

Socioeconomic Neurophysiology

Exploring the relationship between a
child's environment and their
neurocognitive development

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Preface

Declaration

This thesis is the result of my own work and includes nothing which is the outcome of work done in collaboration except as declared in the preface and specified in the text. It is not substantially the same as any work that has already been submitted before for any degree or other qualification except as declared in the preface and specified in the text. It does not exceed the prescribed word limit for the School of Clinical Medicine Degree Committee.

Chapter 3 in this thesis has been adapted for publication in a peer-reviewed journal. As the lead author I was responsible for the data analysis, illustrations, and drafting of the paper, in collaboration with my supervisor.

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Abstract

This thesis investigates the impact of socioeconomic status (SES) on the neurophysiology of children's brains. Human beings develop within a variety of social and economic environments. This variability is inevitably reflected in cognition and associated brain activity. This includes stark negative impacts on the lower end of this spectrum. Research is often limited to one measure of SES, such as income or housing. There is also a tendency to limit analysis to one outcome, like a cognitive test or a particular form of brain scan. However, both SES and neurocognitive development are multi-faceted. If we are to understand their interactions fully, this complexity must be considered. I endeavour to address this complexity in the current thesis, by considering multiple measures of SES across structural, functional and task-based neuroimaging. I apply data-driven techniques including general linear modelling, auto-regressive models, and graph matching. Chapter 1 reviews the current literature on SES and development. I put forward a multi-level approach to build upon previous work. In Chapter 2 I compare different methods of modelling brain networks and contrast their suitability for capturing SES related variance. I find a distributed network of connections which relate to different elements of SES. I also show that functional neurophysiological methods are superior in capturing this variance. In Chapter 3, I investigate how neurophysiological activity during a passive phonological task predicts SES. I find that later processing is specifically related to subjective parental ratings of SES. In Chapter 4 I extend this approach to an actively involved visual working memory task and find differential associations with objective and subjective measures. In Chapter 5 I integrate these findings with existing theories and models. I find my results support theories connecting SES, inhibition, and language processing. I also reflect on the many distributed associations that *do not* fit these parsimonious models. Most importantly, this thesis showcases a new approach to SES research in cognitive neuroscience, and the importance of considering SES as multi-factorial.

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Chapter 1: General Introduction

1.1. Inequality and Education in the UK

The United Kingdom, and the broader western world, are fundamentally unequal. Individuals and families vary in their income, access to healthcare, quality education, community resources and exposure to crime. We can conceptualise this variance with a measure called socioeconomic status (SES). As the name implies, this aims to capture both social and economic aspects of an individual, family or community. As an academic construct, it can be defined in different ways, I cover this later in the introduction. However, it does reflect a spectrum of subjective and objective factors. Those who fall on the lower end of this spectrum experience huge disadvantages across their lifespan: they are more likely to suffer abuse (Alink et al., 2013; Trickett et al., 1991) commit suicide (Denney et al., 2009; Kim et al., 2016; Lewis et al., 1988) develop substance use issues (Fitzgerald & Zucker, 1995; Galea & Vlahov, 2002; Williams & Latkin, 2007)), have poorer healthcare outcomes (Clark et al., 2009; McEwen & Gianaros, 2010; Nandi et al., 2014), and at the end of their lives are more likely to suffer from dementia (Karp et al., 2004; Russ et al., 2013). Additionally, this SES effect worsens with adverse global events, like financial crises (e.g. health status: Bartoll et al. 2015; cardiovascular disease: Kollia et al., 2016; abuse: Kontos et al., 2017; addiction Mateo-Urdiales et al., 2020; old-age cognitive health: Whetung & Bhattacharyya, 2020), or more recently, with the ongoing coronavirus pandemic (e.g. cancer detection: Chen et al., 2021; mental health: Nagasu et al., 2021; general wellbeing: Wanberg et al., 2020). A socio-economic disadvantage may also have indirect impacts upon longer-term outcomes, via co-occurring risk factors like alcohol usage, diet, and mental health. Given the multitude of negative impacts, it is unsurprising that socioeconomic inequality is also reflected in an individual's cognitive and neural functioning. The broad aim of this thesis is to characterise this variability in childhood.

The UK has seen consistently improving living standards over the last century. This has lifted many out of the levels of absolute poverty seen in 19th century Britain

(Gazeley, 2003). Much of this change was catalysed by the creation of a welfare state (Nullmeier & Kaufmann, 2010). Despite this, we still have a steadily widening relative gap between the most affluent and those experiencing the greatest disadvantage (Browne & Hood, 2016). In recent years, even the positive changes in absolute poverty rates have begun to regress (Barry et al., 2021; Bernard et al., 2017). Children have no control over this; they could be born into an affluent household in a wealthy area, or into a household reliant on food banks in an area with few amenities. These environmental differences have a causal impact on physical development, health, cognitive functioning, and education (Duncan & Magnuson, 2012). Whilst some appear to display some resilience to these circumstances (Cicchetti, 2013; Netuveli et al., 2008; Werner, 2013), many children do not. Even those who appear to have overcome these burdens can still suffer longer-term consequences. Such as low SES teenagers who show resilience through improved self-regulatory skills, but at a cost of increased epigenetic ageing of cells (Miller et al., 2015). Should they have their own children, those who themselves experienced socio-economic disadvantage are often forced to raise their children in relative poverty, and the cycle continues. In the UK, the single most important predictor for escaping this inter-generational trajectory is the educational attainment of children (Department for Work and Pensions, 2014).

Lifting children from relative deprivation with education has long been a motivation for charities and public policy (Lawton, 2004; Platt, 2005). This began in earnest with the establishment of mass public education in the mid-nineteenth century and the introduction of mandatory child education in 1870 (Musgrave, 2013). The logic is intuitive: education gives children the opportunity to earn more and therefore improve their access to resources as an adult. However, this does not *eliminate* the impact of low SES. The most recent data¹ from the Department of Education showed 96% of pupils had a full primary school attendance (Department for Education, 2020), but despite this attendance, a relationship between low SES and poor outcomes persists. A move to equality of opportunity, in theory, does not fully confer more equitable

¹ 2019 - later figures are skewed due to the impact of the 2020 Coronavirus Pandemic on school attendance

outcomes for these children in practice. There are two potential reasons for this lack of translation: firstly, there are differences in the quality of education given to children from different SES backgrounds; and secondly, that children show SES-related variability in their *response* to education. Both are likely to be true. Whilst differences in education provision is a question best suited for policy and educational researchers, cognitive neuroscience can shed light on the reasons behind why children with the same provision show — sometimes dramatically — different outcomes.

1.2. Education, Genetics, and Cognitive Neuroscience

Part of the answer to this lack of translation between increased educational opportunity and outcomes can be identified by looking at genomics. Between ~15-40% of the variance in educational outcomes can be explained by genetic factors (Benjamin et al., 2012; Rietveld et al., 2013), with a large part of this variance being explained by the genes associated in other studies with cognitive functioning (Davies et al., 2016; Tambs et al., 1989). Marioni et al. (2014), in a UK sample, showed that the SES of individuals had a modest genetic component. von Stumm et al., (2020) found that *both* SES and genetic factors combine additively to predict educational attainment across schooling. Genes predicted 14% of the educational attainment and SES 23%. The studies used to model these relationships are genome-wide association studies (GWAS), this approach has several limitations. GWAS is largely blind to the specific mechanisms which produce association (Hirschhorn & Daly, 2005; Tam et al., 2019), and in many studies, most variations occur in non-coding regions of the genome (Tak & Farnham, 2015). Interpretation of GWAS in terms of associated behavioural and social traits can be particularly challenging due to the distal relationship with biology, relative to say a clinical disease (Abdellaoui & Verweij, 2021). The relationship between SES and outcomes in GWAS studies is also somewhat complex. Marees et al. (2021)'s meta-analysis revealed that SES moderates all types of GWAS relationships between mental health and that this was potentially confounded with hidden geographical co-variance and other relationships.

This strong genetic influence may appear demotivating for those studying SES. Why bother looking at mechanisms influenced by SES if such a large chunk of variance in education and later life outcomes is determined by the genome? Such conclusions are premature. An individual's present genetic expression is *not* a straightforward reflection

of the parent's genomes. Many mutations occur from conception, and throughout the lifespan. Most have little impact, but some can have a large impact on neurocognitive development (Clement et al., 2012; Tischfield et al., 2005). Also, epigenetic changes — alterations in the expression of the gene based on the environment — impact how the genome translates into outcomes. Methylation is one such epigenetic process, it regulates the expression of genes and is necessary for healthy functioning, however, it can be disrupted by many environmental factors, including stress (Meaney & Szyf, 2005). As an example, Kaminski et al. (2018), studying a large group of adolescents, showed that increased methylation of a gene that codes for frontal dopamine receptors (DRD2 cg26132809) led to a decrease in IQ scores. This correlation explained 2.7% of total variance *after* accounting for variance explained by fMRI activation, and other genetic factors. This is only a single marker, and it is likely there are many epigenetic contributors to educational outcomes. To complicate things further, these changes can occur across multiple generations. Adverse parental environments can impact methylation in gametes, which eventually become their offspring (van Otterdijk & Michels, 2016). This trans-generational epigenetic mechanism can even extend to grandchildren if extreme changes occur when the child is in the womb, such as starvation (Heijmans et al., 2008). To summarise briefly: despite genetics being important, they are not deterministic. The environment an individual grows up in will have a considerable impact on outcomes, in part due to epigenetic effects both within and across generations. Crucially, all these influences likely culminate in their impact on neurocognitive development, and the proximal impact this has on educational progress. For that reason, many researchers have focused on the intersection between cognitive neuroscience, SES and education.

Linking educational attainment and cognitive neuroscience has been a focus of a great deal of work since the late-1990s (Antonenko et al., 2014; Blakemore & Frith, 2005; Byrnes & Fox, 1998; Varma et al., 2008). One motivation is to make teaching more equitable through evidence-based approaches (Sigman et al., 2014). The field even has an acronym - Mind, Brain, and Education (MBE) (Fischer et al., 2010). Multiple neurocognitive mechanisms have been identified as contributing to the educational performance in childhood. Indeed, this field is so large that I cannot cover everything in this initial introduction. Instead, I have provided a high-level overview. A good place to start is Blakemore & Bunge (2012) who provide a comprehensive summary of what the authors call 'foundational cognitive skills'. Skills related to self-regulation or control are

a broad theme here, with genetic contributions at play (Klaus et al., 2017). Self-regulation is the general ability to assert control over emotions, actions, and internal states in support of goal-directed behaviours (McClelland & Cameron, 2012). This is important, as one benefit of self-regulation is a child's increased ability to form relationships with teachers and other peers. This, in turn, supports learning (Duckworth & Carlson, 2013). It is these relationships that further feed backwards into increased self-regulation abilities (Zee & de Bree, 2017). The converse is that those who struggle to self-regulate often experience a negative cascade. The children who fail to get on this circular reinforcing improvement in regulatory processes lose out relative to their peers (Fernandez-Rio et al., 2017).

Given self-regulation's observed importance in educational attainment, it is foreseeable that it might play a role in the mediation of attainment by SES. This role has been on the radar of researchers for decades. For example, in the context of delaying rewards, Green & Fisher (1988) suggest the ability to control oneself and receive a greater future reward is impacted negatively by SES. More recently, Evans & Rosenbaum (2008) demonstrated that low SES predicts low self-regulation and later lower school attainment. They show that this pathway is independent of any improvement due to an enriched cognitive environment (e.g. more books, music lessons etc). Moilanen et al. (2010) followed the trajectory of inhibitory control (self-regulation assessed through parent questionnaires), along with observations of parenting. SES made contributions to slower development of this skill, beyond the impact of parenting attributes. Predisposition to lower self-regulation can even occur before birth. A recent study described how maternal immune activation (as measured by cytokine activity) impacted their child's later self-regulation. This negative factor explained about one-tenth of the SES-related differences in the skill (Yu et al., 2020). It appears, therefore, that self-regulation is not only important in how SES relates to attainment, but it is independent of direct attempts to enrich the environment, and the impact may be triggered before the child is even born.

Self-regulation itself is an umbrella term and relies on a broad range of cognitive skills. *Executive Function* (EF) is a term that overlaps highly with self-regulation but is more commonly preferred in the cognitive literature. Tasks which require EF are particularly sensitive to a child's SES (Duncan et al., 1998; Noble et al., 2007). EF itself covers cognitive constructs such as inhibitory control, action planning, attentional

flexibility, error detection and correction, and resistance to distractors (Carlson, 2005). These constituent factors are also negatively impacted by SES. Suppression of distractors —one measure of selective attention — is poorer in children from low SES backgrounds, with children showing higher evoked responses to irrelevant auditory stimuli (Stevens et al., 2009). In addition to replicating this effect, more recent research has demonstrated a mediating effect of cardiovascular load on this relationship — suggesting children from low SES backgrounds bear a greater biological burden when exerting selective attention (Giuliano et al., 2018). The recognition and processing of mistakes is another indicator of EF. The error processing — measured by children watching familiar puzzles being solved incorrectly — elicited weaker frontal theta oscillations in toddlers from low SES backgrounds, with one aspect of SES, parental education, being particularly predictive (Conejero et al., 2018). These studies connect the SES impact on behavioural cognitive measures, with the potential neurophysiological substrates. I build on this later in the thesis: in Chapter 3, using electrophysiological error signals to assess phonological processes, and in Chapter 4 with a working memory task in the MEG scanner.

Beyond EF, other cognitive skills which predict attainment are also influenced by SES. For instance, mastering spoken and written language is a key skill for educational, professional, and social success. The cognitive processes supporting language are a very plausible candidate for providing a link between SES and educational outcomes. Compared to other cognitive skills, one of the strongest relationships is between SES and language development (Bus et al., 1995; Pungello et al., 2009). Some of the selective attentional research discussed above used spoken language as stimuli (Giuliano et al., 2018; C. Stevens et al., 2009), illustrating how interconnected language is with outcomes in the SES literature. The acquisition of oral language is reliant on specific and time-sensitive neurocognitive mechanisms: moving from lower-level word sounds to complex syntactic rules, then higher-level language over several years (Stromswold, 2000). In turn, the development of oral language skills is the biggest known predictor of written language mastery (Hagtvet, 1993; Honig, 2007). The gradient of this language development trajectory is impacted by SES. For instance, the development of reading across primary/pre-school children is negatively impacted by lower SES (D'Angiulli et al., 2004). This to great extent likely reflects language exposure in a child's home. Romeo et al. (2018) showed increased white matter connectivity in the brain related to

adult-child conversational experience, and that this contributes to SES related language gaps in children.

Combining many aspects of the cognitive neuroscience SES literature, Noble and colleagues have posited a dual-path model through which SES impacts brain development (and therefore future attainment) (Noble et al., 2012; Ursache & Noble, 2016). One path posits that SES impacts a child's language skills through the linguistic environment at home, which in turn leads to structural differences in the brain, specifically in the left inferior frontal and left superior temporal gyri. A second pathway links low SES with increased stress. This second pathway influences multiple brain areas, and in turn constrains social-emotional processing, memory, and self-regulation. In line with this model, research has shown that SES does indeed moderate the relationship between task-measured phonological language performance and left fusiform gyrus activation. (Noble et al., 2006) selected children matched in phonological skill, but from a range of SES backgrounds and had them perform a pseudo-word reading task during fMRI. Lower SES children's brain activity appeared to moderate task performance, whereas higher SES children showed an attenuated relationship. This was apparent in the left fusiform and perisylvian regions. The second pathway's main mechanism is through stress-induced changes to the neuroendocrine system. Evidencing this, low SES children have shown to exhibit both very low and very high levels of cortisol, which influence cognition negatively (Badanes et al., 2011; Blair et al., 2011). Areas with high densities of cortisol/corticosteroid receptors include the hippocampus, amygdala, and prefrontal cortex, involved in memory, emotion, and executive functions respectively (Ursache & Noble, 2016). Long-term extremes in cortisol levels cause a lack of inhibition in these cognitive systems underlaid by dysregulation of the hypothalamic-pituitary-adrenal axis (Arnsten, 2009; Lupien & Lepage, 2001). Providing further support cortisol has been linked to changes in activation in the prefrontal cortex during executive function tasks (Blair et al., 2011), amygdala during emotion regulation (Kim et al., 2013), and hippocampus during memory tasks (Arnsten, 2009).

