group differences in right dorsomedial prefrontal activity in Experiment 6, the possibility that ambiguous statements require some aspect of executive function (at least in the low AQ sample) cannot be excluded.

A logical extension of the investigation of the TiP framework would be to compare our ambiguous verification statements with tests of executive functioning in their sensitivity to individual differences in verbal-visuospatial strategy preferences among individuals with low versus high AQ scores. Such a study could incorporate dual-task and/or neuroimaging approaches to ascertain whether restricted verbal processing as argued under the TiP framework is specific to executive functioning (Williams et al. 2012), or if individuals with subclinical but high AQ traits might generally have intact verbal thinking. Adding a clinical ASC sample to a design that includes high and low AQ groups would help clarify whether differences in verbal-visual thinking biases span across the autism spectrum. Nevertheless, some aspects of cognition were similar to autistic individuals in that our participants with high levels of autistic traits exhibited stronger visuospatial abilities and alongside weaker verbal abilities, although the high AQ sample did not exhibit a cognitive bias towards visual thinking. The next section focuses on discussing the relationship between cognitive abilities and strategy preferences within the TiP account, for the low and high AQ samples.

8.6 Dissociation between Cognitive Abilities and Cognitive Biases in the TiP account of Autism

This thesis examined the relationship between cognitive abilities (mental proficiency) and cognitive biases (preferred modality in information processing) within the TiP framework, by assessing how the profile of verbal and visuospatial abilities was linked with strategy preferences on the ambiguous verification statements. If cognitive abilities are inherently linked with cognitive biases, it is expected that proficiency in a particular (verbal/visuospatial) domain should be associated with greater engagement of processing strategies within the same domain.
While the high AQ sample exhibited relative strengths in visuospatial abilities and weaknesses in verbal abilities, they were not more likely to favour use of visuospatial processes to solve ambiguous statements, compared to their low AQ counterparts. Correlational analyses between participant scores on Wechsler verbal and visuospatial ability measures and indices of the degree of language and visuospatial cerebral activity associated with the ambiguous statements were non-significant for each of the high AQ and low AQ groups (see Experiment 5, Table 5.3; Experiment 6, Table 7.0). Using both fTCD and fMRI, cerebral responses in regions subserving language and visuospatial functions were found to be unrelated to the profile of verbal and visuospatial abilities for the low and high autistic trait samples.

In Experiment 2, cross-modality effects were observed where participants in the high AQ sample who had stronger visuospatial abilities, appeared more susceptible to performance trade-offs when verbal processing was blocked via articulatory suppression (see Table 2.2). In contrast, for the low AQ sample, participants with stronger verbal ability showed more pronounced performance costs when visuospatial processing was impeded via spatial tapping. Taken together, these results suggest that a strength in processing in one domain may be associated with a vulnerability in interference in the alternate domain. While such cross-modality effects have not been previously reported, Holland and Low (2010) found that cognitive abilities and strategy preferences were directly linked within the same modality in their neurotypical comparison group. More specifically, weaker verbal ability in the neurotypical sample was found to be associated with greater verbal interference from articulatory suppression. The pattern of dual-task interference found in this thesis and from Holland and Low (2010) suggest that susceptibility in utilising (verbal/visual) information processing strategies might be impinged by weaker ability in the same modality or stronger ability in the alternate modality.

Three previous studies have alluded to the idea that verbal and visuospatial abilities are closely aligned with preferred processing strategy in autistic individuals. Using a stratified-design, Williams et al. (2008) divided autistic and neurotypical children based on verbal mental age (i.e., calculating an age-equivalent level in which the individual performs verbal tasks) and examined their profiles of short-term memory recall. Similar to their neurotypical peers, autistic children with a verbal mental age above 7 years showed poorer recall for pictures with similar-sounding names (e.g. “cat, bat”) than for pictures with different-sounding names (e.g. “dog,
cow”), taken to reflect verbal encoding or rehearsal of pictures in short-term memory. By contrast, this phonological similarity effect was not found in neurotypical and autistic children with a verbal mental age below 7 years, suggesting that poor verbal abilities might restrict verbal encoding or rehearsal (Williams & Jarrold, 2010). Similarly, Lidstone et al. (2009) showed that autistic children with better verbal than visuospatial abilities (i.e., a verbal > visuospatial profile based on 2.5 year difference in age-equivalent level) suffered pronounced performance costs on mathematical set-shifting during articulatory suppression, unlike autistic children with weaker verbal than visuospatial abilities (i.e., a verbal < visuospatial profile based on 2.5 year difference in age-equivalent level). These findings lend support to the idea that verbal ability, or perhaps the discrepancy between verbal and visuospatial ability might play a crucial role in influencing whether autistic individuals can engage verbal thinking to support cognitive performance.

To further investigate whether verbal and visuospatial abilities may have moderated strategy preferences in the present research, data from Experiments 2, 5 and 6 were re-analysed based on a discrepancy profile. Given psychometric issues associated with using mental age to create discrepancy groups (Wechsler, 2008), as was done by Lidstone et al. (2009), the two AQ groups in each experiment were divided into two subgroups by subtracting scaled scores from the Wechsler Vocabulary and Visual Puzzles subtests. For each of the low and high AQ samples, participants were categorised in the subgroup with a verbal > visuospatial profile if their Wechsler Vocabulary scores were larger than Visual Puzzles scores, with the remaining participants in the subgroup with a verbal ≤ visuospatial profile. Within the low and high AQ groups, the two subgroups were compared as to the interfering effects of articulatory suppression and spatial tapping on the ambiguous statements (Experiment 2), along with LIs for the ambiguous statements (Experiment 5) and degree of visuospatial activation in the right dorsomedial prefrontal cortex during ambiguous statement verification (Experiment 6). These analyses yielded non-significant subgroup differences (largest $t(34) = 1.73, p = .09, d = .59$), suggesting

5 Within the high AQ sample, a non-significant trend indicated greater articulatory suppression interference for participants with a verbal > visuospatial profile, than for participants with a verbal < visuospatial profile (Chapter 3, Experiment 2). Given that this finding did not satisfy statistical significance, there was limited support that a verbal < visuospatial profile in individuals with high levels of autistic traits is associated with restricted verbal processing (Lidstone et al., 2009)
that irrespective of the direction of the verbal and visuospatial discrepancy, participants from the low and the high AQ samples appeared to utilise verbal and visuospatial processing to a similar degree to facilitate sentence comprehension.

Thus, results from this thesis do not fit with those reported by Lidstone et al. (2009), as the relative profile of verbal and visuospatial ability in our high AQ samples was found to be independent of information processing strategies. Failure to find relationships between verbal-visuospatial discrepancy profile and processing strategy could be because our ambiguous verification statements were not sensitively picking up individual differences in verbal-visual strategy preferences. Lidstone et al. (2009) might have found relationships between discrepancy profile and use of verbal processing in their autistic sample due to demands on executive functions associated with mathematical set-shifting (Williams et al., 2012), which might not be shared with our verification task.