Taken together, the neurocognitive literature provides several candidate mechanisms that might provide a vehicle for the relationship between SES and attainment in childhood. This research suggests SES likely impacts outcomes via multiple mediating pathways, not to mention that SES is likely itself highly multivariate.

The result is that any researcher or theoretician must be selective. Often researchers are forced to choose tasks, domains of cognition, elements of SES, or even in some cases specific brain regions. However, as I will outline, these selection choices can themselves have a massive impact on the conceptual conclusions we draw.

1.3. Dimensions of Socioeconomic Status

SES is not a unitary construct. As its name implies, it consists of both social factors, like education and economic factors, like income. However, all too often developmental studies characterise SES using a single measure, such as income (Case et al., 2002), parental education (Hoff, 2003), affluence of the child's school (Lupien et al., 2001; Perry & McConney, 2013), household facilities (Ryu et al., 2016), or neighbourhood (Martens et al., 2014). This creates an issue of comparability, as the mechanisms by which these factors influence developmental trajectories are likely to be different. For example, should we expect a measure that reflects household income and a measure which reflects parental education to impact the brain in the same way? Probably not. To provide a concrete example: one study showed that children schooled in a poorer area had higher stress-related hormone secretion (cortisol) but found no difference for these groups in memory or attention (Lupien et al., 2001). This finding stands in contrast to a large body of research showing a relationship between SES and these cognitive measures (Lawson et al., 2018). This lack of replication is likely to have arisen because grouping children based on school is not a sufficiently sensitive measure of SES when compared to parental education and income which are necessarily individual-specific. But the group differences in cortisol were strong enough that an individual approach was not needed. There are other explanations. For instance, child salivary cortisol can vary with diet (Toda et al., 2004), and there was no mention of accounting for food consumption. So small group differences in when the child ate breakfast could have driven this effect, but then diet may itself be another indicator of SES. This illustrates issues with many studies in the literature – SES is differently defined. Even when multiple measures are used there is a tendency to combine them into a composite risk score. Whilst this might maximise predictive power, it obscures the potential specificity of relationships (Duncan & Magnusson, 2003; Tarullo et al., 2020).

I am not the first person to identify this challenge. This tricky issue of measurement is discussed in the review by Ursache & Noble (2016). They point out that even income can be measured differently. For instance, it can be grouped into quartiles or can be more precisely estimated by comparing it to the outgoings of the household in an income-to-needs ratio, or as total affluence considering assets and debts. Occupational prestige can be measured using categorical scoring schemes like the Hollingshead factor scales (Hollingshead, 1975), with caution taken to update them to modern standards. They also describe subjective measures of SES, such as the MacArthur Scale of Subjective Social Status (Adler et al., 2000), where parents rank themselves within their community on a 10-runged ladder. This is posited to represent either a more sensitive measure (as the parents combine information about themselves more accurately) or an additional measure based upon the independent psychological interpretation of their relative inequality. Ursache & Noble (2016) suggest that researchers should aim to include measures of income, education and occupation. Encouragingly, recently these suggestions have been taken up. Tarullo et al. (2020), for instance, conducted a multi-dimensional analysis of variation between SES, and various measures of cortisol in children. They replicated a general impact on SES, but breaking this down, found that food insecurity, household environment and neighbourhood all made specific contributions to specific biomarkers of stress (as measured by parent cortisol, child cortisol and hair cortisol). Furthermore, they found these unique contributions were independent of household income or parental occupation. Tarullo et al.'s results illustrate how previous studies may have missed the complexity of relationships and illustrate the importance of multiple measures.

In this thesis, to capture a broad measurement of SES, I have chosen to assess multiple indicators of SES. These measures include subjective SES rated by the ladder measure above, household income equalised for the number of people, both parent's highest educational level, both parent's occupations, personal ratings of the neighbourhood, Index of Multiple Deprivation (IMD) for their postcode, extra-curricular activities, number of books in the home, household appliances, household bathrooms, and whether a child has their own room. This represents a lot of data, and

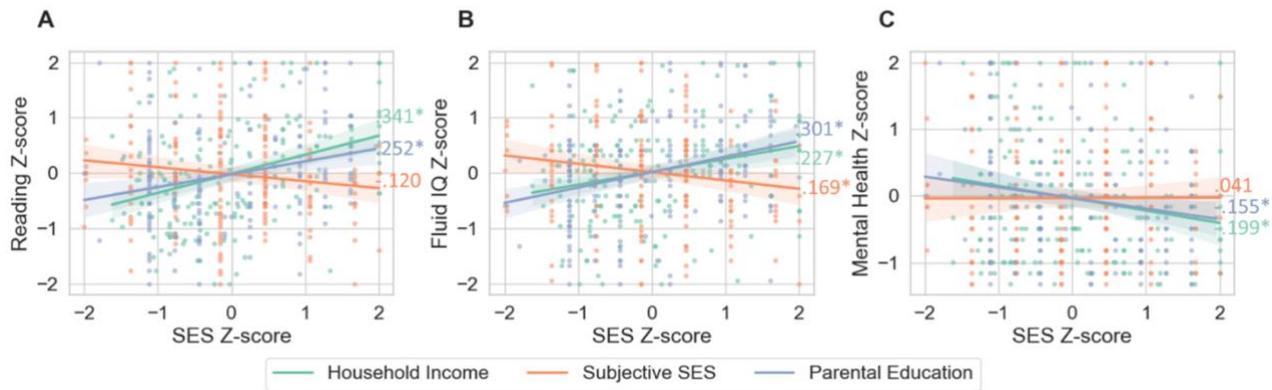


Figure 1. Different trends of factors of SES on education, cognitive and mental health measures. Data from the combined samples in this study, 172 children. Linear regression lines are plotted with a bootstrapped 95th confidence interval. Coloured numbers are Spearman's rho coefficients, with * indicating a significant effect at below .05 adjusted for multiple comparisons. Household income is derived from equivalised household income, subjective SES from self-rating, and parental education score according to the UK National Qualifications Framework. **A)** Reading z-score derived from Woodcock Johnson Reading test. **B)** Fluid IQ z-score derived from the WASI Matrix Reasoning subtest. **C)** Mental Health Z-score derived from the total difficulties score from the SDQ.

as covered above some will share variance, but other factors could have differential relationships. I decided to conduct a small analysis to illustrate this potential issue. I conducted a simple correlation analysis across the samples used within this thesis. I arbitrarily picked three of these SES measures (household income, subjective SES, and parental education), against three outcomes of: educational attainment (reading), cognitive functioning (fluid IQ) and mental health (Strength and Difficulties Questionnaire - SDQ). As expected, and in line with previous work, these variables were all associated with some measure of SES. However, illustrated in **Figure 1**, the degree of association is variable dependent on measure. **Figure 1.A** shows that reading ability increases with household income and parental education but is not significantly correlated with a care-givers subjective rating of SES. **Figure 1.C**, capturing a measure of mental health shows the same pattern, with scores on the mental wellbeing questionnaire getting worse (higher) with lower income and education. But most strikingly **Figure 1.B**, illustrating Fluid IQ, shows a different pattern: IQ scores become higher in lower subjective SES ratings, whereas household income and parental income show a positive relationship. If we were to simply look at one of these SES measures in isolation, we would get a partial picture — and in the worst case of Fluid IQ, we would see a trend that flips direction depending on the way of defining SES.

I do not wish to disparage the previous literature; the decision to use only one or two SES measures in previous studies is often a pragmatic one. It becomes very

challenging to conduct complex analytical procedures - especially with neuroimaging methods - if one has multiple continuous SES variables. The purpose of many of the studies is not to study directly SES, but just to control for it (more than half in the Lawson et al., 2018 meta-analysis), so it is not reasonable to expect huge methodological adaptations. Additionally, there is *still value* in studies that do not cover the full range of potential SES-related constructs. Lawson et al. (2018), found that the variability in the choice of measures of SES did not moderate the relationship between SES and EF. Although I must point out that a lack of findings alone is not the same as evidence for its non-existence, and this is not consistent with the small analysis above. Even in the case of this thesis, it is not possible to use the 12 separate measures of SES in every analysis, especially as many of these predictors are collinear (linear combinations of each other), which is an issue for the linear models used (Farrar & Glauber, 1967). On that subject, some studies that *do* include multiple measures of SES fail to adjust for this collinearity, potentially skewing the results (e.g., Tarullo et al., 2020). However, there *is* a way to address the issue, whilst still capturing the components of SES. The compromise I make, which is described in the empirical chapters, is to reduce the many measures into a few statistically orthogonal factors (i.e., *not* collinear). This approach allows me to examine the association between SES and neurocognitive functioning in a data-driven fashion, whilst avoiding the potential pitfalls illustrated in **Figure 1**. As far as I could detect, this approach has hitherto not been taken in the literature. It provides a novel means of capturing potential specificity, without violating the assumptions of linear regression models.

1.4. Characterising Multi-level Models of Impact

So far, I have established two potential sources of complexity that are relevant for this thesis: first, SES is not a singular construct; second developing brain-cognition relationships are complex. The potential scope of this thesis is therefore broad, and this has necessitated several pragmatic decisions as to my focus.

One potential conceptual structure is to hierarchically nest the levels of understanding that I aim to study (McClamrock, 1991). Examples of these approaches include David Marr's characterisation of the computations of neural circuitry (Marr & Poggio, 1976), and Zenon Pylyshyn's application of architectural and algorithmic levels (Pylyshyn, 1980). Indeed, one paper already discussed applies a multi-level approach,

understanding cortisol's involvement in the hypothalamic–pituitary–adrenal axis. Tarullo et al. (2020) characterise this as a multilevel process, lower levels of instant measurements (from saliva at different times), versus higher-level biomarkers of chronic stress from hair samples. I hope to apply this conceptual approach to the study of cognitive processing and SES.

This concept of multi-level models can be of some value when approaching my data. I can characterise different analytical levels of a child's processes and outcomes. For simplicity, I will split these into three levels – with the rough names of Network Architecture, Passive Processes, and Active Processes (see **Figure 2**). I say 'rough names' because these could be named alternatively, but identifying the right labels is not the purpose here. The purpose is to investigate SES correlates from more than one angle. The levels are organized along opposite axes indicated by the arrows on the left. 'Granularity' describes the level of detail an analysis can go down to, whereas 'Context' is the conceptual distance to observed behaviour. The first level: 'Network Architecture' represents our most granular level², it relates to the physical attributes of the brain, and large-scale general-purpose networks at rest. Analysis conducted here are the most removed from context. The second level is 'Passive Processes' and this describes the passive processes which occur in response to the structured environments. These are more focused processes which operate on the architectural level to achieve representations and predictions for perception. For example, areas of the brain which process phonological information show reduction in brain activity when an unexpected stimulus (like an error in pronunciation) occurs (Pulvermüller & Shtyrov, 2006). This is not just a physical connection; this is an active process involved in perception. The third level, I have named 'Active Processes', these are specific large-scale systems and networks of areas, which support higher level cognitive processes like working memory or language. These are at least partly active systems, which we can measure in relation to an individual performing some task. For instance, activation in the networks of areas underpinning performance in fluid intelligence tasks (G. J. Duncan & Magnuson, 2012; Gray et al., 2003; Tschentscher et al., 2017). I hope by focusing on these levels

² Of course, we could go more granular — neurotransmitters, cellular work, genetics — but I am fundamentally limited by time and resources.

separately, this thesis can report a fuller account of the impact of SES than if I were to focus on a single level.

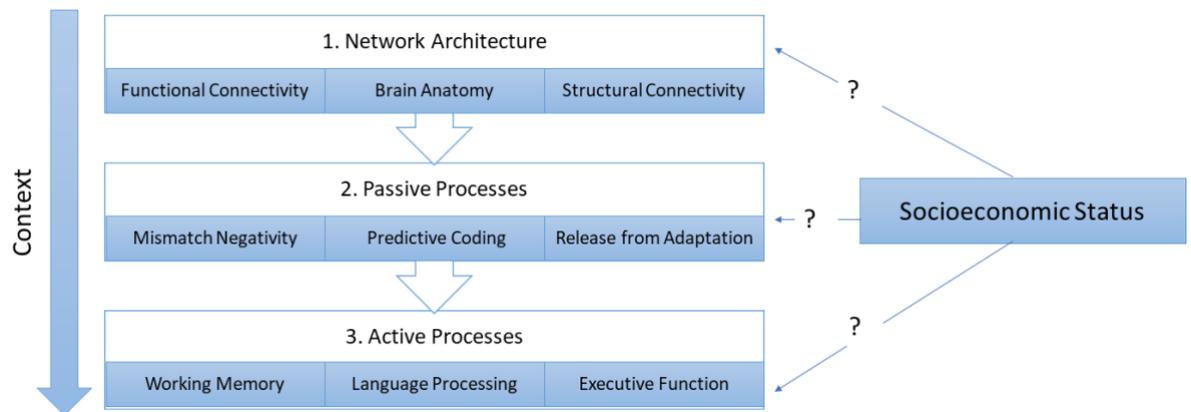


Figure 2. Cartoon diagram illustrating different levels of explanation. Examples of measures included each in light blue. The vertical arrow illustrates how each level relates to context.

The specific details of models like Marr's have been somewhat debated since their creation (Stevens, 2012), and there are other competing approaches for characterising complex systems. Keeping this in mind, it is worth pointing out that my aim with this model is primarily to structure an exploration, rather than to condone any specific model of development or functioning of the human brain. Additionally, I make a distinction between 'active' and 'passive' processes. This comes close to the debate around the 'automaticity' of cognitive and perceptual processes (see Moors, 2013 for an overview). I intentionally avoid addressing this issue, as I use the model to spread my focus, rather than ask abstract questions about the nature of the levels. The terms 'active' and 'passive' are more closely tied to the nature of the tasks rather than delineating the bounds of consciousness. For instance, the oddball task in Chapter 3 may involve orienting of attention and conscious awareness, however the task itself involves no active response by design. Indeed, focusing on constructs, with competing multilevel models, and assessing their fit to neuroimaging and cognitive data would be a very tempting subject for a thesis. However, this would be a distraction from my primary aim of investigating SES. I therefore consider this model as a utilitarian tool for structuring the following chapters.

Going forward with the levels above. The focus of several previous SES studies falls within only one of these levels. For instance, SES association with cortical thickness (Piccolo et al., 2016), cognitive function (assessed by questionnaire) (Meyer et al., 2018),

mental health (Gilman et al., 2002), or educational achievement (Sirin, 2005). Commendably, there *are* several studies which aim to integrate across more levels. For instance, SES with event-related potentials and selective attention (Herdman et al., 2008; C. Stevens et al., 2009), or cortical grey-matter volume and school achievement (Mackey et al., 2015). However, these are usually limited to two levels at most. Those observations are all singularly interesting, characterising certain aspects of the relationship between SES and a given measure. However, we must move towards integrating between these levels if we are to produce insights which could eventually inform policymaking. In this spirit, the present project aims to gather information across several domains – brain structure and function, cognition, attainment, mental health, and social adaptation.

I have structured the empirical chapters along the lines of the multi-level system. As mentioned above, I am somewhat limited by time and resources, so I have chosen to characterise a tranche of investigations, slicing through the levels above. Beginning with Network Architecture, I first begin with an analysis of the structural connectome in comparison to the functional connectome and investigate what these properties might be associated with. I then investigate neurophysiological patterns within a passive task – a phonological oddball task – and how these co-vary with SES. This is the ‘Passive Processes’ level. Finally, I select an actively involved task whilst the children are in a scanner, a visual working memory task. This characterises the relationship on the ‘Active Processes’ level. By taking this approach I can then focus on the commonalities and differences between these levels, to gain a more nuanced picture than previous research

1.5. The General Linear Model

Above, I’ve spoken about the need to utilise multi-level approaches towards capturing the interplay between SES and cognitive neuroscience. However, this leaves us with a statistical requirement to compare multiple predictive factors from SES against brain signals and contrasts involving huge dimensionality. I have multiple different forms of structural, task based and resting-state brain data, along with demographic information and behavioural performance. To tie this together in a comparable way, I need a general purpose and robust statistical approach. A general linear model (GLM) framework may provide such an approach. It is helpful to describe what this is, and

particularly why I choose to use this tool and its extended versions in all the following empirical chapters.

The GLM I elected to use is based on a linear regression algorithm called Ordinary Least Squares (OLS), specifically extended for both multiple regressors, and to predict higher dimensionality data. This approach considers the data (data from the brain in our case) to be explained by a linear combination of multiple predictors (e.g., age, cognitive scores and demographics), a constant regressor, and residual error. This concept is represented with example regressors in **Equation 1**.

$$Y_{scans} = \beta_{intercept} + \beta_1 X_1 + \beta_2 X_2 + \beta_3 X_3 + \beta_4 X_4 + \beta_5 X_5 + \epsilon$$

Equation 1. Ordinary Least Squares formula. Y_{scans} represents the neuroimaging data. This is explained by a combination of regressors weighted by beta values and residual error ϵ . $\beta_{intercept}$ is a constant regressor, the numbered β_i each represent individual weights which are applied for each matched X_i regressor. X_1 is Age, X_2 is WASI Matrix Reasoning, X_3 is Objective SES, X_4 is Objective SES, and X_5 is Household SES.

The beta (β) weights (or coefficients) estimated are the key statistics of interest, as they represent the degree each predictor impacts values in the data matrix. These weights are estimated using a procedure which aims to minimise the summed squares of the residual errors for each regressor. This minimisation treats all regressors together, each estimated value is the impact of *that* regressor whilst the *other* regressors are held. This is extremely helpful for our purposes here. For example, this means the predictive value of a measure like Matrix Reasoning on the data will be independent of Age, so long as Age is included as another regressor. As this thesis includes measures of SES, Age, and IQ, all of which are likely to be associated with each other and our various brain measures, this type of model allows us to separate these effects rather than confound them.

$$T = \frac{\beta_1}{se(\beta_1)} \quad (1)$$

$$se(\beta_1) = \sqrt{\frac{RSS}{(n-2)S_{xx}}} \quad (2)$$

Equation 2. *T*-statistic equation for a single β coefficient **(1)** the coefficient value is divided by its standard error. Standard error of the coefficient **(2)** is calculated as the square root of the residual sum of squares (RSS) divided by the sample size minus two and multiplied by the square of de-meaned regressor (S_{xx}).

T statistics can also be calculated for each regressor. This is helpful because *T* represents both the strength of the predictor *and* its consistency (i.e., variance).

Equation 2 represents the process for calculating *T* from a single beta weight. I use this statistic frequently to establish significance across the high-dimensional brain data. For this purpose, I avoid the typical approach of obtaining a *p* value from reference distributions. This typical approach comes with a raft of assumptions, such as that data and regressors are parametric, which does not hold for the brain data frequently used in this thesis. When using the typical approach, it is also necessary to correct for each contrast, which reduces the statistical power of the model. Instead, I utilise a permutation approach in which the null distributions of *T* statistics are generated by shuffling each predictor many times and re-calculating. Unlike the reference distributions used in the standard approach, permutation testing is non-parametric, the null distributions are fitted perfectly to the intrinsic properties of the high-dimensional scan data, and we are not required to correct for multiple comparisons on this level (Nichols & Holmes, 2002).

Additionally, multiple comparisons on the level of contrast (e.g., multiple group-level regressor contrasts, like the independent effects of Age vs IQ) are also accounted for in the permutation scheme. The Monte-Carlo *p* value in our GLM differs from parametric tests, as it is a conditional probability generated from the data and design matrix, rather than tabulated from reference tables and adjusted for multiple comparisons based on number of tests (such as in a Bonferroni correction) (Maris & Oostenveld, 2007; Salmaso & Pesarin, 2010). The risk of false alarms does not increase, within each contrast-permutation other regressors are held constant in the design matrix and therefore accounted for in synchronous permutations, so the final Monte-Carlo probability does-not need to be further adjusted for other contrasts (Camargo et al.,

2008; Winkler et al., 2014, 2016). This multivariate GLM-permutation inferential method has been used extensively (e.g. Kocagoncu et al., 2020; Proudfoot et al., 2017; Quinn et al., 2018; Singh et al., 2003). Here I use several different types of permutation across the thesis, which are explained within the relevant sections.

The combination of GLM and permutation testing is particularly flexible and can be adapted to suit many different types of data. Within the thesis, for example, I use the combination to predict evoked electrophysiological signals, with a clustering step to aid in interpretability; connection weights in brain networks; principal component scores, and metrics of behavioural task performance. GLM's can also be layered, with beta-weights or t-statistics carried forward from participant-level models to group-level models. I also used this in the auto-regressive models, with a temporally extended OLS algorithm, in which output statistics on the participant level are piped into a group level GLM. This procedure is also utilised in a comparison of different types of scans for a high-level comparison MEG and DTI GLM's - where beta weights are used to mask an upper-level regression. Put simply, this combination of a GLM alongside permutations is robust and multi-purpose, making it a perfect swiss-army knife to use as a recurring methodological tool.

1.6. The Present Study

To summarise the above: I have reviewed literature showing that cognitive skills are key in understanding how SES influences different outcomes of children in education and then later in life. I've also discussed that to understand this, I factorise the complex component of SES, and apply it to three investigations that fall across a multi-level model of the cognitive neuroscience of SES.

In Chapter 2, the first of these investigations is a mass-correlational analysis of how structural and functional networks co-vary with Age, IQ, and SES factors. I also attempt to match these networks together and compare their predictive ability. This analysis also combines the two large samples used in later sections to maximise statistical power. I use the results of this chapter to select two functional tasks for further analysis. In Chapter 3 I look at how SES impacts upon the electrophysiological correlates of an automatic phonological processing task. Chapter 3 uses the prediction-error mechanisms of underlying brain networks, operating at the middle of the levels I discuss above. Finally, in Chapter 4, I use an active task with a visual working memory

(VWM) retro-cue design, to investigate potential SES associations on a functional task level.

There are a broad set of questions that I would like to address in this thesis. Firstly, which elements SES will be most predictive of the neurocognitive data? As explored above, some estimates like income and parental education are highly correlated so could lead to similar negative patterns, others like subjective SES may lead to more unexpected relationships. Secondly, which functional systems will be most associated with these SES elements? Noble and other's models would suggest we could see dual, but separable, impacts along both language-related processes and systems, versus self-regulation/socio-emotional processes and systems (Noble et al., 2012). Will we replicate these influences, or will we identify other sets of relationships? Lastly, will there be convergence between the structural and functional neuroimaging methods in terms of which SES measures they are most sensitive to, and is one modality more sensitive than another.

Chapter 2: The Connectome and Socioeconomic Status

2.1. Introduction

As covered in Chapter 1, childhood deprivation and related adverse experiences are associated with the developing brain. This association has been documented across many developmental processes and measures of brain health, with downstream consequences for cognition (Brito & Noble, 2014; Dalmaijer et al., 2019; Johnson et al., 2016). Previous research has outlined broad anatomical correlates of low SES — such as a more linear trajectory of cortical thickness (Piccolo et al., 2016) or a decreased developmental slope in total grey matter volume (Hanson et al., 2013). This kind of broad characterisation is important because it demonstrates the likely effects of socioeconomic factors at multiple levels of brain development but leaves open many questions about specific circuits and outcomes. In contrast, a number of previous studies have focused on associations with specific systems, such as the prefrontal cortex and the amygdala, which display reduced activity during emotion regulation in low SES groups (Kim et al., 2013). Kim et al. (2013), for example, reported that adults who spent their childhood in low-income households were less able to suppress amygdala activity when regulating negative emotions.

The above study is one of many possible examples in which a particular brain area, or set of brain areas, are selected *a priori*. Whilst this can have valuable statistical benefits, it also risks giving the false impression that emotion regulation or SES associations are restricted to, say, the amygdala. The overall contribution of whole brain activation is downplayed, and this can limit our understanding of potentially large scale network involvement (Raizada & Kishiyama, 2010). The localist perspective that naturally flows from analysing data only from regions of interest, which can have knock-on conceptual consequences elsewhere in the literature. Indeed, in some cases, claims about neuro-cognitive systems in specific brain areas are made without the use of neuroimaging *at all*. The assumption is made that particular brain areas are activated by

specific behavioural tests (Farah et al., 2006), and thus direct brain measures are not needed. This type of evidence leads to circular reasoning, which artificially inflates the evidence for a given region being involved in a process. There is an alternative approach, however.

2.1.1 Characterising distributed patterns of brain activity

An alternative *data-driven* approach is slowly emerging within the field, that looks beyond the activity patterns of individual areas in isolation. The analysis of whole-brain networks has the potential to uncover the much wider set of associations between system-wide brain development and SES. One approach in this field is whole-brain connectomics, where areas across the entire brain are conceptualised as connected nodes in a network (Sporns et al., 2005). Let's consider why using this approach may be particularly appropriate. The increased exposure to early life stressors that come with lower SES may enact changes across a large array of systems — through epigenetic changes, hormonal damage and dysregulation (Miller et al., 2011). However, this system-wide information is lost by focusing on a single brain area, or even a restricted set of regions. Whole brain connectomics provide an approach that combines both global associations, and potential importance of specific areas within that global context. This approach also allows for the possibility of capturing heterogeneity of association. Within any sample a particular brain correlate of SES could have differential effects depending upon its profile of connectivity across the individuals within that sample. Show-casing the strength of this whole-brain approach, Bathelt et al. (2018) show that voxel-wise comparisons of white-matter explain far less variance in cognitive performance, relative to connectivity properties of the network more broadly.

For this thesis we have data that can be used to form structural networks (Magnetic Resonance Imaging/MRI scans) and functional networks (functional MRI/fMRI and magnetoencephalographic/MEG scans). Both have been used to investigate the neural correlates of SES within the developing brain, however they likely measure different but partially overlapping neurodevelopmental processes. I decided that a sensible first step in this thesis is to establish how these two scan types – structural neuroimaging in the form of diffusion tensor imaging, and functional neuroimaging in the form of resting-state MEG – relate to each other within the same sample, and more crucially how each is predicted by SES and other covariates of

interest. This then provides an informed platform for subsequent task-based chapters of the thesis.

There are many ways of deriving connectivity metrics with structural and functional data. Here I limited myself to a single functional method and a single structural method, in order to construct connectomes for each datatype. Whilst it would be interesting to compare connectivity metrics, this would be a large methodological task and not allow time for addressing the central SES questions of the thesis.

For the functional data I used resting-state MEG scans. These data provide a high temporal resolution because they are sensitive to the electrophysiological basis of connectivity itself. We can also obtain information on the frequency of brain activity and interregional connectivity (this is further outlined below).

For the structural data I used Diffusion Tensor Imaging (DTI), which gives a measure of white matter tracts between different areas. DTI is a common way of constructing structural connectomes (Bullmore & Bassett, 2011; Sporns et al., 2005), using the diffusion of water molecules and 3D tracing to estimate white matter tracts in the brain. DTI-derived connectivity appears to be related to the functional elements of the connectome, as captured by fMRI. This correspondence seems to apply to both individual areas, like the medial frontal cortex (Johansen-Berg et al., 2004) and on a global network level (Honey et al., 2009; Osmanlıoğlu et al., 2019; Silva et al., 2020). To our knowledge, DTI has not been directly compared to MEG derived connectomes, but because it is the most widely used structural connectivity tool within the literature, it should act as good yardstick against which to compare our MEG connectomes. For example, DTI-derived connectomes have already been shown to vary according to IQ (Kocevar et al., 2019a), Age (Zhao et al., 2015) and SES (Johnson et al., 2021).

Connectomics and graph theory provide a formal framework for handling structural and functional brain data and testing how brain organisation co-varies with individual differences in cognition, behaviour (Cao et al., 2014; Shen et al., 2017; Sporns, 2012). These tools have been leveraged to investigate the developing brain, in resting state MEG (Dimitriadis et al., 2013), functional (Gracia-Tabuenca et al., 2021; Zhou et al., 2021), and structural (e.g. Kim et al., 2019) MRI data. However, it is rare that these different types of connectivity are considered in parallel within the same participants. The purpose of this chapter is to create both DTI- & MEG-derived connectomes,

explore their interrelationship and the relative unique contribution of each scan type towards explaining variance in SES.

2.1.2 Socio-economic predictors of network connectivity

As outlined in the General Introduction, the purpose of this thesis is to robustly characterise the association between SES and developing brain processes. However, SES is a complex construct, that cannot always be well captured by parental income or occupation (Adler et al., 2000; Rubin et al., 2014), and different elements of this construct can predict outcome measures differentially – illustrated in the General Introduction where I show that Subjective and Objective SES measures can predict fluid IQ in opposite directions. To address this, the approach I have taken is integrate potentially distinct socio-economic indicators using an exploratory factor analysis. The details of the factor reduction are included below, but to summarise, its results in three orthogonal factors: the first relating to parental income and education; the second relating to subjective perceptions of SES, and the third representing aspects of the household (rooms, appliances, neighbourhood). This allows us to integrate these different factors within our GLM.

For our covariates I chose to investigate Age and fluid IQ, as these represent common and important cofactors of interest in the literature (Age: Coquelet et al., 2020; Zhao et al., 2015), fluid IQ: Kocevar et al., 2019; Simpson-Kent, Fried, et al., 2020; Simpson-Kent, Fuhrmann, et al., 2020, SES: Brito & Noble, 2014; Johnson et al., 2021; Kim et al., 2019. As mentioned in the GLM section of the General Introduction, their inclusion in the GLM means the SES factors we are seeing on the brain are independent of Age and IQ.

In summary, the purpose of this first empirical chapter is to construct structural (DTI) and functional (MEG) connectomes within the same participants. Then, using a GLM-permutation combination, to test whether *and how* these connectomes are associated with multiple elements of SES, IQ, and Age. Because the tools needed to construct the connectomes are somewhat bespoke to each modality, I have divided this chapter into the following sections: First, the construction and analysis of the resting-state MEG connectomes; Second, we deploy a novel PCA-based analysis to make those MEG results digestible; Third, the construction and analysis of the DTI connectomes; and Fourth, the direct comparison of the functional and structural connectomes.

2.2. Resting State MEG Connectomes

Resting state functional connectivity networks derived from fMRI exhibit excellent spatial resolution and allow fine parcellations. This approach has been used to study impact of early adversity in children (Demir-Lira et al., 2016; Rakesh, Zalesky, et al., 2021). However, the method is affected by non-neural physiological signals and is limited in the temporal domain (Logothetis, 2008). MEG, in contrast, allows the inclusion of oscillatory frequency information not available using fMRI functional connectivity (Hipp & Siegel, 2015). Multivariate vector autoregressive modelling (MVAR) (Fasoula et al., 2013) enables us to split connectivity into discrete frequency bins, and metrics such as partial directed coherence (PDC) (Baccalá & Sameshima, 2001), which allow us to describe directionality in these networks. Direction information is valuable, as functional networks in the brain are themselves directed, with this direction changing in line with frequency (Hillebrand et al., 2016).

These directed oscillatory networks are likely to be important factors in investigating the association between SES and the brain. For example, cognitive control and associated directed pre-frontal networks are negatively impacted by early stress and low SES (Demir-Lira et al., 2016; McEwen & Gianaros, 2010; Xie & Pisano, 2019). In their review Helfrich & Knight (2016) explore the literature around pre-frontal cognitive control networks. They show that oscillatory dynamics – such as coupling across frequencies and phase resetting by task cues – underpin control of these networks, and support integration from other areas during various goal-directed tasks. They also show there is an inherent directional component to these oscillatory networks.

To my knowledge, this is the first use of directed functional connectivity in the brain (in fMRI or MEG) in combination with socio-economic metrics. It is reasonable to predict that the inclusion of this additional information has the potential to explain more variance in the demographic and behavioural regressors than structural or non-directed functional information alone. This very concept is assessed later in this chapter.