Differences between the high AQ samples in the present research and the autistic samples used in the previous studies can also provide reasons for discrepant results. Participants in the high (and low) AQ groups were drawn from an undergraduate student cohort ($M = 20.31$ years age, $SD = 4.55$ years) and so were considerably older, with verbal and visuospatial skills that were more developed than the autistic children from Lidstone et al. (2009) ($M = 10.91$ years age, $SD = 1.75$ years) and Williams and Jarrold (2010) ($M = 12.25$ years age, $SD = 3.10$ years). Furthermore, since low verbal skills would typically preclude entry to university, our high AQ samples are likely to have more advanced verbal skills compared to people from the general population who would otherwise lie on the same point of the autism spectrum (i.e. with similar AQ scores). This is relevant because while the recruited high AQ groups show comparative strengths in visuospatial over verbal abilities, their verbal skills are unlikely to be impaired. Consequently, the discrepancy profile in our recruited high AQ samples are likely to be less pronounced relative to autistic individuals or wider population samples with high levels of autistic-like traits. Either way, preserved verbal abilities or a less discrepant profile might render our high AQ undergraduate sample capable of utilising verbal processing strategies during ambiguous sentence verification. Comparison studies involving ASC and neurotypical samples, or, low and high autistic trait samples drawn from the general population would provide a more
sophisticated test of the influence of verbal-visuospatial discrepancy profile on strategy preferences, as proposed by Lidstone et al. (2009).

By combining dual-task behavioural methods, fTCD and fMRI neuroimaging, this thesis provides preliminary evidence that cognitive abilities and preferences for verbal-visual information processing in our high AQ samples are not as inherently connected as in individuals with ASC. A stronger visuospatial than verbal profile in individuals with high levels of autistic traits did not, in and of itself, necessitate a concomitant bias towards visual thinking (or away from verbal thinking). Finding conceptual distinctions between cognitive abilities and strategy biases in individuals with high levels of autistic traits appears to be consistent with the broader literature on neurotypical cognition. For instance, using a self-report measure of strategy preference, the Verbaliser-Visualiser Questionnaire (Richardson, 1977), two studies have shown that subscale scores on the visualiser and verbaliser domains in neurotypical individuals do not correlate with Wechsler measures of visuospatial and verbal abilities, respectively (Kraemer, Rosenberg, & Thompson-Schill, 2009). Furthermore, using a factor analytic approach, Mayer and Massa (2003) found that measures of thinking style and measures of spatial ability loaded onto distinct factors. Our findings suggest that, similar to neurotypical individuals, people with high levels of autistic traits may not resort to a “default” visuospatial representational mode on cognitive tasks, even if they might possess comparatively stronger visuospatial abilities and weaker verbal abilities.

Different to autistic individuals, people with high levels of autistic traits might show more flexible use of verbal and visuospatial information processing to support sentence comprehension. This raises the question of whether atypical neural mechanisms affecting ASC might be different to mechanisms underlying subclinical autistic-like traits (Gregory & Plaisted-Grant, 2016). Although our data cannot directly address this issue, this thesis also examined how cerebral lateralisation in the low and high AQ samples might relate to language and visuospatial abilities. Before discussing the results on cerebral lateralisation, the next section focuses briefly on the utility of the sentence verification task in localising language and visuospatial functions.
8.7 Limited Utility of Verbal and Visual Verification Statements in Assessing Language and Visuospatial Lateralisation

The word generation and visual short-term memory tasks are currently considered benchmark measures for assessing language and visuospatial cerebral laterality (Bishop et al., 2009; Groen et al., 2012; Whitehouse et al., 2009). However, a single task examining the two cognitive functions could potentially shorten the scanning procedure in the investigation of people on the autism spectrum. Sets of verbal and visual verification statements were developed and were compared against the word generation and visual short-term memory tasks to evaluate the utility of such statements in assessing cerebral lateralisation in young adults (Experiments 3 and 4) including those selected for low and high AQ scores (Experiment 5). Before discussing these results, one caveat to be noted is that methodological issues concerning the fMRI version of the visual short-term memory task resulted in failure to localise participants’ dominant visuospatial cerebral hemisphere (discussed more in Section 8.8). Consequently, it was not possible to test the utility of the verification statements against the gold standard laterality tasks in Experiment 6, and interpretation rests mainly on the fTCD results from Experiments 3, 4 and 5.

Quantification of the strength of cerebral lateralisation (i.e. LI) from the verification task showed poor correspondence with the established laterality measures. This was the case for the low and high AQ samples as well as participants not selected for particular levels of autistic traits. Individual LIs for the visual statements did not correlate with LIs for the visual short-term memory task, and, similarly, the LIs measured for the verbal statements and for the word generation task were not associated (see Table 5.5, and Appendix C, Tables C.1 and C.2). That is, people who showed stronger language or visuospatial lateralisation on the gold standard tasks did not also show more pronounced lateralisation on the corresponding sentence types for the verification task.

Using fMRI and fTCD, several studies have provided evidence that LIs on language tasks may vary between receptive and expressive tasks (Buchinger et al., 2000; Pillai & Domineco, 2011; Stroobant et al., 2009). In these studies, strongest activation was found in left hemisphere frontal regions on expressive language tasks (e.g. object naming, narrating a story), but superior activation in left hemisphere
temporal regions was observed on receptive language tasks (e.g. listening to jokes or poems). If expressive and receptive tasks draw differently on cerebral regions within the frontal-temporal language network, then it is reasonable to expect that LIs during (receptive) comprehension of verbal statements might not perfectly correlate with LIs during (expressive) word generation.

Intriguingly, when the verbal verification statements were assessed for congruence with the gold standard word generation task with regard to identifying the cerebral hemisphere dominant for language functions, the two measures showed good consistency. Among those participants with language and visuospatial functions in separate hemispheres, a majority from Experiments 3 and 4 (31 out of 38, 81.57%) and Experiment 5 (low AQ = 18 out of 22, 81.82%; high AQ = 14 out of 15, 93.33%) showed dominant activation in the same (language) cerebral hemisphere, across the verbal statements and the word generation task. Hence, while the verbal verification statements differed from the word generation task with regard to degree of lateralisation, the verbal statements had reasonably good sensitivity in localising participants’ language cerebral hemisphere. However, it cannot be inferred that the utility of the verbal statements in localising the hemisphere dominant for language functions was a consequence of particular content within the statements, since the other two statement conditions yielded very similar patterns of hemispheric activation.