2.2.1 Methods

Participants

The data came from a large developmental cohort collected at the MRC Cognition and Brain Science, at the University of Cambridge. A total of 142 participants were recruited across two sub-samples. The first targeting areas in Cambridgeshire (UK), with high relative deprivation, and the second recruiting from both high and low deprivation areas. The participants took part in the scans on two separate visits. Due to the family's availability, and study attrition, only 104 participants provided fully usable MEG scans. Twenty-two participants were excluded because a high noise level left their MEG data rank deficient for signal leakage correction. The remaining group ranged from 6.82 - 12.77 years old, with an average age of 9.23 (SD = 1.43). The equivalised household income of this group had a mean of £27,870.07 (SD = £16,121), 22.11% of the sample (23 children) lived in households below the relative poverty line (60% of the English median for the year reported).

Behavioural, Demographic and Socioeconomic Data

Parents completed a questionnaire that established information about the children and their households. From this questionnaire we derived the values of interest for the later analyses. The children's date of birth was confirmed by the parent, which formed the age values in years, months and days, on the day of assessment. We administered a series of cognitive assessments, which included the matrix reasoning subtest of the Wechsler Abbreviated Scale of Intelligence (WASI) (McCrimmon & Smith, 2013) -- this was used as a measure of 'fluid IQ'. The WASI matrix reasoning sample-standardised score was calculated as-per the user manual. This score accounts for age, which is included as another regressor in the GLM, using this score reduces the degree of collinearity between the two – a potential issue in regression models (Farrar & Glauber, 1967).

The parent questionnaire was used to derive our various measures of socioeconomic status and was given to the primary caregiver. The salaries of each parent were used to calculate the total Equivalised Household Income (Anyagbu, 2010). A subjective SES rating was given where parents marked themselves on a 10-rung ladder representing their family's position in society (Adler et al., 2000; Anwyl-Irvine et al.,

2021). We recorded the occupations of each parent and then used the most recent (2016) Nam-Powers-Boyd Occupational Status Scale to calculate a socioeconomic score for the parent's occupations (Nam & Boyd, 2004). We asked the parents for their highest level of education, and gave each a score from 1-7 based on the Hollingshead four-factor index of SES (Hollingshead, 1975). The household's postcode was used to ascertain the neighbourhood deprivation level, utilising the 2019 English Indices of Multiple Deprivation, provided by the UK Ministry of Housing, Communities & Local Government (McLennan et al., 2019). Lastly, we recorded whether the child was eligible for Free School Meals (FSM), if they had their own bedroom, and how many books were in the home.

Our SES measures are likely correlated. For instance Noble et al., (2015) found that income and parental education were highly correlated. The GLM approach can tolerate some shared variance, but this shared variance within the SES data is likely too large. To address this, I undertook a factor analysis to reduce these measures into relatively orthogonal factors. A scree plot of the eigenvalues of these measures for each participant indicated that a three-factor solution would be most appropriate (see **Supplementary Figure 1**). I used Factor Analysis function of the psych package in R (Revelle, 2017), with the Minimum Residual fitting method and the ten Berge method to extract the individual factor scores and weights (ten Berge et al., 1999). Extracted factors were named according to their weight profiles. They were labelled: "Objective SES" - the factor weighted most on income, education and employment; "Household SES" - weighted most on whether the child had a bedroom and books in the home; and "Subjective SES" - weighted most highly on the subjective SES measurement. These weightings are reported in **Table 1** below.

	Labeled Factors & Weightings			Item Statistics		
	Objective SES	Household SES	Subjective SES	Variance Explained	Residual Variance	Item Complexity
Equivalised Household Income	0.81	-0.11	-0.03	0.73	0.27	1
Subjective SES	-0.02	0.02	0.73	0.54	0.46	1
Average Parental Education	0.68	0.15	-0.08	0.45	0.55	1.1
Parental Occupation Score	0.59	-0.01	0	0.35	0.65	1
Free School Meal Status	-0.41	-0.14	-0.04	0.15	0.85	1.2
Index of Multiple Deprivation	0.52	-0.09	0.22	0.31	0.69	1.4
Number of Books	0.23	0.35	0.03	0.12	0.88	1.8
Own Bedroom	-0.07	0.66	0.01	0.47	0.53	1

Table 1. Factor analysis weightings and item-level statistics for SES component decomposition

As mentioned above, the data were collected for this study in two recruitment runs. It is possible that SES variance within these two runs create a binary effect, where an association is being driven by one group but not the other. To see if this was the case, I ran a MANOVA (Pillai test) with the three factors as dependent variables and study run as a fixed factor. This model indicated a significant impact of study run on factor scores ($F(115)=7.271, p<.001$). However, post-hoc t-tests indicated the only factor score that differed significantly was the Household SES score ($t(117)=4.497, p<.001$). I did not want to regress out this study run factor, for fear of obscuring important effects. Instead, we have reported bifurcation plots of any results based on this factor, to ensure this is not driving an effect.

Neuroimaging

MEG resting state scans were captured using the 306 Channel Elekta Neuromag Vectorview system, consisting of 204 planar gradiometers and 102 magnetometers. Three pairs of electrodes were attached to generate electro-oculograms (horizontal & vertical), and electrocardiograms, assisting in later denoising through detecting heart-beat, eye movement, and blink related artefacts. The position of the participant's head

was monitored via coils fixed behind each ear, on the crown, and two on the forehead. The scalp shape was captured using approximately 150 points, in addition to head fiducials and sensor positions with the Polhemus pen. This process permitted co-registration with MRI scans taken on a separate visit.

Participants were positioned in the scanner helmet in a seated position, they sat with their eyes closed and were instructed to not think of anything and to relax for ten minutes. They were also instructed to keep movements to a minimum.

To localise the MEG signals we captured structural MRI data. During a separate visit, participants took part in an MRI scan, which yielded T1-weighted images from a Siemens 3T Prisma-fit system, using a 32-channel quadrature head coil. For these images, a Magnetisation Prepared Rapid Acquisition Gradient Echo (MP RAGE) sequence with 1mm isometric image resolution, 2.98ms echo time and 2250ms was used.

Preprocessing and parcellation

Raw data underwent Signal Source Separation (SSS), Temporal Extension (SE), and movement compensation using Maxfilter 2.2. These data were loaded into MNE-Python and then high-pass filtered at 0.1Hz and notch filtered at 50hz. This filtering was minimal to reduce the chances of artifacts in the later MVAR modelling. In order to remove noise associated with heartbeats and blinks, a two-stage Independent Component Analysis (ICA) denoising procedure was used. An ICA was applied using *fastica* with 25 components specified. Stage 1 involved automatic rejection of components that correlated with ECG or EOG electrodes more than 0.3. Stage 2 involved manual checking of excluded component topography, and selection of components to exclude for participants with insufficient ECG or EOG electrode signal. Data for each child was visually checked before and after to ensure the components were not still present.

FreeSurfer (Fischl, 2012) was used to construct the whole brain surface from MRI scans, using the recon-all command. A single layer Boundary Element Model (BEM) of the inner skull was constructed using the FreeSurfer watershed method. A source space was made using the cortical surface from the FreeSurfer output. Our inverse model consisted of this one-layer BEM, and the method used to invert the evoked signals was

the MNE toolbox's implementation of minimum norm estimation, using a lambda value of $1./9$. Empirical whitening was undertaken using a noise-covariance matrix taken from empty room recordings, which I found to produce the most consistent results. Participants who lacked an MRI or moved too much during the MRI scan ($n=2$) had models created using FreeSurfer's FSAVERAGE model.

Parcel time-courses were then extracted from this source localised data. We used the Desikan-Killany (Desikan et al., 2006) cortical parcellation – consisting of 34 parcels in each cortex. The parcellation was specific to each participant's FreeSurfer cortical model, except for the FSAVERAGE models used for missing MRI data. The mean values of each vertex within a parcel were combined for each timepoint, yielding a time-course for each parcellation which represented average activity within that parcel.

Connectome Construction and Analysis

Multivariate Autoregressive Modelling

In order to identify frequency-specific directional relationships between different parcellations, a multivariate vector autoregressive modelling (MVAR) approach was taken. MVAR models are used to characterise dependencies between nodes in a time-varying network based on the past activity of those nodes. We used an Ordinary Least Squares MVAR model on each participant's resting state parcel time courses. This approach models values for each parcellation in our resting state data as a weighted linear sum of the previous values of all parcels. A frequency vector, consisting of discrete bins across a frequency range, is also fed into this model, allowing connectivity to be estimated across the frequency spectra. Once the model is built, connectivity was estimated using the metric of Partial Directed Coherence (PDC) (Baccalá & Sameshima, 2001). PDC estimates direct flows between source channels (parcels in our case), representing this with a value between 0-1. These coherence values are partial, meaning they are residual correlations after the network mean has been subtracted — this maximises detection of differences between areas. The output data are directed and shows both feedforward and feedback connections for any given parcel. The output given per-participant is a parcel-by-parcel directed (i.e., non-symmetric) connectivity matrix for each frequency bin. In our case this was a $68 \times 68 \times 36$ matrix of PDC values for each participant.

As MVAR models are sensitive to the sampling rate, signal leakage, and noise in the data, I undertook some extra preparation of each participant's parcel time-courses. The data were down-sampled to a lower sampling rate of 75Hz as MVAR models deal better with a lower sampling rate, this did limit our modelling spectrum to approximately 0-36Hz due to Nyquist frequency limits. Noisy segments were detected and removed using a generalised Extreme Studentized Deviate (ESD). The time-courses of each parcel were then orthogonalised to correct for potential signal leakage (Colclough et al., 2015).

The number of previous samples used in modelling each value – the ‘model order’ or number of ‘delays’ – needed to be determined. The higher this value, the more complex, but less parsimonious, the model. There is no absolute procedure for setting this parameter. In order to choose this value, I considered two tools: the Akaike information criterion (AIC) and Welch's spectrogram. AIC aims to capture the quality of the model by combining information about the fit of the model with its complexity. For each participant I generated a series of MVAR models with delays of 2-35. The AIC values reached an elbow on average across participants at a delay of 25 – indicating that this was the point of diminishing returns in the trade-off between complexity and explanatory power. The average elbow plot can be seen in **Supplementary Figure 2**. To further confirm the quality of the model, the Welch's spectrum of parcel time-courses were visually compared with that of the MVAR model, which revealed that the spectral density of the original was roughly comparable, with the models. These reconstructed and original power spectra can be seen in **Supplementary Figure 3**. This did reveal that the MVAR model overstates frequency peaks (particularly a peak at around 13Hz), however this is likely due to unavoidable noise in the resting state scans of children sat in an adult scanner and changing number of delays and down-sampling further did not improve this without overfitting (i.e., going beyond the AIC scree plot elbow). I used the Python toolbox Spectral Analysis in Linear Systems (SAILS) (Quinn & Hymers, 2020) to create these models, perform leakage correction, and bad segment detection.

Mass General Linear Model

A mass multivariate General Linear Model (GLM) was used to investigate the group-level relationships between Age, IQ, the SES factors, and the individual partial

directed coherence matrices. I used an Ordinary Least Squares (OLS) approach to estimate the beta-weights and error terms.

The data matrix consisted of PDC values in the shape 104x68x68x36 (Participants x Parcel drivers x Parcel receivers x Frequency band). A 104x6 design matrix was created with a constant regressor (to represent the intercept), and parametric regressors for z-scored Age (in weeks) and fluid IQ (WASI Matrix Reasoning), Objective SES, Subjective SES and Household SES. All regressors contained one observation for each participant (104). For each regressor I generated a simple contrast, consisting of '1' for the regressor and a '0' for all the other regressors. This means our beta weights represent the effect of the regressor of interest when all other regressors are held at zero.

The output of the fit model produced a 68x68x36 matrix of metrics for each contrast. I used two metrics of interest from the GLM - t statistics (representing both the magnitude of the contrast effect and consistency across the sample) and the beta weights (representing the weighting of that effect on the data).

The statistical significance of each contrast at each frequency and connection was assessed using a non-parametric permutation test, which controls for Family-wise Error rate (T. E. Nichols & Holmes, 2002). This involved shuffling the regressor of interest in the design matrix, so that the participant's data no longer matches that regressor, whilst all other regressors remain unshuffled. The GLM is then re-calculated, and the t statistics are saved. This is repeated 5000 times per contrast to produce a null distribution of t statistics for each. I classified any t-statistic from the original GLM that was above the 99th Percentile of the null distribution as significant (i.e., Monte-Carlo $P < .01$).

It is possible to utilise the methods of clustering in an extra step within the permutation testing procedure. This would ideally allow the statistical matrices to be reduced somewhat into interpretable groups of activity and generate a null distribution for each of these clusters, rather than a distribution for each value in the matrix. Ultimately for the analysis in this chapter I was unable to use the clustering approach. The clustering steps require information about how each value is connected to the next — in the case of MEG parcel data, this would specify which parcels were next to each other. We defined such an adjacency matrix for our data (68 x 68) and extended this

matrix on the frequency dimension (frequencies were considered adjacent if they were sequential). It also requires a threshold which dictates the size of the clusters. This can be set by the researcher to maximise cluster size, or it can be calculated using procedures like Threshold-free Cluster Enhancement (TFCE). Unfortunately, no combination of usage of the adjacency matrix, TFCE or specifying thresholds manually yielded easily interpretable clusters. The clusters would either be the size of one value in the matrix of statics (i.e., the same as not clustering), select arbitrary values forming sparse and non-adjacent clusters, or select the entire dataset as a single cluster. This is likely due to the large variation between adjacent frequencies in the frequency dimension (illustrated in network averages in Supplementary Figure 7 and along parcels of interest Supplementary Figure 8), which disrupts formation. An alternative to this is a PCA approach which I describe in a later section.

Whilst making the results less parsimonious, avoiding the cluster step does mean that my initial analytical approach is not limited by some of the inferential drawbacks of cluster or dimension-pooled permutation testing (Sassenhagen & Draschkow, 2019). It also means that the significant MVAR connections identified would have a 1-1 mapping across frequencies and with the DTI analysis carried out later in this chapter.

Selecting parcels of interest

For the MEG-MVAR GLM results, the matrices of significant connections are relatively difficult to interpret holistically due to the dimensionality and density of the connectomes. Each contrast produces a 68x68x36 matrix with 166,464 potentially significant connections. In order to make the results interpretable I reduce this space down by thresholding and then a subsequent peak frequency selection.

I first calculated a t statistic weighted degree for each parcel. This was the sum of all significant outgoing and incoming connections for each of the 68 parcels. I used the t statistic as this represents both the magnitude and consistency across the sample of each connection. Next, only the parcels across all contrasts which were in the top 10% were used - chosen based on the percentile distribution in **Figure 5**. This leaves us with the significantly associated specific brain areas with the strongest and most consistent connections.

2.2.2 Results

Network-level

Figure 3 shows the relative distribution of t-statistics produced by each regressor in the GLM. Objective SES and Subjective SES have the longest tails, with several parcels having much larger values than the mean. The points in the plot represent parcel-summed T Statistics, rather than individual edges within the graph; this metric is also known as the weighted degree of each parcel and is used later to select parcels of interest for further exploration.