Accordingly, the visual statements of the verification task were less successful in isolating the cerebral hemisphere dominant for visuospatial functions. While a majority of the participants exhibited right lateralised visuospatial activation on the gold standard visual short-term memory task, left lateralised activation was evident for the visual verification statements (see Figures 3.6, 4.4 and 5.4). Finding pronounced left hemisphere (presumably language) activation on the visual verification statements was surprising, given that mental representation of visuospatial content is associated with a right hemisphere bias in parietal-occipital responses within the visuospatial network (Bottini et al., 1994; Kosslyn et al., 1995; Mellet et al., 1996, 1998). In these previous neuroimaging studies, participants were instructed to visualise common objects read aloud to them (e.g. anchor) (Kosslyn et al., 1995), listen to sequential spatial instructions (e.g. “right-down-down-back-back-up-up-back-back-right”) (Mellet et al., 1996), or evaluate the plausibility of imaginable statements (e.g. “The old man had a head full of dead leaves”) (Bottini et
The slightly longer length of our visual verification statements (9 to 15 words) could impose higher demands on verbal resources (subvocal rehearsal, phonological working memory) associated with temporary storage and manipulation of information, resulting in a leftward bias in language hemispheric activity.

Relative to the gold standard visual short-term memory task, the notion of hemispheric specialisation for visuospatial functions might not be as absolute during reading comprehension (Mason & Just, 2004; Virtue, Haberman, Clancy, Parrish, & Beeman, 2006). In the initial stages of reading, decoding of written statements requires a combination of visuospatial processing (registering the print information) and verbal processing (registering print information as meaningful words). This occurs even before the content from the visual statement is transformed and visuospatially represented during reading comprehension (De Beni et al., 2005). Such involvement of verbal processing, at least in the early stages of reading, could obscure the expected rightward lateralised effects in the course of comprehending visual statements. Alternatively, the long length of the visual statements could place demands on verbal processing in the form of inner speech (Baddeley, 2010; Caplan & Waters, 1999), which might not be required when encoding location information in visual short-term memory. Notably, while fMRI results from Experiment 6 show that our visual statements recruited the highest ROI activation in the visuospatial network and lowest ROI activation in the language network compared to the other statement types from the verification task (see Table 6.9), the visual statements have limited utility in the assessment of visuospatial hemispheric dominance.

In addressing why our verbal and visual verification statements did not produce distinct lateralisation effects to the left and right hemispheres, respectively, it is also important to consider how the stimuli were selected in the self-report strategy study (Experiment 1). More specifically, the cut-offs for selecting visual statements (mean ratings ≤ -1) and verbal statements (mean ratings ≥ +1), meant that a couple of statements in each of the two categories received less extreme ratings than the rest of the statements in their category. While overall mean ratings for the verbal statements and the visual statements were substantially different (see Figure 1.1), use of a more stringent selection criteria could have produced a stronger pattern of hemispheric lateralisation to discriminate the two sentence types.

Based on the fTCD and fMRI results from Experiments 3, 4, 5 and 6, the verbal and visual verification statements are not reliable alternatives to the word
generation and visual short-term memory tasks in quantifying cerebral lateralisation. With this in mind, the results on language and visuospatial laterality for the low and high AQ samples will be discussed with reference to the word generation and visual short-term memory tasks.

8.8 Cerebral Laterality of Language and Visuospatial Functions and Autistic Traits

Experiments 5 and 6 sought to clarify the pattern of language and visuospatial cerebral lateralisation in individuals with low and high levels of autistic traits in two main ways. The first way was to investigate whether atypical cerebral lateralisation is a potential mechanism underpinning altered language and visuospatial cortical responses documented in the TiP literature. The second way was to explore how the cerebral organisation of language and visuospatial functions might relate to the profile of verbal and visuospatial abilities from a TiP standpoint.

fTCD and fMRI were used to examine whether participants with high AQ scores would show a departure from typical left-side language and right-side visuospatial lateralisation compared to their low AQ counterparts. Subtle but significant differences in right hemisphere cortical responses were identified in participants with high levels of autistic traits on the word generation and visual short-term memory laterality tasks. Relative to the low autistic trait sample, the high autistic trait participants showed weaker right hemisphere visuospatial lateralisation (Figure 5.1), along with stronger responses in right hemisphere subcortical language regions during word generation (Figure 6.3). Where neuroimaging studies on subclinical participants scoring high on the AQ have documented altered cerebral networks associated with social cognition (Nummenmaa et al., 2011; von dem Hagen et al., 2011), this research demonstrates for the first time that functional activation differences extend to domains of language and visuospatial functions.

The finding that individuals with high levels of autistic traits demonstrated weaker, not stronger, right hemisphere visuospatial specialisation than their low autistic trait counterparts is novel. During visuospatial task performance autistic individuals have been found to show over activation of right hemisphere parietal-occipital regions, accompanied by under activation in left hemisphere frontal regions relative to neurotypical individuals (Lee et al., 2007; Manjaly et al., 2007; Ring et al., 1999; for review, see Mottron et al., 2006). This pattern of group differences
suggests that autism might be associated with a more pronounced rightward bias in visuospatial lateralisation, and remains in direct contrast with finding weaker visuospatial lateralisation in our high AQ sample.

On the one hand, augmentation in the degree of visuospatial lateralisation for the low AQ group could reflect enhanced engagement in visuospatial processing strategies during visual short-term memory when compared to the high AQ group. On the other hand, cognitive advantages in visuospatial abilities in our high AQ sample could render them more efficient in neural processing (Reichle, Carpenter, & Just, 2000), with less cognitive effort then associated with smaller visual short-term memory LIs. While the former interpretation suggests that visual thinking characterises the lower end of the autism spectrum and challenges the TiP account, the latter suggestion seems to support the TiP framework. These conflicting interpretations highlight a conundrum with neuroimaging research, in which higher or lower cerebral activation can be difficult to interpret conclusively (Preslar et al., 2014).

In some ways, the pattern of group differences in visuospatial lateralisation found in this thesis fits with more recent evidence of reduced right hemisphere involvement in visual attention in individuals with high levels of autistic traits, relative to those with low trait levels (English et al., 2015, 2017, 2018). According to English and colleagues, one consequence of right hemisphere visuospatial specialisation is that neurotypical individuals generally attend more to the left versus the right visual field, resulting in a leftward spatial bias on line bisection (judging the centre of a line) and greyscale (judging which side of a graded bar has darker luminance) tasks. As well as showing a less pronounced leftward attention bias on such visual attention tasks (English et al., 2015, 2017), English et al. (2018) demonstrated that right hemisphere excitatory tDCS stimulation on individuals with high AQ scores increased the degree of leftward bias, to levels similar to those found in a low AQ group under no tDCS stimulation.