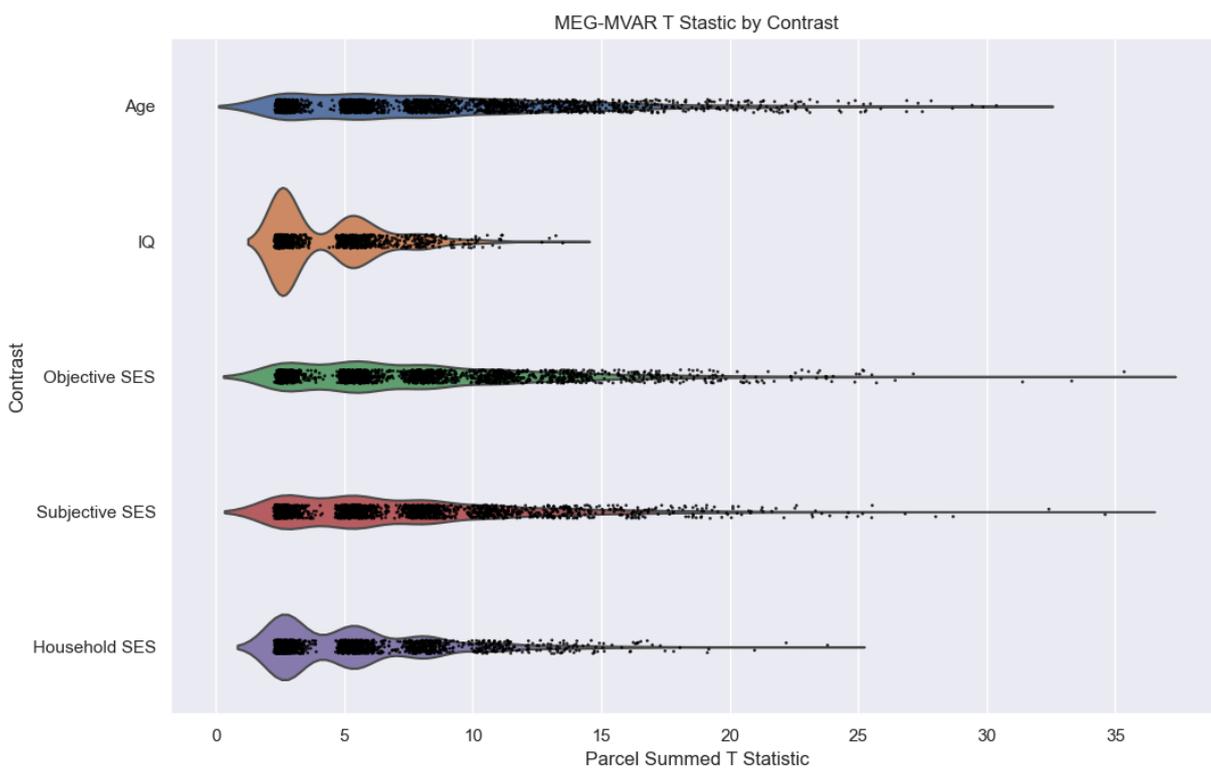


Figure 3. Distribution of Summed *t*-statistics by parcel (Weighted Degree) for each contrast in the MEG-MVAR data. Only connections which survived permutation testing are included here. The statistics are summed over connections and 36 frequency bands.

If we take the associated significant beta weights of these contrasts, we can investigate the data further. The beta weights represent the proportional weighting any regressor has on the directed coherence itself, irrespective of t statistic (which represents the magnitude of statistical significance). The scale of the beta-weights is the same used in the PDC metric, so represents the proportion of signal explained in other parcels by that parcel in the network. As with the t statistics, summing the beta-weights of each connection attached to a given parcel gives a weighted degree, representing the influence that parcel has in the network. We can consider each high degree parcel as a 'hub node'. **Figure 4**, shows the average weighted degree of these parcels for each contrast broken down by lobe membership. This shows some interesting patterns, for example: you can see that the beta weighted degree of parcels in the Objective SES related connectome are much higher in the Occipital Lobe than anywhere else.

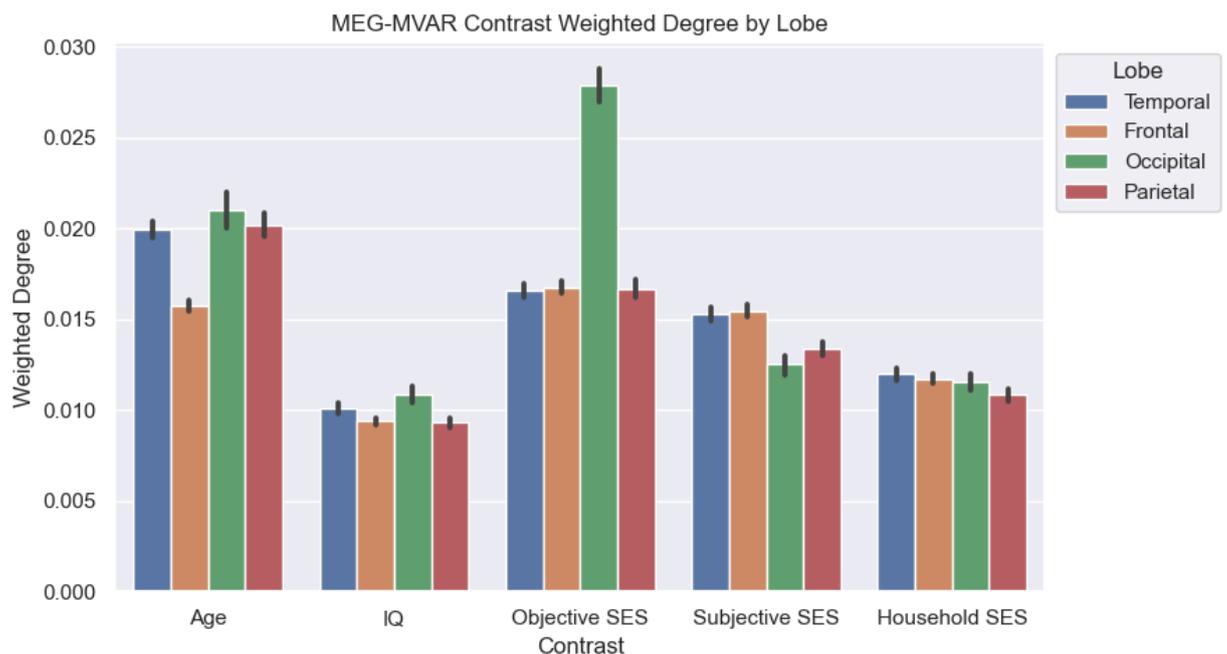


Figure 4. Mean Beta Weight Weighted degree across parcels, broken down by contrast and lobe. Error bars represent the standard error. Desikan-Killiany parcel lobe membership was determined using the grouping published in (Klein & Tourville, 2012). The beta weights are summed across connections, parcels and 36 frequency bands. The graph shows a clear increase in occipital lobe connectivity related to Objective SES factor (this maps onto job, income and living area affluence).

Parcel-level

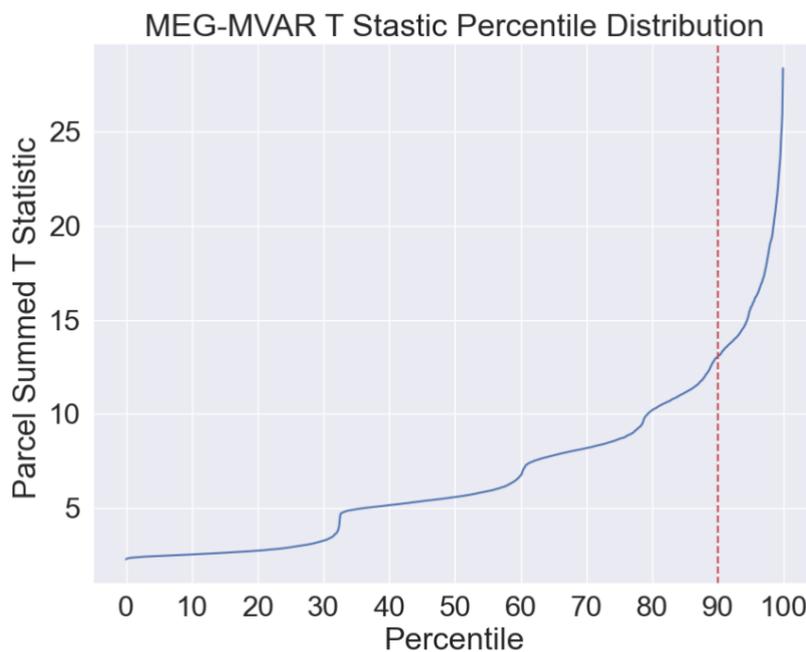


Figure 5. Distribution of parcel T statistics across all contrasts and frequencies with 10% upper threshold shown at the red dotted line.

As mentioned above, the outcome statistics from the GLM, even after being reduced by permutation testing, are highly dimensional so require some thresholding. Parcels with a higher level of connectivity represent the strongest and most connected in each contrast. **Figure 5** shows the distribution of t statistic weighted degrees across contrasts and frequencies. The dotted line shows the top 10% threshold I used. This illustrates that the parcels and contrasts chosen below represent the highest magnitude of effects.

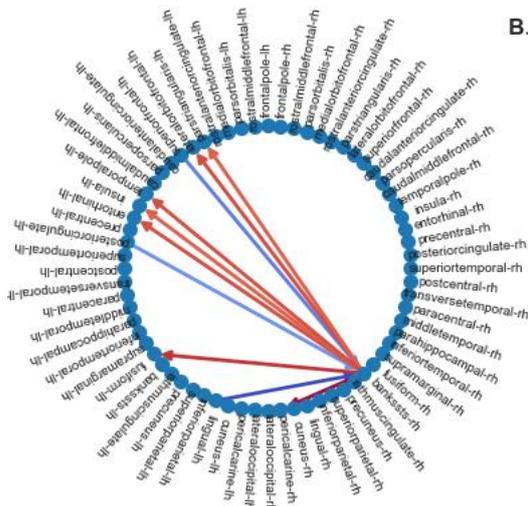
Across all the significant contrasts, four parcels crossed this 10% threshold. These combinations were: Subjective SES & Right banks of the superior temporal sulcus (bankssts-rh) (**Figure 6**), Subjective SES & right hemisphere frontal pole (frontalpole-rh) (**Figure 7**), Age and left parahippocampal gyrus (parahippocampal-lh) (**Figure 8**), Objective SES & left pericalcarine sulcus (pericalcerine-lh) (**Figure 9**). Barplots in Supplementary Figure 6, showing the average across frequencies for each parcel and each contrast, further confirms that the four parcel-contrast combinations chosen to investigate further represent a much higher strength of association than the rest of the results.

Each combination also represents a frequency peak, the frequency distributions of each parcel-contrast combination are shown in Supplementary Figure 7. These peak frequencies are as follows: right banks of the superior temporal sulcus & Subjective SES - 19Hz (Beta); right frontal pole & Subjective SES - 10Hz (Alpha); left parahippocampal gyrus & Age - 35Hz (low Gamma); left pericalcarine sulcus & Objective SES - 28Hz (Beta).

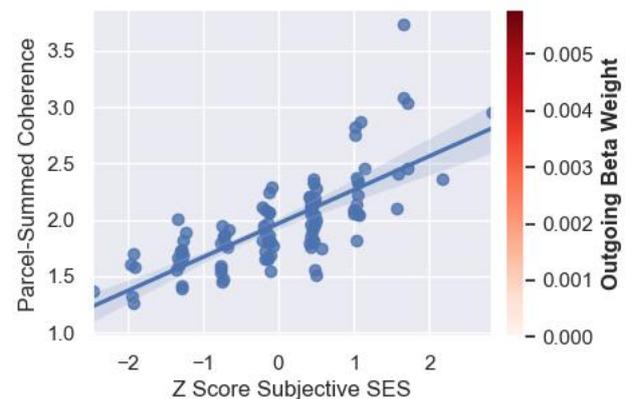
Figures below give a detailed graphical overview from each of these combinations. The MVAR model allowed a directional network to be formed, and this is illustrated with red arrows for outgoing and blue arrows for incoming connections.

Subjective SES related connectivity in bankssts-rh at 19 Hz

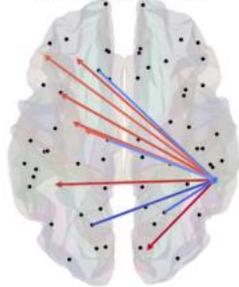
A. Circular Connectivity Graph



B. Correlation between Parcel Coherence and Subjective SES



C. Coronal View



D. Additional View

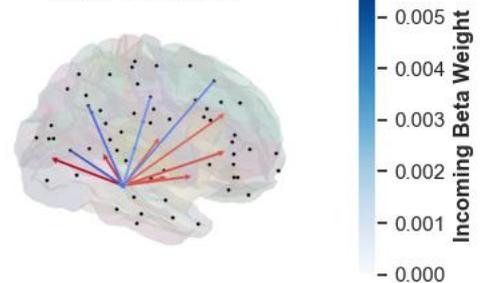
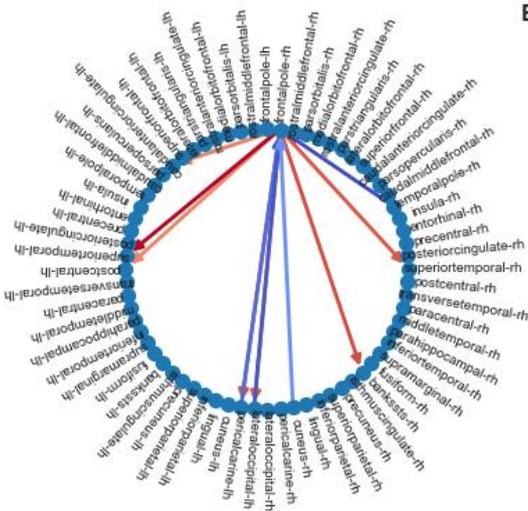


Figure 6. Summary of Subjective SES related connectivity of the right banks of superior temporal sulcus parcellation at 19Hz. **A)** Shows a circular connectivity plot, blue arrows are incoming connections and red arrows are outgoing connections. **B)** A scatterplot with a trend line, showing the summed coherence of this parcel for each individual against individual Subjective SES score. **C)** and **D)** show the connectivity arrows within a glass brain, dots represent parcel centroids.

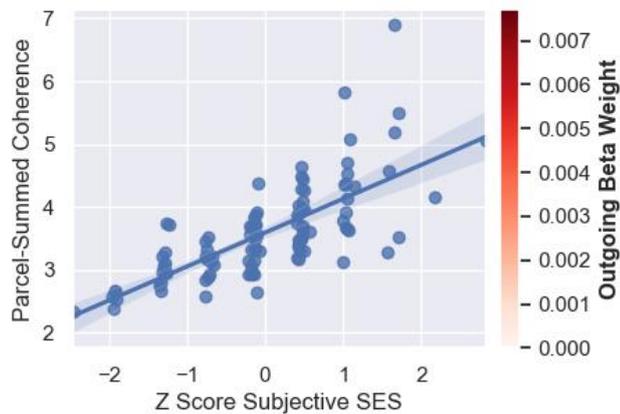
Figure 6 shows connections to the right bank of the superior temporal sulcus (bankssts-rh). The peak frequency was at 19Hz, which falls in the beta frequency. The weighted degree of this parcel is given by a mix of outgoing and incoming connections. **Figure 6.A, C** and **D** show the spatial organisation of these connections. There is an apparent bias to cross-hemispheric connections (9 out of 11). Two strong connections seem apparent. The first is an outgoing intrahemispheric connection to the right pericalcarine cortex (i.e., calcarine sulcus) it has a beta value of 0.00556, the second is an incoming cross-hemispheric connection from the left lingual cortex, this has a beta value of 0.00577.

Subjective SES related connectivity in frontalpole-rh at 10 Hz

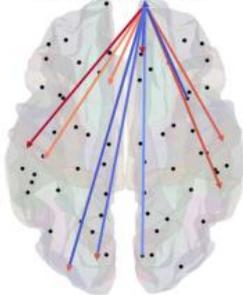
A. Circular Connectivity Graph



B. Correlation between Parcel Coherence and Subjective SES



C. Coronal View



D. Additional View

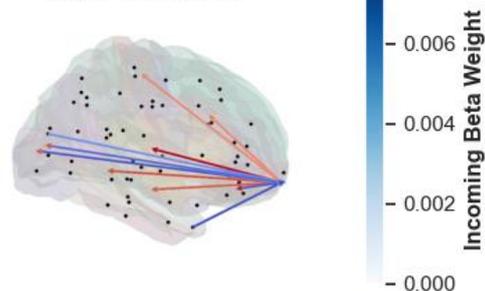


Figure 7. Summary of Subjective SES related connectivity of the right frontal pole at 10Hz. **A)** Shows a circular connectivity plot, blue arrows are incoming connections and red arrows are outgoing connections. **B)** A scatterplot with a trend line, showing the summed coherence of this parcel for each individual against individual Subjective SES score. **C)** and **D)** show the connectivity arrows within a glass brain, dots represent parcel centroids.

Figure 7 Illustrates a second Subjective SES-related parcel. Connections with the right frontal pole at 10Hz, which falls into the Alpha range. Again, like the previous graph, this shows a mix of outgoing and incoming connections. Two connections: left lateral occipital (out beta: 0.00594, in beta: 0.0658) and left pericalcarine (out beta: 0.00624, in beta: 0.00590), are reciprocal. However, unlike the other Subjective SES-related parcels, connectivity is relatively balanced between intra and inter-hemispheric. The highest weighted connection here is outgoing to the left superior-temporal gyrus with a beta weight of 0.00770.

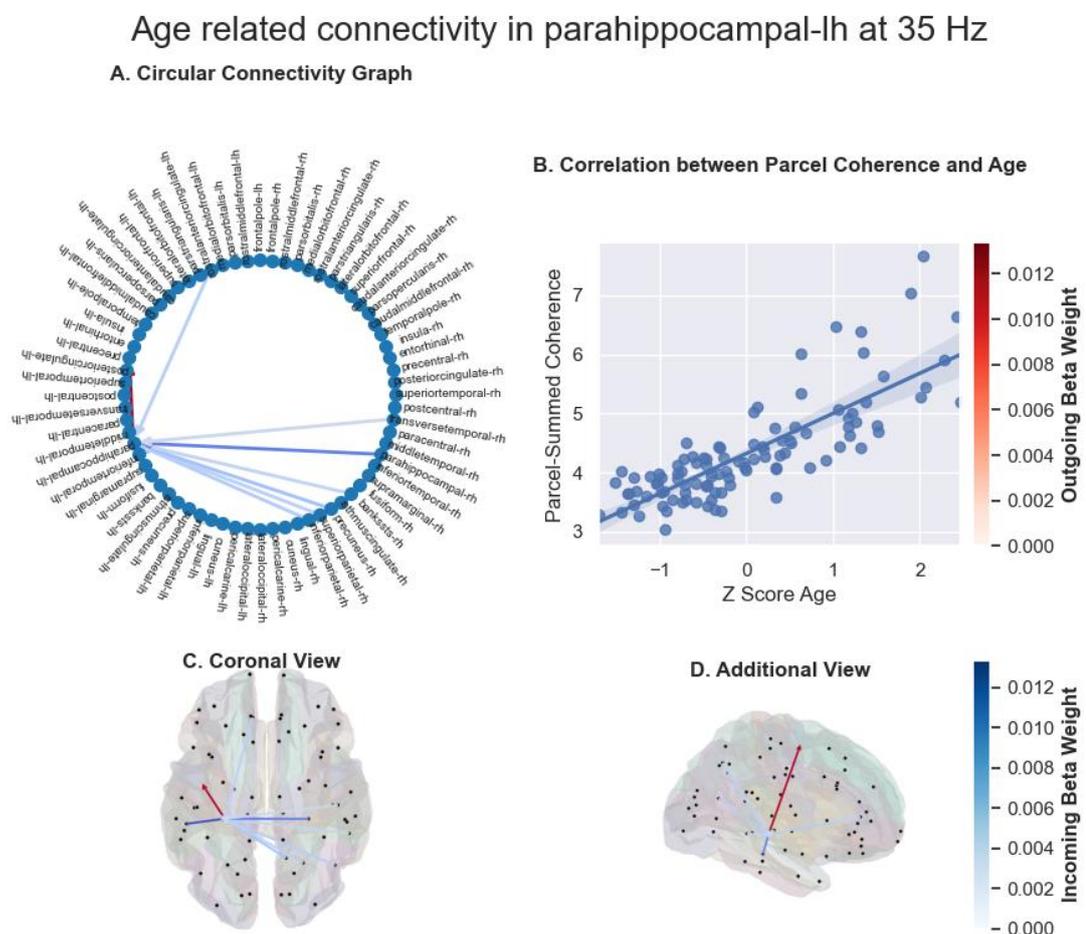


Figure 8. Summary of Age related connectivity of the left parahippocampus at 35Hz. **A)** Shows a circular connectivity plot, blue arrows are incoming connections and red arrows are outgoing connections. **B)** A scatterplot with a trend line, showing the summed coherence of this parcel for each individual against individual Age scores. **C)** and **D)** show the connectivity arrows within a glass brain, dots represent parcel centroids.

Figure 8 shows the third parcel above the threshold. Age related connections with the left parahippocampal gyrus at 35Hz. This frequency falls into the gamma range. This parcel has a high proportion of incoming connections (7 out of 8). The single outgoing connection projects to the left precentral gyrus and has a beta weight of 0.00614. The strongest connections are incoming ones, one from the contralateral (right) parahippocampal gyrus (beta weight 0.0108), and another from the left inferior temporal gyrus (beta weight 0.013). These are both relatively weighty connections, in the top 98th percentile of significant beta values (right parahippocampal gyrus: 98.58 percentile score, left inferior temporal cortex: 99.66 percentile score). Connections appear to be both ipsi- and contra-lateral.

Objective SES related connectivity in pericalcarine-lh at 28 Hz

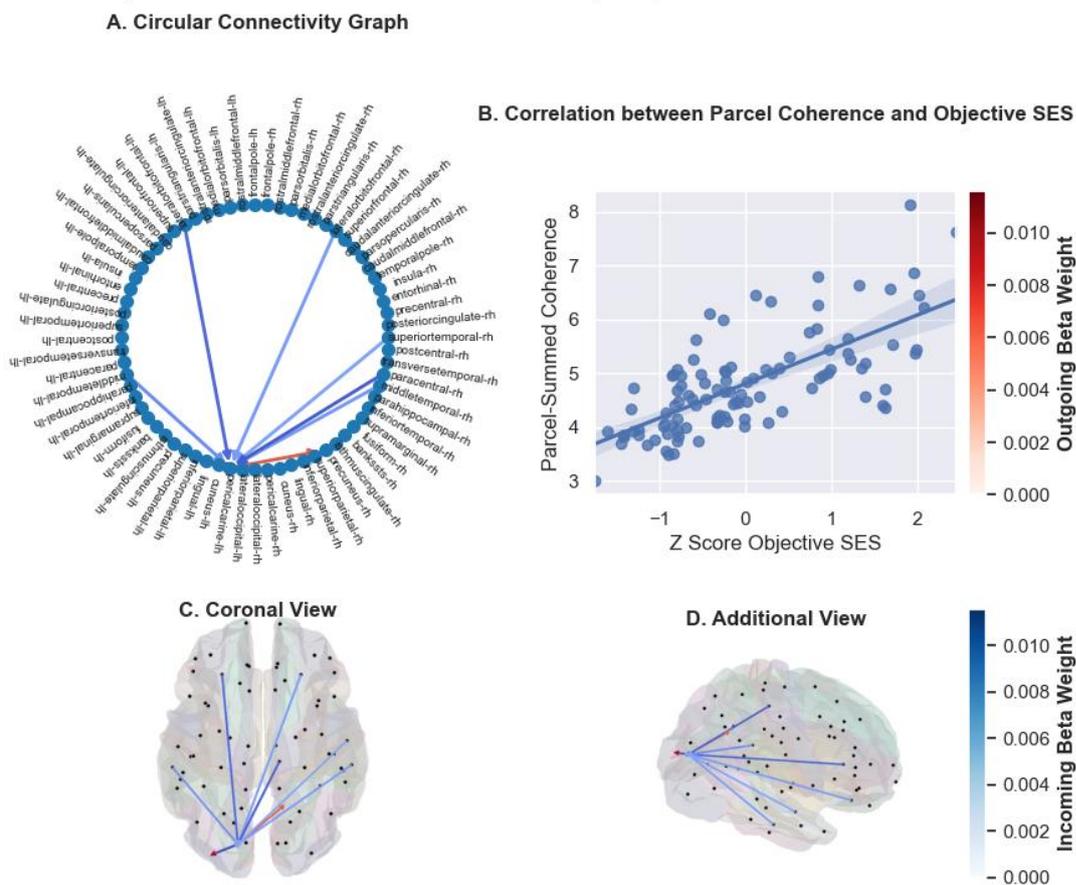


Figure 9. Summary of Objective SES related connectivity of the left pericalcarine cortex at 28Hz. **A)** Shows a circular connectivity plot, blue arrows are incoming connections and red arrows are outgoing connections. **B)** A scatterplot with a trend line, showing the summed coherence of this parcel for each individual against individual Objective SES score. **C)** and **D)** show the connectivity arrows within a glass brain, dots represent parcel centroids.

Figure 9 illustrates the final parcel combination that passed the threshold. This shows Objective SES related connectivity between the left pericalcarine sulcus at 28Hz. This frequency is in the beta range. Much like the pattern in **Figure 8**, there is a dominance of incoming connections over outgoing (7 out of 9). In another similarity there is a relatively strong connection driving the high weighted parcel degree (beta weight of 0.0115, 99.10 percentile score), an outgoing connection to the adjacent lateral occipital cortex. Again, the connections appear to be distributed across both hemispheres.

To give some further context to the beta values of the reported individual connections, readers may refer to the threshold distributions shown in Supplementary Figure 9. Comparing this supplemental graph to the above results, it's notable that the Subjective SES parcels in **Figure 6** and **Figure 7** have connections that fall in the middle of these distributions, so their high degree is driven by having many connections. Whilst the Age and Objective SES related parcels in **Figure 8** and **Figure 9** have connections within the higher tails of the distributions — which seems to be driving their higher degree, suggesting narrower, but stronger connections.

2.2.3 Interim Discussion

This first section investigated the hub nodes across different frequencies of resting state MEG networks in a large group of children. The approach yielded many statistically significant connections associated with all the covariates of interest. These connections were ranked across frequencies, and I report the areas with the most consistent and strongest relationships. Across all frequencies and parcels, the Age and SES measures seemed to have the higher weighted beta values.

One of the hub nodes identified in the Subjective SES contrast was in the right frontal pole at 10Hz. The summed coherence of this node increases with the subjective SES rating. The nature of MEG scans in children means I cannot claim granular specificity of the frontal pole at the parcel level, this finding likely surrounding frontal areas also. These surrounding areas are likely involved in general frontal control networks. This falls nicely in-line with work discussed above on how frontal control networks are impacted by low SES (Demir-Lira et al., 2016; McEwen & Gianaros, 2010; Xie & Pisano, 2019). It also replicates previous electrophysiological studies, which show SES differences in frontal activity (Herdman et al., 2008; Kishiyama et al., 2008), and

work showing resting state frontal alpha power (the same band of our hub node) increases with SES in school-aged children (Maguire & Schneider, 2019).

The second hub node, related to Subjective SES, was the right bank of the superior temporal sulcus (STS), which shows distributed connectivity to areas on the contralateral (left) side of the brain in the Beta band. Displaying both outward and inward coherence to areas in all right lobes is perhaps unsurprising, as the STS is claimed to be a key area in many different research areas (Hein & Knight, 2008).

Finally, the third SES-associated parcel related to Objective SES (equivalised income, local affluence). This is a difficult finding to interpret, as the pericalerine sulcus deals with primary visual processing, and its coherence increases with objective SES. Given that subjects were at rest with their eyes-closed, this was unexpected. Occipital Beta oscillations at rest have been related to individual differences in problem solving. Kounios et al. (2008) suggest that increased resting state occipital Beta activity reflects analytical approaches to problem solving. However, given the direction of our association here, we can only guess that this might reflect differing problem-solving approaches.

More generally, a serious limitation of the interpretations made in this interim discussion is that we are interpreting very specific peaks of a wide distribution of significantly associated connections. There are many parcels which approach the selection threshold (see Supplementary Figure 6). Their inclusion could change the interpretation of the results significantly. Additionally, as mentioned above in discussion of the frontal pole, individual small parcels in MEG data are likely to also represent adjacent areas, so focusing on these isolates may represent an unrealistic level precision. There is, however, another analytic approach without this thresholding drawback and which represents broad areas – using a data-driven method of dimension reduction. This is what I explore in the next section.

2.3. PCA derived global patterns in the MEG connectome

The preceding section focuses on the granular identification of specific parcels and narrow frequencies which contribute to covariate-related networks. There is however an alternative possibility, which may also enable us to identify relationships

between our covariates and global spatial patterns of interest across broad frequency bands. This approach is to reduce the MVAR metrics for each participant using Principal Component Analysis (PCA). PCA attempts to find vectors or axes (eigenvectors) which describe the largest amount of variance, with the fewest number of components (K. Pearson, 1901). In our case we can use PCA to identify the common axes in which our networks vary across participants, with each axis representing a weighting of connections forming a new network. We can call these Principal Component networks, or PC networks. These PC networks attempt to explain the most variance across participants, whilst reducing the dimensionality of our connectivity matrices. The first PC network explains the most variance, the second slightly less, and so on. This approach is an adjustment of the method used by Quinn et al. (2021) who used PCA in a larger MEG analysis that described individual oscillatory components across participants. The PC networks of Quinn et al. identified spatial differences associated with different frequencies and allows for simultaneous positive and negative variations. Some connections in a PC network increase in strength, whilst at the same time others decrease. Elsewhere, PCA-based dimension reduction has also been used to explore EEG topographies related to heart-beats, blinks and brain activity (Artoni et al., 2018), and to identify a global MEG connectome which characterises Mild Cognitive Impairment (MCI) (Dimitriadis et al., 2013).

We can extend PCA to produce a loading score for each individual against each PC network. If we think of a principal component as an axis of variation, this loading score represents where each individual falls along that axis. So, in our case, how well each component network represents any given participant's brain activity. By entering these scores into a GLM, we can interrogate the degree that each PC network is associated with SES and other variables across the sample. We are characterising association with networks, rather than individual connections. Because of this, my approach should be well-placed to capture network-level variance, rather than the hub-nodes identified in the section above.

2.3.1 Methods

To make the frequency domain more interpretable, the [parcel x parcel x frequency] matrix of PDC values for each participant was reduced to four frequency bands - Theta (1-7Hz), Alpha (7-13Hz), Beta (13-30Hz) and Gamma (30-75Hz). For

each participant the peak frequency within each band was calculated by taking the frequency with the highest absolute mean PDC value - the distributions are included in **Supplementary Figure 4**. This individual approach was taken, as the peak frequency of each band varies between individuals (Quinn et al., 2021), so by using this selection method we were getting the best network characterisation for each individual.

Following this, a separate Principal Component Analysis (PCA) was conducted on each band to identify common spatial patterns of variation across participants. There are different flavours of PCA, which vary in the estimation of the eigenvectors. I used the Singular Value Decomposition (SVD) approach as this has been shown to be more numerically stable (and therefore reproducible) than others (Partridge & Calvo, 1998). The matrices were vectorized into two dimensions [participants x parcels x parcels], the group mean was subtracted from each value. Demeaning and centering maximises the differences between each individual and fulfils the requirements of the analysis approach. Finally, PCA was used to extract the principal components and a score for each component from every participant.

As in the behavioural data factor analysis and MVAR model order selection, to decide how many of these components we should take forward in the analysis, scree plots were generated for the Eigenvalues of each band-model (**Supplementary Figure 5**). The elbow of these plots indicated that providing more than two factors does improve the variance explained — so we can carry these two principal components forward for later analysis.

This PCA reducing step then allows us to extract participant scores, which are a single value for each band and component. These scores represent how much each participant contributes to these component networks and are then used in the GLM against the behavioural covariates. This procedure was identical to the one used above, but the data matrix of participant's component scores greatly reduced in comparison. Each participant now has a 4x2 (Band x Components) matrix of 8 network scores, as opposed to a 68x68x36 (Parcel x Parcel x Frequency) matrix of 166,464 individual connections - a 20,808-fold reduction. This process can then tell us which of these 8 component networks are significantly related to the covariates - Age, WASI score, and the SES components.

2.3.2 Results

The eight component networks identified, i.e., the principal axes of variation across participants, are shown in **Supplementary Figure 11**. For Alpha, Beta, and Gamma PCAs, the stronger connections in component networks appear to be prominent within the posterior regions of the brain - connections between the Occipital and Parietal areas, whereas the Theta networks seem to be more distributed. The variance explained for each network is included in **Table 2**.