Right hemisphere under-activation in individuals with high levels of autistic traits, as argued by English et al. (2015, 2017, 2018), is consistent with weaker right hemisphere visuospatial specialisation in our high AQ sample and might reflect reduced allocation of spatial attentional resources to the left visual field during the visual short-term memory task. A crucial test of the proposal from English et al. (2015, 2017, 2018) would be to combine eye tracking with functional neuroimaging...
(for review, see Dawson, 2016) to link neural mechanisms to visual fixation patterns among samples selected for low and high AQ scores. Such a study could administer a more sophisticated version of the visual short-term memory task, where the test stimuli are distributed across the left and right visual fields. Using eye tracking, it would be possible to monitor the amount of time participants fixate on the left and right visual fields during visual memory encoding. Concurrent recording of neural activity would also provide a test of AQ group differences in left and right hemisphere activation and could indicate whether these differences are related to the extent of left visual field bias demonstrated under eye tracking. This research design also has potential to extend the TiP account by examining whether atypical visual attention is a cognitive mechanism linked with enhanced visuospatial performance in individuals with high levels of autistic traits.

Turning to the pattern of results on the language laterality task, right hemisphere subcortical areas which were deactivated in the low AQ sample during word generation, were even less suppressed in the high AQ sample. Where an over-activation of language areas in the (atypical) right hemisphere has been reported in autistic individuals (Boddaert et al., 2003; Eyler et al., 2012; Redcay & Courchesne, 2008; Takeuchi et al., 2004), fMRI beta fit signals of right hemisphere insular and putamen ROIs for the high AQ sample were characterised by less deactivation than that observed in the low AQ sample. During verbal fluency, subcortical regions of the language network such as the insular cortex subserve motor planning and coordination of inner speech functions (Ardila et al., 2014) and have been found to show a relative drop (rather than increase) in fMRI beta fit signals (Hutchinson et al., 1999).

While the precise mechanisms causing reduced subcortical language deactivation in our high AQ group are difficult to pinpoint (Wood et al., 2001; Kannurpatti & Biswal, 2004), there is some suggestion that altered frontal connectivity within the language network could play a role. A functional connectivity study investigating the effects of increasing task difficulty of verbal fluency has shown excitatory effects on activation in the middle frontal gyrus, but inhibitory influences on regions downstream of the language network (Fu et al., 2006). This is relevant to this thesis because if the middle frontal gyrus exerts suppressive mechanisms on subcortical language areas as an adaptive response in
self-regulating task difficulty, deactivation could be expected in insular and putamen ROIs during verbal fluency.

Consistent with the idea that frontally-mediated difficulties with coordinating language (Williams et al., 2012) might influence less subcortical language deactivation in individuals with high levels of autistic traits, our high AQ sample also showed behavioural trends towards poorer verbal fluency (in Experiment 6). Connectivity studies have provided more direct links showing pronounced disconnections between frontal regions and other areas (e.g. superior temporal) of the language network in autistic children with more severe language difficulties (Verly et al., 2014). Other studies have proposed reduced ‘long-range’ connectivity between the frontal cortex and other regions in autism (for reviews, see Courchesne & Pierce, 2005; Schipul, Keller, & Just, 2011). Further clarification of connectivity patterns between frontal-temporal language regions of individuals with low and high levels of autistic traits would be necessary. This could be addressed by examining the time course of activity between frontal-temporal ROIs associated with verbal fluency task performance using the collected fMRI data. Such a study could inform whether the recruited high autistic trait sample show evidence of altered frontal connections, and also if connectivity with regions downstream of the language network might be more affected, relative to the low autistic trait sample.

Despite group-level differences in right hemisphere activity on the word generation and visual short-term memory tasks, rates of atypical cerebral lateralisation in the high AQ samples were found to be equivalent to the rates observed in the low AQ samples. In contrast with my predictions, most participants with low and high levels of autistic traits were found to exhibit the typical pattern of left lateralised activation for word generation (see Figures 5.2 and 6.5) and right-lateralised activation for visual short-term memory (see Figure 5.2). Altered right hemisphere neural responses on the language and visuospatial laterality tasks in the high AQ sample did not translate to group difference in rates of atypical cerebral lateralisation compared to the low AQ sample. fMRI-measured differences in right hemisphere putamen and insular activation between the low and high AQ groups were focal, and when pooled across the frontal-temporal regions of the language network, were not significant enough to differentiate the two AQ groups on language laterality. Though, the fMRI results on visuospatial laterality showed poor correspondence with fTCD, where elevated rates of atypical (bilateral) lateralisation
were found across the low and high autistic trait samples on the fMRI visual short-
term memory task (Figure 6.5).

Inconsistent findings on the pattern of visuospatial lateralisation for our low
and high AQ samples can be explained by methodological differences in the baseline
conditions used in the fMRI and fTCD short-term memory tasks. In the fTCD visual
short-term memory task, cerebral activation associated with visual memory was
compared against a rest baseline condition that did not require any task to be
performed. In comparison, the fMRI visual short-term memory task incorporated an
attention baseline condition that matched the experimental condition on low-level
processing (e.g. visual encoding, memory recognition) but differed on visual
memory retention demands (see Figure 6.2). The fMRI task-design was predicted to
yield a robust measure of visuospatial lateralisation. However, difference in cerebral
activity for the visual memory condition minus the attention baseline condition was
more evenly distributed across the two hemispheres than the fTCD difference for the
visual memory condition minus the rest baseline condition. It was argued that if the
attention baseline required some degree of visuospatial processing (i.e., visual
encoding, memory recognition), potentially eliciting right-lateralised activity, then
fMRI block-subtractions from the visual memory condition potentially explains a
more (symmetric) bilateral pattern of visuospatial lateralisation, found across the low
and high AQ samples.

With regard to examining whether the pattern of cerebral lateralisation was
linked with the verbal and visuospatial ability profile in individual with low and high
levels of autistic traits, there was no support for this. Correlations between strength
of cerebral laterality (as measured by fTCD) and Wechsler scores on the verbal
(Vocabulary) and visuospatial (Visual Puzzles) ability measures were all not
significant, for the low and high AQ groups. In other words, although the high AQ
sample showed weaker visuospatial lateralisation, this reduction did not seem to be
linked with enhanced visuospatial abilities, relative to the low AQ sample. Similarly,
relatively weaker verbal abilities in our high AQ sample did not seem to correspond
with group differences in the strength (or directionality) of language laterality, when
compared to the low AQ sample.

The results from this thesis build on the TiP framework by showing that
visuospatial strengths and verbal weaknesses in individuals with high levels of
autistic traits are not underpinned by the pattern of cerebral lateralisation. This
suggestion is in agreement with other fTCD studies showing that people from the general population who exhibit atypical lateralisation do not experience worse language (Knecht et al., 2001) or visuospatial skills (Groen et al., 2012), compared to age-matched peers with typical lateralisation. Different to neurotypical development, there appears to be a closer link between cerebral lateralisation and language functions in various clinical populations. In particular, atypical language lateralisation has been documented in clinical conditions for which language skills are commonly affected, including ASC, developmental language disorder and specific learning disability with reading impairment (for a review, see Bishop, 2013).

While systematic reviews and meta-analyses of autism research have implicated left hemisphere language dysfunction (Preslar et al., 2014; Sperdin & Schaer, 2016) marked by underactivity, a more recent meta-analysis (Herringshaw et al., 2016) has implicated augmented right-lateralised language activation in ASC. Herringshaw et al. (2016) found that where autistic individuals showed poorer performance on verbal tasks compared to neurotypical controls, the ASC group was more likely to show heightened responses in right hemisphere inferior frontal and superior temporal regions on language tasks. This notion that atypical cerebral laterality in ASC is linked with poor language has been further corroborated with structural MRI revealing reductions in the size of left hemisphere language (e.g. inferior frontal) areas (Abell et al., 1999; Boddaert et al., 2004; Knaus et al., 2010; McAlonan, 2008) and even enlargement of right hemisphere regions serving visuospatial functions (e.g. inferior parietal area) (Floris et al., 2016).

Of the current functional and structural MRI studies that have examined language laterality in ASC, some have demonstrated atypical lateralisation in autistic individuals with comorbid language impairments, but not in autistic individuals without language impairments (Anderson et al., 2010; De Fosse et al, 2004; Floris et al., 2016). One longitudinal study (Lombardo et al, 2015) has also demonstrated that atypical language lateralisation at 12 months of age predicts poorer language outcomes in children with ASC. Conversely, typical lateralisation at 12 months of age was associated with better childhood language outcomes in ASC (Lombardo et al, 2015). These findings highlight the suggestion that atypical lateralisation might be linked with language impairments rather than ASC specifically, or possibly present in subgroups of autistic individuals. This explanation potentially accounts for the lack of group differences in language lateralisation between our high and low AQ
undergraduate participants, with the former group unlikely to experience significant language impairments. There might be a threshold beyond which maladaptive language impairments in autism begin to be associated with atypical language laterality. In which case, atypical language laterality might not be detected where subtle language weaknesses exist in undergraduate samples with high levels of autistic traits.

8.9 Summary, Implications for Autism and Future Directions

In sum, the findings presented in this thesis provide preliminary evidence that relative advantages in visuospatial over verbal abilities in individuals with high levels of autistic traits are not associated with a visual thinking bias, and are not underpinned by atypical cerebral lateralisation. Consistent with the TiP account (Kunda & Goel, 2011), the uneven profile of stronger visuospatial and weaker verbal abilities in our high AQ samples relative to the low AQ samples fits with the notion of a broader verbal and visuospatial phenotype in autism. These results highlight the importance of accounting for verbal and visuospatial abilities in future investigations of the TiP framework. Intriguingly, the relative profile of verbal and visuospatial abilities did not appear to restrict or facilitate the way in which the low and high AQ groups recruited verbal or visuospatial processing strategies on ambiguous verification statements, further expanding on the TiP framework. The relative profile of verbal and visuospatial abilities in the low and high autistic trait samples was also unrelated to the pattern of cerebral lateralisation for language and visuospatial functions. While the task-development studies and use of behavioural (dual-task) and neuroimaging (fTCD and fMRI) approaches provided a comprehensive investigation of the TiP framework, the findings are not without limitation and future research is required to explore the limits of these results.

The most obvious constraints are that these studies involved low/high AQ comparisons, rather than neurotypical/ASC comparisons. While cognitive advantages in visuospatial over verbal abilities in our high AQ samples overlap with the profile seen in ASC, dissociations between cognitive profile, cognitive biases and cerebral lateralisation challenge the notion that common neural mechanisms affecting autism might span beyond clinical ASC. It was not clear if language proficiency of our recruited samples rendered them more capable of recruiting verbal
processing, and if our finding of typical language lateralisation across the low and high AQ samples reflects sufficiently developed language in both groups (Herringshaw et al., 2016). It will be necessary to examine relationships between verbal and visuospatial abilities, cognitive biases and cerebral lateralisation in an autistic/neurotypical comparison study to test the boundaries of our findings.

The number of recruited participants in our fTCD and fMRI studies are comparable with previous research that has assessed language and visuospatial functions in clinical ASC/neurotypical controls as well as high/low autistic trait comparison groups. In particular, previous studies have typically compared group differences between ASC and neurotypical groups on fMRI BOLD responses on sentence comprehension and cerebral lateralisation (Anderson et al., 2010; Eyler et al., 2012; Harris et al., 2006; Just et al., 2004a; Lee et al., 2007; Manjaly et al., 2007; Redcay & Courchesne, 2008; Ring et al., 1999; Silk et al., 2006; Takeuchi et al., 2004), and examined group differences between individuals with high and low levels of autistic traits on visuospatial behavioural tasks (Grinter et al., 2009; Stewart et al., 2009 Fugard et al., 2011). Using results from these studies, effect sizes for the reported analyses were estimated. For the ASC studies, statistics comparing differences in BOLD responses between clinical ASD and control groups have ranged from $t = 3.15$ to $4.79$, with effect sizes of $r = .55$ to $.71$. For the AQ studies comparing differences in high- and low-AQ groups on various visuospatial tasks, the statistical values ranged from $F = 4.17$ to $6.54$, with effect sizes of $r = .37$ to $.45$. Using the lower and upper boundaries of these effect sizes ($r = .37$ to $.71$), statistical power for our fTCD and fMRI studies was estimated using a minimum sample size of $n = 24$. Power for our studies was estimated to range between $.60$ (for $r = .37$) and $1.00$ (for $r = .71$), which represent moderate to large power estimates. Thus, the sample sizes used in the present study are reasonable when assessed against power for effects reported in similar research designs.

One limitation is that while our ambiguous verification statements were designed to measure cognitive biases within the TiP framework, the results reported in Experiments 3 and 4 provided limited support that these statements differentiated typical individual differences in verbal and visuospatial processing. Considering that our verification task assesses comprehension of written information, all three statement types likely require some verbal semantic retrieval from long-term knowledge stores when participants verify the truth of the statement content. In other
words, incidental language activity associated with solving ambiguous verification statements could override or obscure subtle (localised or hemispheric) differences in visuospatial cerebral responses that might be evident among individuals with high versus low levels of autistic traits.

Another explanation for the lack of AQ group differences in verbal thinking is that limitations in verbal thinking in the autism spectrum only begin to emerge on cognitive tasks which impose demands on executive functions (Williams et al., 2012). If our ambiguous verification statements do not draw extensively on executive functions, then individuals with high levels of autistic traits might be sufficiently able to draw on verbal processing without resorting to visuospatial compensatory strategies to support sentence comprehension. In which case, the ambiguous verification statements might not be ideal in distinguishing individuals with low versus high levels of autistic traits on verbal and visuospatial strategy preferences.