Frequency	Explained Variance (%)			GLM R Squared	
	PC 1	PC 2	Total	PC1	PC2
Theta (1-7Hz)	5.13%	3.80%	8.94%	17.05%	3.26%
Alpha (7-13Hz)	6.73%	4.44%	11.17%	4.13%	2.75%
Beta (13-20Hz)	11.07%	7.11%	18.18%	3.59%	9.61%
Gamma (30-75Hz)	4.91%	4.30%	9.21%	14.22%	7.2%

Table 2. Explained variance of each frequency band PCA and GLM R squared value. PC 1 refers to the first component in each PCA and PC 2 refers to the second, the total column is a sum of both. The R squared values represent the explained variance in the component networks by all the regressors (Age, WASI and SES factors) - higher indicates that factor was better explained by these things.

There were three PCA components with associations with covariates that survived permutations. These were: the second component in the Beta band, which was associated with Subjective SES ($t=2.476$, $beta=.243$, Monte-Carlo $p=.007$) shown in **Figure 10**; the first component in the Gamma band with WASI Matrix Reasoning ($t=2.586$, $beta=.269$, Monte-Carlo $p=.006$) shown in **Figure 11**; and finally the first component in the Theta band, with Age ($t=2.626$, $beta=-.247$, Monte-Carlo $p=.007$) shown in **Figure 12**. The layout of the circular plot with names included and colour key are available in **Supplementary Figure 10**. These component networks also represent the networks with the highest proportion of variance explained by the predictors - Beta PC2 9.61%, Gamma PC1 14.22%, and Theta PC1 17.05% (**Table 2**).

Beta PC2 and Subjective SES

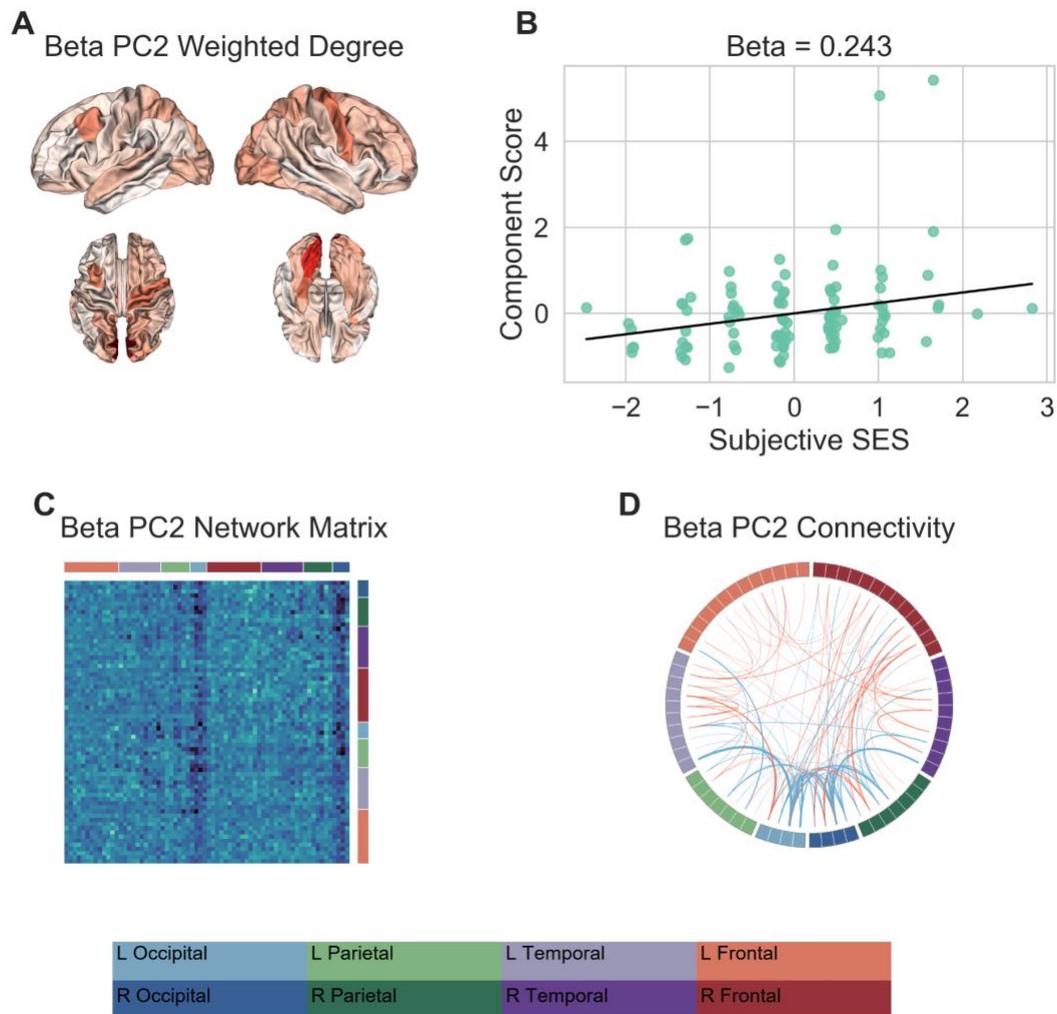


Figure 10. Overview of the Beta PC2 network and its significant relationship with participant's subjective SES score. **A)** Shows a spatial representation of the network through weighted degree of each parcel in the brain. **B)** Shows the component score for everyone against their Subjective SES component score, the line represents the beta value. **C)** Shows the thresholded network matrix columns represent outgoing connections and rows represent incoming connections, with darker being stronger. **D)** Is a thresholded circos connectivity plot, representing the top 5% of connections, negative connections are in blue and positive connections in red, thickness varies by strength. Both matrix and circos plots are grouped by lobe and hemisphere using colors shown in the key.

Gamma PC1 and WASI Matrix

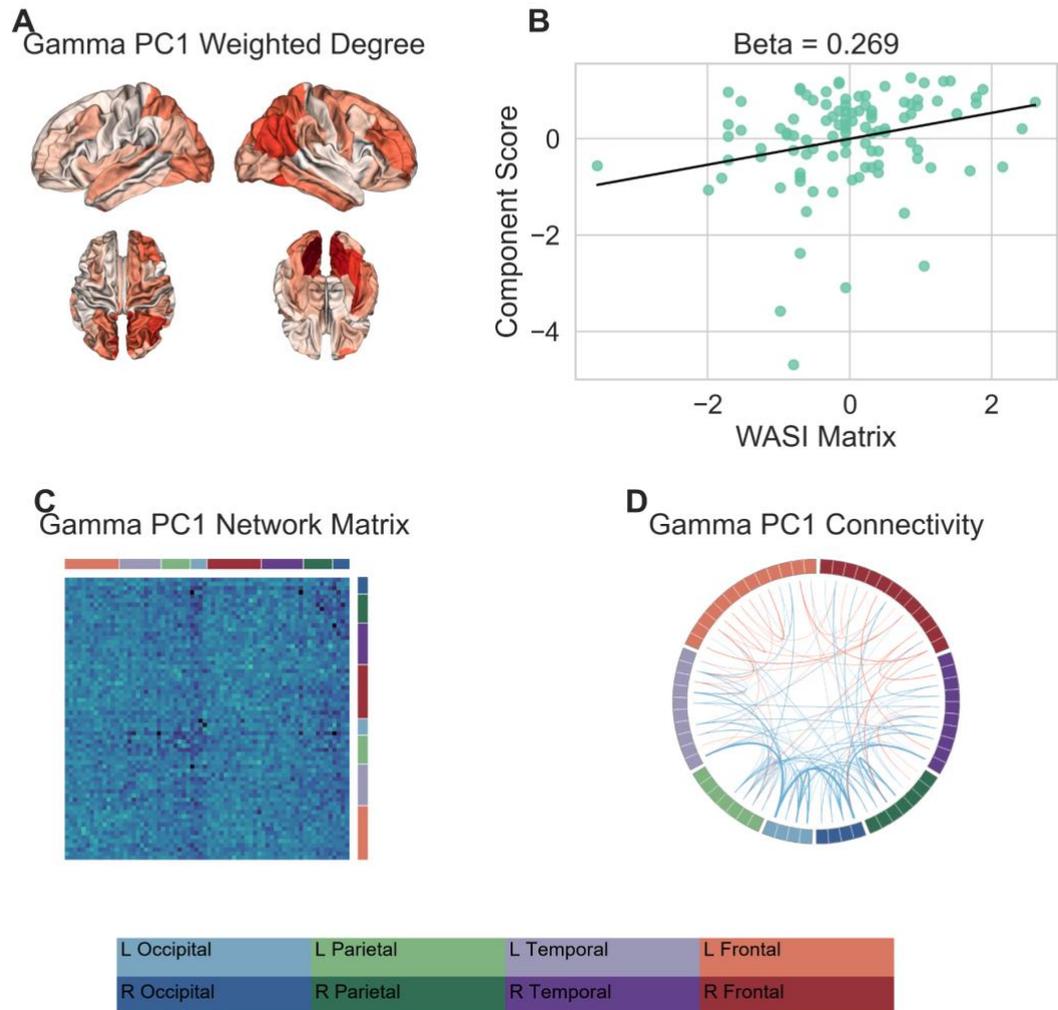


Figure 11. Overview of the Gamma PC1 network and its significant relationship with participant's WASI Matrix Reasoning score. **A)** Shows a spatial representation of the network through weighted degree of each parcel in the brain. **B)** Shows the component score for each individual against the z-scored WASI Matrix Reasoning score, the line represents the beta value. **C)** Shows the thresholded network matrix columns represent outgoing connections and rows represent incoming connections, with darker being stronger. **D)** Is a thresholded circos connectivity plot, representing the top 5% of connections, negative connections are in blue and positive connections in red, thickness varies by strength. Both matrix and circos plots are grouped by lobe and hemisphere using colors shown in the key.

Theta PC1 and Age

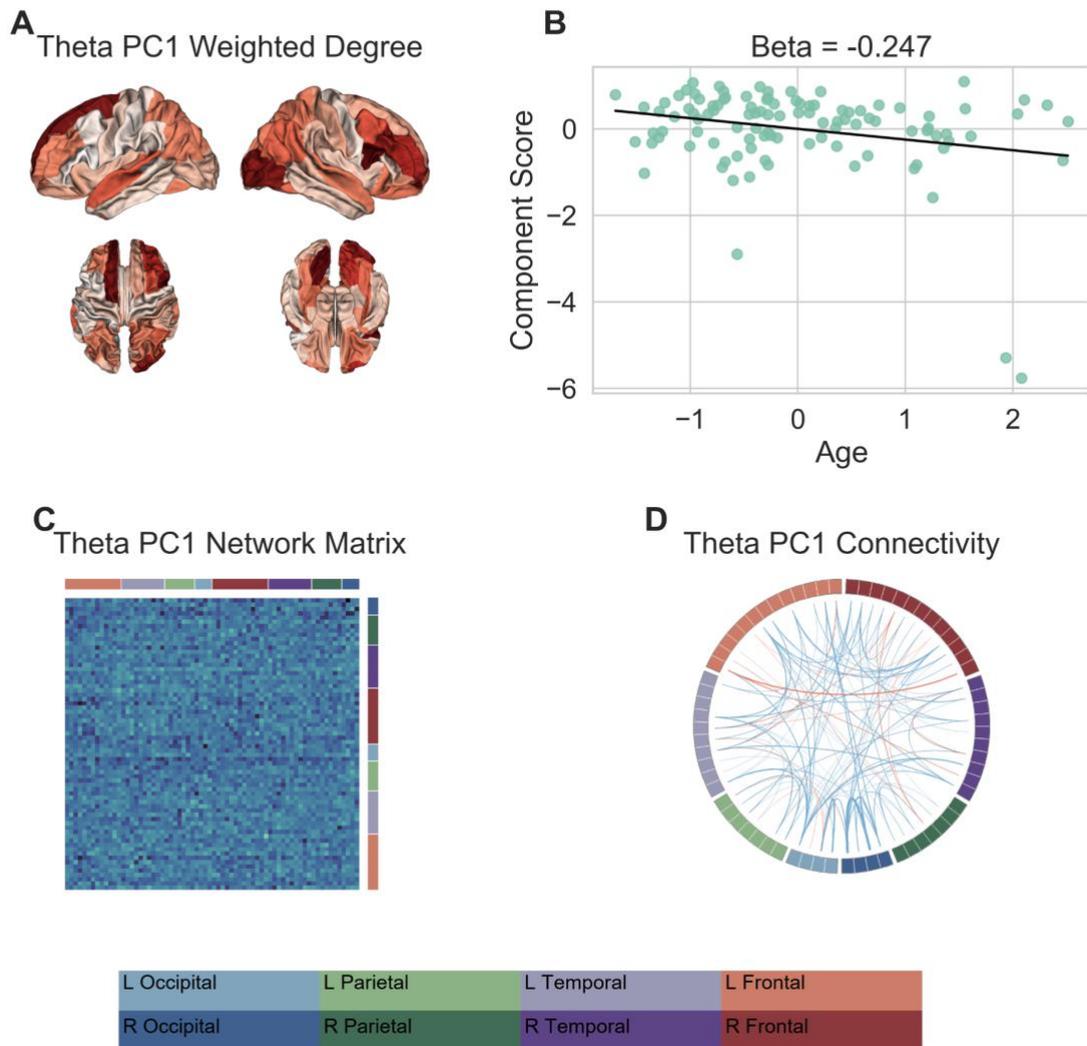


Figure 12. Overview of the Theta PC1 network and its significant relationship with participant's Age. **A)** Shows a spatial representation of the network through weighted degree of each parcel in the brain. **B)** Shows the component score for each individual against z-scored Age, the line represents the beta value. **C)** Shows the thresholded network matrix columns represent outgoing connections and rows represent incoming connections, with darker being stronger. **D)** Is a thresholded circos connectivity plot, representing the top 5% of connections, negative connections are in blue and positive connections in red, thickness varies by strength. Both matrix and circos plots are grouped by lobe and hemisphere using colors shown in the key.

2.3.3 Interim Discussion

The output of the PCA approach achieve the goal of simplifying the results. The significant variance is forced onto reduced key axes, achieving a more parsimonious description. This avoids the pitfalls inherent in interpreting single parcels. However, with this reduction, we do lose the ability to pick out individual areas; these component networks are particularly distributed. That said, upon visual inspection, there does seem to be a common feature in the PC networks (excluding Theta): connections in the occipital and parietal lobes are particularly important, and these connections are polar between the two components (see Supplementary Figure 11). PC1 in Alpha and Beta shows an increase in these posterior connections, and then PC2 shows a decrease. This pattern is flipped for the Gamma band. This tells us that the common axis of variance between participants is in the areas supporting visual processing and sensorimotor integration.

The three network relationships that remain are Subjective SES-Beta; WASI Matrix Reasoning-Gamma; and Age-Theta. It's notable that all show a decrease in occipital-parietal connectivity. This is particularly surprising within the Theta-Age relationship, as previous research has outlined an age related *increase* in theta connectivity. Schäfer et al. (2014), for example, found increases in and between many different functional networks - DMN, Ventral Attention, Visual, Motor and more. However, after closer consideration it appears that the theta increase Schäfer et al. (2014) report is between *adults* and *adolescents*, and there are very few significant increases in theta when they are compared to *children*. This suggests a non-linear developmental trend, where theta connectivity decreases into adolescence, then ramps up again into adulthood. As theta is believed to represent long range inter-regional connectivity (von Stein & Sarnthein, 2000), it is possible this is an observation of a U-shaped trend, which is common in connectivity of several networks across the lifespan (Collin & van den Heuvel, 2013).

It is particularly notable that the PCA components did not explain a particularly high amount of variance in the participant networks (in total between ~9-18%, see **Table 2**). The variance explained does follow the power distribution in the scans — with the Beta band containing the strongest peak in power — so this makes intuitive sense. The nearest comparison for this method is Quinn et al. (2021) who's two

illustrated Alpha components explained 24.0% and 12.7%, so some of my estimates overlap with this. Still, the low explained variance is rather disappointing, and I suspect this may be down to the relatively low signal-to-noise (SNR) levels during scanning, often caused by movements and the relatively small size of children's heads in the adult MEG helmet. The children tend to rest their heads against the back of the helmet, so this may result in the components being particularly weighted towards the posterior, as seen here.