Using dual-task and neuroimaging methodologies, it would be important to compare our verification task with other executive function tasks, to assess whether the breakdown of verbal processing in autistic individuals is specific to executive function tasks (Williams et al., 2012), or spans across all tasks (Kunda & Goel, 2011). Importantly, while executive function tasks like mathematical set-switching and tower planning have been shown to differentiate autistic and neurotypical individuals on relative recruitment of verbal and visuospatial processing, these tasks are not specifically designed to measure thinking style. This gap in the literature could perhaps be addressed by evaluating how behavioural and neural correlates of our ambiguous verification statements and executive function tasks might relate to self-report questionnaires assessing preferences for verbalising-visualising processing styles (e.g. the Verbaliser-Visualiser Questionnaire) (Richardson, 1977).

In weighing up whether standard assessment of cerebral lateralisation is necessary in empirical investigations of the TiP framework, several considerations are necessary. Assuming the fTCD results from Experiment 5 are reliable, a notable proportion of participants from the low (15.36%) and high (37.50%) AQ groups are understood to exhibit atypical language and/or visuospatial cerebral organisation. While these individuals constitute the minority, the inclusion of participants with atypical lateralisation in analyses on the dominant cerebral hemisphere activated on the ambiguous verification statements would have undoubtedly contributed to spurious interpretations regarding their favoured modality (verbal/visuospatial) of
processing in *Experiment 5*. Additionally, despite the fact that most participants within our high AQ samples showed the typical pattern of left-language and right-visuospatial functions, there is compelling evidence from meta-analyses suggesting that atypical cerebral lateralisation is common in ASC, especially within the language domain (Herringshaw et al., 2016; Preslar et al., 2014; Sperdin & Schaer, 2016). If atypical cerebral lateralisation is more prominent in autistic than neurotypical controls, or in subgroups of autistic individuals with language difficulties, these arguments reinforce the importance of accounting for the pattern of language cerebral laterality in neuroimaging investigations of the TiP framework.

The pattern of cerebral lateralisation documented in the low and high autistic trait samples (as well as general population studies) rests on the assumption that the gold standard word generation and visual short-term memory tasks were predominantly approached using language and visuospatial strategies, respectively. It is possible that individual differences in verbal/visual processing might, in part, have influenced the profile of cerebral responses on the word generation and visual short-term tasks. That is, cognitive preferences for verbal-visual thinking could have contributed to ‘noise’ in the LI calculations on measures of cerebral laterality. Future research could examine the extent to which self-reported thinking style influences word generation and visual short-term memory performance. If individual preferences for verbal/visual processing play a critical role in affecting neuronal activity during assessment of cerebral laterality, then LI values of functional cerebral lateralisation would be closely associated with self-reported thinking styles. The results from such a study would have methodological implications on measurement of cerebral lateralisation.

With the use of two neuroimaging methods (fTCD and fMRI) to investigate the TiP framework, questions remain about why individuals with high autistic traits showed a different pattern of language and visuospatial cerebral responses to their low autistic trait counterparts across the two experiments. Where the fTCD study (*Experiment 5*) showed AQ group differences in right hemisphere activity during visuospatial performance, the fMRI study (*Experiment 6*) documented regional differences in left hemisphere areas underlying language and visuospatial functions.

In comparing fTCD and fMRI, differences in spatial resolution, statistical methods for detecting significant activity and task-specific elements related to the
experimental design, are factors that could explain disparate findings across the low and high AQ comparison studies. First, fMRI measures spatially localises brain tissue oxygenation changes, while fTCD detects temporal changes in cerebral blood flow velocity, meaning the two imaging methods capture different aspects of neural responses and isolate activity within the left and right hemispheres with different sensitivity (Deppe et al., 2000; Jansen et al., 2004). Second, the statistical methods for prep-processing fMRI and fTCD data, and statistical thresholds for identifying ‘meaningful’ AQ group differences in cerebral responses are inherently different across the two imaging methods. Finally, the baseline condition, against which the neural responses for experimental conditions were contrasted, differed for the fTCD (experimental versus rest baseline) and fMRI (experimental versus low-level processing baseline) studies, and so could have contributed to variability in strength of activity as well as the quantification of LI. There are many methodological factors which make it difficult to pin-point specific mechanisms underlying AQ group differences in this thesis. As such, our fTCD and fMRI findings are preliminary and require replication in further samples selected for low and high autistic traits, preferably using the same experimental and baseline tasks to interpret results within the context of the TiP framework.

It would also be important to investigate functional connectivity of language and visuospatial networks in ASC to assess whether differences in language and visuospatial responses reported in the TiP literature might be the consequence of altered connections. For the results reported in Experiment 6, it was difficult to identify the mechanisms causing the differences in responses in the right hemisphere language (insular cortex, putamen) and visuospatial (dorsomedial prefrontal) regions that distinguished the low and high AQ samples. Relative to the low autistic trait group, participants with high levels of autistic traits showed considerably less deactivation in subcortical language areas and less frontally-mediated visuospatial activation. These results seem contrary to predictions from the TiP account if, for the high AQ group, less deactivation of language areas reflects more linguistic processing, while less activation of visuospatial areas reflects less pronounced use of visuospatial processing. On the other hand, interpretations of lower/higher activation levels are not straightforward and depend on the nature of connections (excitatory/inhibitory) in the cerebral network (Fu et al., 2006; Hutchinson et al., 1999). For instance, during verbal fluency, if subcortical language areas are typically
suppressed by inhibitory connections from the frontal cortex, then less deactivation in the high AQ sample could stem from disconnections in the frontal regions of the language network (Courchesne & Pierce, 2005; Schipul et al., 2011). A closer examination of functional connectivity in individuals on the autism spectrum might confirm the pattern of results in this thesis and provide new insights into how the language and visuospatial circuity might be affected in autism.
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# Appendix A: Sentence Verification Task

Stimuli

<table>
<thead>
<tr>
<th>Table A.1. Final set of verbal statements.</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Verbal statements</strong></td>
</tr>
<tr>
<td>Double negatives</td>
</tr>
<tr>
<td>There is not a living being that would survive without water.</td>
</tr>
<tr>
<td>Wearing sunscreen does not increase the likelihood of getting sunburnt.</td>
</tr>
<tr>
<td>If drinking not enough fluids, we are unlikely to be hydrated.</td>
</tr>
<tr>
<td>It is uncommon for people to not have baby teeth during adulthood.</td>
</tr>
<tr>
<td>Overeating does not contribute to a higher likelihood of being obese.</td>
</tr>
<tr>
<td>Without sunlight, it is not impossible for green plants to make oxygen.</td>
</tr>
<tr>
<td>It is not against the law to take other’s property without their permission.</td>
</tr>
<tr>
<td>An unhealthy diet does not increase likelihood of heart disease.*†</td>
</tr>
<tr>
<td><strong>Word oddities</strong></td>
</tr>
<tr>
<td>Of the words expose, uncover and investigate, investigate is the odd one out.</td>
</tr>
<tr>
<td>Of the words outstanding, spectacular and famous, outstanding is the odd one out.</td>
</tr>
<tr>
<td>Of the words transform, begin and evolve, transform is the odd one out.</td>
</tr>
<tr>
<td>Of the words notice, engage and occupy, engage is the odd one out.†</td>
</tr>
<tr>
<td>Among perfume, incense and candle, incense is the odd one out.†</td>
</tr>
<tr>
<td><strong>Word synonyms</strong></td>
</tr>
<tr>
<td>Of the words cease, discontinue and pause, cease is most similar to discontinue.</td>
</tr>
<tr>
<td>Of the words imply, explain and clarify, explain is most similar to clarify.</td>
</tr>
<tr>
<td>Of the words pointless, ordinary and trivial, trivial is most similar to pointless.</td>
</tr>
<tr>
<td>Of the words separate, connect and attach, attach is most similar to connect.</td>
</tr>
<tr>
<td>Of the words accommodate, divide and provide, divide is the odd one out.†</td>
</tr>
<tr>
<td>Of the words foundation, construct and build, construct is most similar to build.†</td>
</tr>
<tr>
<td>Of the words, capable, potential and accomplish, potential is most similar to accomplish.</td>
</tr>
<tr>
<td>Of the words monitor, revise and modify, modify is most similar to monitor.</td>
</tr>
<tr>
<td>Of the words, console, support and assist, assist is most similar to console.</td>
</tr>
<tr>
<td>Of the words select, classify and choose, classify is most similar to select.</td>
</tr>
<tr>
<td></td>
</tr>
<tr>
<td>-----------------------------</td>
</tr>
<tr>
<td><strong>Word synonyms</strong></td>
</tr>
<tr>
<td><strong>Verbal analogies</strong></td>
</tr>
<tr>
<td></td>
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<tr>
<td></td>
</tr>
<tr>
<td></td>
</tr>
</tbody>
</table>
Table A.2. Final set of visual statements.

<table>
<thead>
<tr>
<th>Visual statements</th>
<th>True</th>
<th>False</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Alphanumeric manipulations</strong></td>
<td>The numbers 3 and 1 touching sideways can make capital letter B.</td>
<td>Erasing the left-half of the number 8 forms capital letter E.</td>
</tr>
<tr>
<td></td>
<td>The small letter p, when rotated looks like a musical note.</td>
<td>The McDonalds sign can be rotated to look like the letter Z.</td>
</tr>
<tr>
<td></td>
<td>Putting your right hand over your left foot, the pinky lies above the big toe.</td>
<td>During a sit-up, lifting shoulders towards knees looks like the letter W.</td>
</tr>
<tr>
<td></td>
<td>Kneeling while leaning back, with hands forward forms the letter Z.</td>
<td>The letter X placed within a circle makes four diamonds.†</td>
</tr>
<tr>
<td></td>
<td>Joining two capital letter Ts together can form capital letter I.†</td>
<td>†</td>
</tr>
<tr>
<td></td>
<td>A circle with an arrow pointing northeast denotes the male gender symbol.†</td>
<td>†</td>
</tr>
<tr>
<td><strong>Clock positions</strong></td>
<td>At 8:50pm, both clock hands are on the left half of the clock.</td>
<td>At 4:25pm, the long and short clock hands overlay each other.</td>
</tr>
<tr>
<td></td>
<td>At 5:45pm, the long hand of the clock points West.</td>
<td>At 12:30am, the short hand of the clock points South.</td>
</tr>
<tr>
<td></td>
<td>On a clock, Number 1 is North of Number 5.</td>
<td>On a clock, Number 7 is East of Number 5.</td>
</tr>
<tr>
<td></td>
<td></td>
<td>On a clock, Number 4 is North-East of Number 8.‡</td>
</tr>
<tr>
<td></td>
<td></td>
<td>At 5:55pm, both clock hands are on the right half of the clock.†</td>
</tr>
<tr>
<td><strong>Map representations</strong></td>
<td>On the world map, Australia has a shorter vertical length than width.</td>
<td>Turning the world map upside down, Australia is below Asia.</td>
</tr>
<tr>
<td></td>
<td></td>
<td>On the world map, Africa can be folded vertically, forming a symmetrical shape.</td>
</tr>
<tr>
<td><strong>Telephone keypad</strong></td>
<td>On a telephone keypad, pressing 4, 8, 3 forms a tick symbol.</td>
<td>On a telephone keypad, pressing 1, 6, 7 forms an arrow pointed leftwards.</td>
</tr>
<tr>
<td></td>
<td>On a telephone keypad, pressing 4, 6, 8 continuously forms a triangular shape.</td>
<td>On a telephone keypad, pressing 1, 5, 7 forms a vertical line.</td>
</tr>
<tr>
<td></td>
<td>On a telephone keypad, pressing 7, 2, 9 forms an upward arrow.</td>
<td></td>
</tr>
<tr>
<td></td>
<td>On a telephone keypad pressing 1, 8, 3 forms a “V” shape.</td>
<td></td>
</tr>
<tr>
<td>Table A.2 (continued)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>-----------------------</td>
<td>---------------------------------------------------------------------------------------------</td>
<td></td>
</tr>
<tr>
<td>Telephone keypad</td>
<td>On a telephone keypad pressing 2, 8, 9 forms an “L” shape.‡</td>
<td></td>
</tr>
<tr>
<td>Visual oddities</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Among wrist, ankle and chin, ankle is the odd one out.</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Among donut, cracker and bagel, bagel is the odd one out.</td>
<td></td>
</tr>
</tbody>
</table>

*Trials not administered in Experiments 3, 4 and 5.
†Trials not administered in Experiments 6.
Table A.3. *Final set of ambiguous statements.*

<table>
<thead>
<tr>
<th>Ambiguous statements</th>
<th>True</th>
<th>False</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Alphabet representations</strong></td>
<td>In the alphabet, C is three letters before F.</td>
<td>In the alphabet, Q is three letters after O.</td>
</tr>
<tr>
<td></td>
<td>In the alphabet, T is two letters before V.</td>
<td>In the alphabet, G is three letters before K.</td>
</tr>
<tr>
<td></td>
<td>In the alphabet, M is three letters before P.</td>
<td>In the alphabet, L is two letters after I.</td>
</tr>
<tr>
<td><strong>Anagrams</strong></td>
<td>The letters N, G A, W can be rearranged to spell “gnaw.”</td>
<td>The letters S, Y, I, N, can be rearranged to spell “sign.”</td>
</tr>
<tr>
<td></td>
<td>The letters D, B, E, T can be rearranged to spell “debt.”</td>
<td>The letters M, T, I, H can be rearranged to spell “myth.”</td>
</tr>
<tr>
<td></td>
<td>The letters Y, O, K, L can be rearranged to spell “yolk.”</td>
<td>The letters N, E, T, I can be rearranged to spell “knit.”</td>
</tr>
<tr>
<td></td>
<td>The letters S, O, R, U can be rearranged to spell “sour.”*†</td>
<td>The letters O, T, M, B can be rearranged to spell “tomb.”†</td>
</tr>
<tr>
<td><strong>Mental arithmetic</strong></td>
<td>The number 34 plus the number 57 is equal to 91.</td>
<td>The number 54 minus the number 27 is equal to 37.</td>
</tr>
<tr>
<td></td>
<td>The number 25 plus the number 27 is equal to 52.</td>
<td>The number 55 plus the number 29 is equal to 84.</td>
</tr>
<tr>
<td><strong>Syllogisms</strong></td>
<td>If Pete is hairier than Craig and Craig is hairier than Luke, Pete is hairiest.</td>
<td>If Rob is happier than Scott and Scott is happier than Paul, Rob is saddest.</td>
</tr>
<tr>
<td></td>
<td>If Jane is shorter than Kim and Jane is taller than Ruth, Kim is tallest.</td>
<td>If Meg is thinner than Trish and Trish is thinner than Liz, Trish is thinnest.</td>
</tr>
<tr>
<td></td>
<td>If Eve is slower than Rose and Eve is faster than Brooke, Rose is fastest.†</td>
<td>If Grace is sweeter than Jill and Jill is dryer than Kate, Jill is sweeter.</td>
</tr>
<tr>
<td></td>
<td>If Troy is stronger than Dave and Troy is weaker than Jim, Dave is strongest.†</td>
<td>If Troy is stronger than Dave and Troy is weaker than Jim, Dave is strongest.†</td>
</tr>
<tr>
<td><strong>Verbal-visual oddities</strong></td>
<td>Among fan, dryer and windmill, dryer is the odd one out.</td>
<td>Among razor, tweezers and comb, tweezers is the odd one out.</td>
</tr>
<tr>
<td></td>
<td>Among diving, kite surfing and sailing, sailing is the odd one out.</td>
<td>Among buffalo, antelope and deer, deer is the odd one out.*†</td>
</tr>
<tr>
<td></td>
<td>Among the countries Japan, Italy and India, India is the odd one out.†</td>
<td>Among the countries Japan, Italy and India, India is the odd one out.†</td>
</tr>
</tbody>
</table>

*†Trials not administered in Experiments 3, 4 and 5. 
†Trials not administered in Experiments 6.
Appendix B: Supplementary fMRI Information

Table B.1. Higher-order contrasts showing brain areas with significantly activated during the visual statements relative to the ambiguous statement condition, collapsed for participants with low and high AQ scores (FWE, $p < .05$, $K_E > 10$ voxels).

<table>
<thead>
<tr>
<th>Cluster size ($K_E$)</th>
<th>MNI coordinates (x,y,z)</th>
<th>Brodmann area</th>
<th>Statistics (Z)</th>
</tr>
</thead>
</table>

**Ambiguous > Visual statements**

**Left hemisphere**
- Middle occipital gyrus: 331 -32 -84 6 18 7.04
- Anterior cingulate gyrus: 193 -1 26 30 32 6.10
- Fusiform gyrus: 64 -30 -66 -10 19 5.83
- Superior temporal pole: 30 -48 10 -2 41 5.46
- Insula: 29 -34 12 2 13 5.89
- Cerebellum (crus 1): 24 -38 -56 -34 - 5.39
- Postcentral gyrus: 17 -60 4 18 44 5.89

**Right hemisphere**
- Inferior occipital gyrus: 229 38 -80 -6 19 6.66
- Middle cingulate gyrus: 138 2 -22 34 23 6.75
- Supplementary motor area: 101 2 0 62 6 6.43
- Precentral gyrus: 26 50 -54 46 39 5.44
- Middle frontal gyrus: 17 28 44 34 9 5.29
- Supramarginal gyrus: 14 56 -46 36 40 5.23

**Visual > Ambiguous statements**

**Left hemisphere**
- Middle temporal gyrus: 112 -62 -50 -2 21 6.30
- Angular gyrus: 75 -44 -72 30 39 6.85
- Calcarine fissure: 44 -10 -62 18 18 5.90
- Inferior frontal gyrus (triangular part): 26 -50 38 2 45 7.64

**Right hemisphere**
- Cerebellum (crus 2): 71 18 -82 -42 - 6.43
Figure B.1. To reconcile differences between our fMRI and fTCD results, follow-up laterality analyses for the word generation and visual short-term memory tasks were conducted based on brain regions perfused by the left and right MCAs (see Table 1, Badcock & Groen, 2017) for the low (left panel) and high (right panel) AQ groups. For each task, an inclusionary ROI mask containing MCA territory, with homologous regions in the left and right hemispheres was built using the Wake Forest University Pickatlas (version 3.0.5) toolbox (Maldjian et al., 2003). The LI analyses were conducted using the LI-toolbox (Wilke & Lidzba, 2007), where participant LIs larger than +.2 denoted left hemisphere lateralisation, while values smaller than -0.2 reflected right hemisphere lateralisation. Bilateral activation was categorised where LIs which fell in between the -.2 to +.2 cut-offs. Referring to the bottom left cells, only a small proportion of participants in the low (n = 2, 12.50%) and high (n = 2, 12.50%) AQ groups were categorised as having the typical pattern of left-side language and right-side visuospatial functions. These results illustrate how LI analyses using middle cerebral artery cortical territory yielded a similar pattern of results to Chapter 7, where of the recruited sample were found to exhibit typical (left-side) language lateralisation and atypical (bilateral) visuospatial lateralisation.
Appendix C: Supplementary fTCD Information

Experiment 3

Table C.1. Pearson correlations between fTCD laterality indices (LI) on the auditory sentence verification task with gold standard language (word generation) and visuospatial (visual short-term memory) measures. Correlations were only conducted on participants with language and visuospatial functions lateralised to separate hemispheres. All correlations had a p-value above .05.

<table>
<thead>
<tr>
<th>Gold standard laterality measures</th>
<th>Language LI</th>
<th>Visuospatial LI</th>
</tr>
</thead>
<tbody>
<tr>
<td>Verbal statement LI</td>
<td>.06</td>
<td>.25</td>
</tr>
<tr>
<td>Visual statement LI</td>
<td>-.23</td>
<td>.10</td>
</tr>
</tbody>
</table>

Experiment 4

Table C.2. Pearson correlations between fTCD laterality indices (LI) on the reading sentence verification task with gold standard language (word generation) and visuospatial (visual short-term memory) measures. Correlations were only conducted on participants with language and visuospatial functions lateralised to separate hemispheres. All correlations had a p-value above .05.

<table>
<thead>
<tr>
<th>Gold standard laterality measures</th>
<th>Language LI</th>
<th>Visuospatial LI</th>
</tr>
</thead>
<tbody>
<tr>
<td>Verbal statement LI</td>
<td>.21</td>
<td>.23</td>
</tr>
<tr>
<td>Visual statement LI</td>
<td>-.14</td>
<td>-.04</td>
</tr>
</tbody>
</table>