The pattern of explained variance in the next step (GLM), however, follows the opposite trend, with the component networks explaining the lowest variance across participants (Theta and Gamma - low and high frequencies), also best explained by the combination of predictors. This implies that component networks like Beta PC1 (highest variance explained at ~11%) are residual noise components (sensor flux, doors shutting etc. that are not fully removed), whereas the remaining components are small but important (like Theta PC1 - 5% explained in PCA, but significantly related to age). This is coherent with the point in the paragraph above, that the PCA is poor at characterising variance due to a higher noise level, and that PCA is 'noise-blind'. It will not distinguish between variance explained by systematic measurement noise (i.e. flux in magnetometers) and variance explained by genuine signal (Bailey, 2012).

Given the explanatory power of these PCA networks, it is unsurprising that the steepness of the regression lines (in **Figure 10**, **Figure 11**, **Figure 12**) are relatively shallow when compared to those in the GLM conducted directly on the individual connections. This is emblematic of the trade-off made between parsimony and the explanatory power of the connection-wise GLM.

In this analysis we are only left with a single predictive SES factor, the subjective rating made by the parents of their own position in society. An increased loading onto the PC network was associated with higher subjective SES. The network itself was in the Beta band and is associated with a seemingly tight decrease in posterior connection weights, and an increase in all other connections (**Figure 10.D** - red connections are increasing and blue connections decreasing). This simultaneous increase and decrease in the same network is difficult to interpret. It's observed in the granular network analysis that resting beta in occipital areas increases with Objective SES. Here we have the opposite pattern with Subjective SES. This could reflect the differential impact of

different aspects of SES. At the very least this confirms the importance of treating these factors separately.

Finding this single SES relationship is interesting because all three SES regressors in the previous section showed connections with very high T statistics (**Figure 3**), and both Objective and Subjective had parcels with a very high weighted degree. In contrast, the beta values from the previous section for the WASI regressor were notably low across lobes (**Figure 4**), whereas in the present results one of the three significant component-relationships is from this same predictor. We can draw two conclusions from these differences: firstly, the global network properties are influenced in a different way by Age, SES, and IQ; secondly, the GLM-PCA does not capture sufficient variance to replicate the findings from the MVAR-GLM.

2.4. DTI Structural Connectome

The next section uses connectomes constructed from Diffusion Weighted MRI scans. Diffusion Tensor Imaging (DTI) covers a number of techniques for capturing white matter fibres in vivo, assuming that water molecules disperse faster along tracts than other surrounding tissue, creating ‘diffusion tensors’ (O’Donnell & Westin, 2011). DTI connectomes are built based on these tracts within the brain (modelled using trajectories called ‘streamlines’). Weighted connectivity in this case, is then the number of these streamlines that connect any two areas (Sporns et al., 2005). Relative to MEG-derived connectomes, there is a much larger literature on relationship between the brain and SES using the DTI connectome. This method has been used in developmental samples, showing correlations with poverty (Kim et al., 2019), fluid intelligence (Kocevar et al., 2019b), and age (Zhao et al., 2015). The structure of white matter – which this method attempts to model – constrains functional activity in the brain (Fernández et al., 2011; Honey et al., 2009), so one possibility is that we will identify overlap with the functional patterns described in the previous section.

As with reporting of MEG connectomes, we can look at both granular and network-level metrics (Yeh et al., 2016). Kim et al. (2019), for example, looked at network-level DTI connectome properties and found that efficiency of the network (the average length of paths between all nodes) was negatively associated with SES. They were also able to probe the connectome by conducting a virtual knock-out procedure to test how each node impacts local efficiency. SES was associated with a general local

pattern of reduced efficiency, but this effect was particularly pronounced in the frontal cortex, insula and cingulate. Using a subset of the sample included in this thesis, but a different parcellation (inclusive of sub-cortical regions) and connectome construction method (fractional anisotropy), Johnson et al. (2021) showed that a distributed pattern of network connections to a variety of areas were associated with SES, and that the connectome mediated the relationship between SES and measures of IQ.

Comparing the DTI connectomes with the MEG variants in the previous section, there are two key differences: sparseness and dimensionality. The MVAR model splits activity into 36 different frequencies, so has an extra dimension. We can therefore skip any frequency reduction in our DTI analysis. These connectomes are not fully connected, as there are some regions in the network which are not considered to share white matter tracts. In contrast, all regions share at least a trace amount of connectivity in the MVAR output. This relative sparseness in the DTI connectomes means the output from the GLM will likely need less thresholding or ranking and we can present networks of predictor-related connections in their entirety, in addition to identify high-degree hub parcels.

2.4.1 Methods

MRI-DTI

Participant's diffusion scans were taken on the same scanner used to acquire the T1-weighted images described above. These scans were echo-planar diffusion-weighted images with an isotropic set of 68 noncollinear directions, using a weighting factor of $b = 1,000\text{s} \times \text{mm}^{-2}$, interleaved with 4 T2-weighted ($b = 0$) volumes. Whole brain coverage was obtained with 60 contiguous axial slices and isometric image resolution of 2 mm. Echo time was 90ms and repetition time was 8500ms. For the MRI-DTI scans I was able to obtain scans for 83 participants, as 20 additional participants were excluded for excessive movement, or insufficient time within the scanner. The range of age was the same for this sample, but the mean was slightly increased at 9.31 (SD = 1.46). This sample was very similar in terms of income, mean equivalised income was £27,576 (SD=£16,423), but a slightly higher percentage of children were under the English poverty line, 22.89% (19 children).

Pre-processing

Diffusion images were converted from the DICOM format to compressed NifTI-1 format. The FSL eddy tool (Smith et al., 2004) was used to correct for motion during the scan, eddy currents and field inhomogeneities. The diffusion images were then processed with non-local means denoising (Buades et al., 2011) using DiPy (v0.11) (Garyfallidis et al., 2014). A Constrained Spherical Deconvolution (CSD) model was used to reconstruct fibre directions (Tournier et al., 2007) from gradient-direction diffusion-weighted images using a localmaximum harmonic order of 8. Whole-brain probabilistic tractography was performed with 8 seeds on all voxels. The step size was set to 0.5 and the maximum number of crossing fibers per voxel to 2. For ROI definition, T1-weighted images were also submitted to nonlocal means denoising in DiPy, robust brain extraction using ANTs v1.9, and reconstruction in FreeSurfer v5.3 (Fischl, 2012). Regions of interest (ROIs) were based on the Desikan-Killiany parcellation of the MNI template with 34 cortical ROIs per hemisphere (Desikan et al., 2006). FreeSurfer v5.3 was used for tissue classification and anatomical labelling. The parcellation here matched the parcellation used in the MEG analysis described above.

Connectome Construction

The connectomes were constructed in the form of connectivity matrices. Going through each ROI pair, the estimated number of streamlines intersecting both was calculated. This leaves us with a 68x68 matrix for each participant representing the count of streamline between ROIs. Self-connections were excluded.

General Linear Model

The design and implementation of the GLM was identical to that used in the MVAR GLM described above. The participant scan data lacked the frequency dimension, so the beta weights and statistics produced were in the form of a 68x68 matrix for each contrast.

The permutation procedure was also identical to the approach used in the MEG-MVAR section above, a null distribution was calculated using 5000 permutations per contrast, and the results were thresholded to a Monte-Carlo p value of .01.

The resulting connectomes were sparser than the MEG connectomes - the MVAR models produced no connections with zero-values, whereas 54% of the DTI connections were zero. Again, this prevents meaningful clustering, or the ability for the PCA model to converge. However, it was not necessary to filter by parcel degree to illustrate important areas, as the permutation procedure on top of the sparsity of the connectomes acted to effectively pre-threshold.

2.4.2 Results

Network-Level

Figure 13 shows the different distribution of the t-statistics for each contrast garnered by the GLM. IQ shows a greater average and maximum statistic, and both Age and IQ appear to outperform the SES measures.

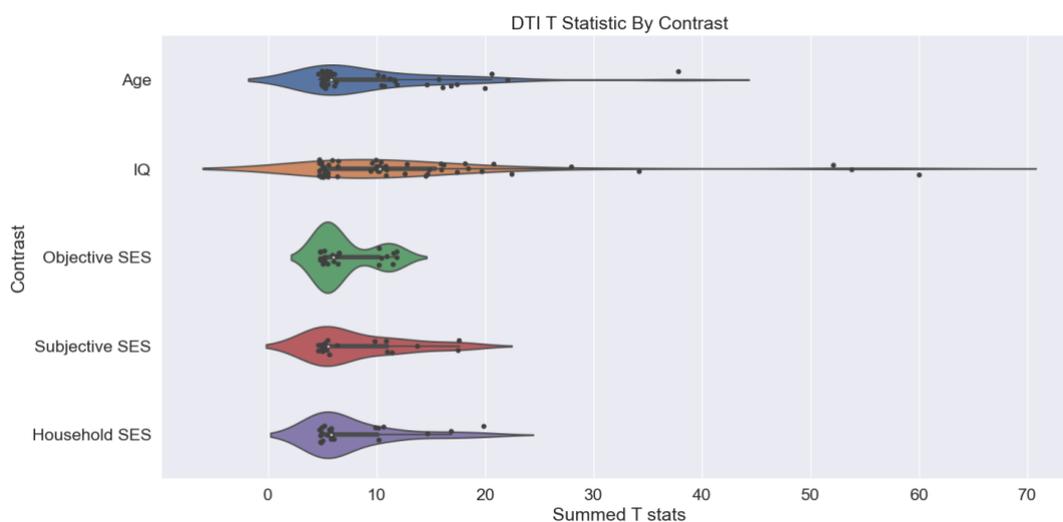


Figure 13. Violin plot Comparison of t-statistic distribution across contrasts from the DTI GLM. Lines within the plot represent the quartiles of the data, around the mean which is represented by a white dot. Individual parcel summed t-statistics are represented by black dots.

Figure 14 shows the distribution of the significant beta weights across lobes of the brain. The variation here is higher than the MVAR-MEG contrasts shown in **Figure 4**, however this is because the original DTI connectomes were sparser than the 100% dense MVAR connectomes. The pattern here is different and illustrates that the magnitude of betas is variable across, and within, contrasts. Specifically, it appears the

SES regressors predict much less variance in the DTI connectomes, and there is a notably large average weighted degree for the frontal lobe in the IQ predictor.

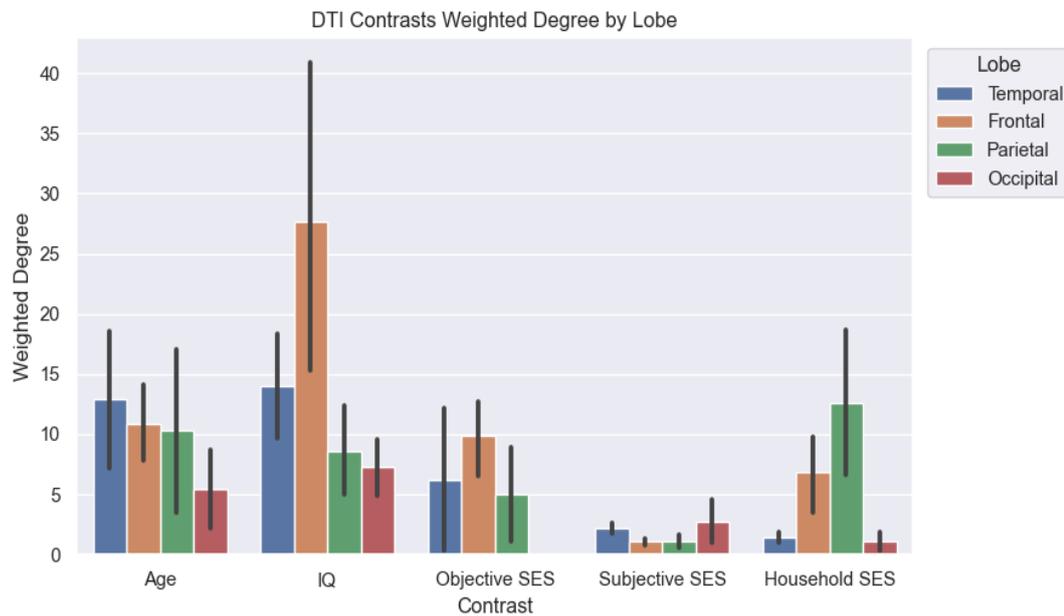


Figure 14. Mean Weighted degree across parcels, broken down by contrast and lobe. Weighted degree for each parcel is calculated by summing the beta-weights, which are on the scale of streamline counts. Error bars represent the standard error. Desikan-Killiany parcel lobe membership was determined using the grouping published in (Klein & Tourville, 2012).

As these DTI were considerably sparser than their MEG-MVAR counterparts, it is possible to present the results of each contrast without any thresholding or parcel selection. These are shown below. For interpretability, and consistency within the chapter, I have also chosen to highlight parcels in each contrast that have weighted degrees beyond the 90th percentile across all contrasts.

Figure 15 shows the first contrast - Age. The largest connections by beta value are intra-hemisphere (this is illustrated best in **Figure 15.D**). The parcel with the highest weighted degree (with the highest sum of streamline beta weights) is the right insular cortex (beta weighted degree 36.02), followed by two areas in the cingulate gyrus: right isthmus of the cingulate (beta weighted degree 32.27), and left rostral anterior cingulate (beta weighted degree 18.61). The high degree of the right insular cortex and the right isthmus of the cingulate is explained by a particularly strong connection between the two, with a beta weight of 28.89 (percentile score of 99.89 - the highest value). The

weighted degree of these parcels can be seen in **Figure 15.B**. The higher value connections are both within their own hemispheres in this contrast.

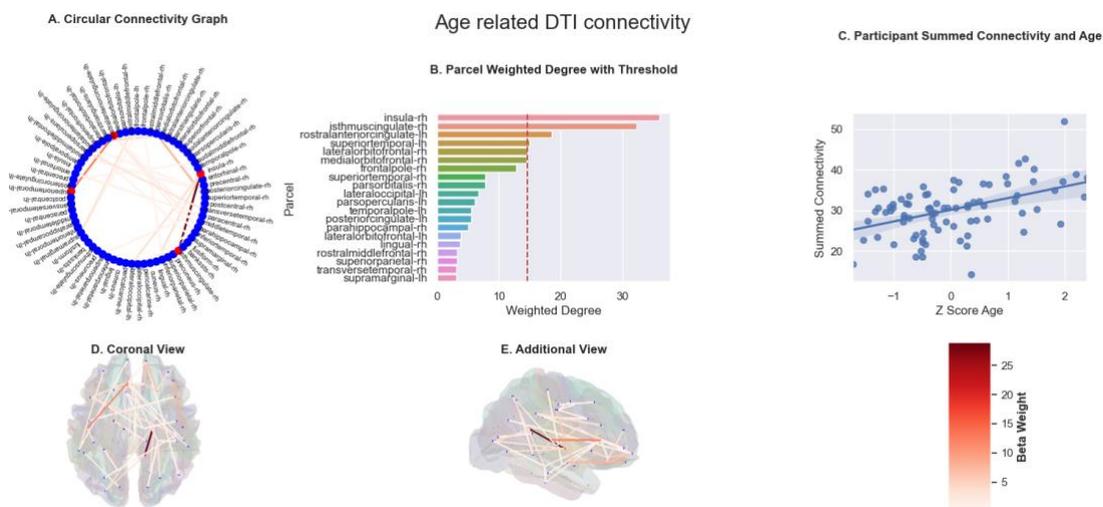


Figure 15. Summary of the Age-related connections in the DTI-connectome. **A)** A circular connectivity graph with parcel names, connections are coloured by beta weight (on the scale of CSD streamline count), the nodes are colored by those which cross the 90% threshold. **B)** The Beta Weighted Degree of each parcel in the brain and the 90% threshold for node highlighting. **C)** average parcel weighted degree of these connections against Z-scored Age, at the level of each participant. **D)** and **E)** the connections plotted on the fsaverage glass brain.

Figure 16 shows the second contrast, fluid IQ. The average parcel weight calculated from edges related to this contrast have a higher average value in the frontal lobe (see **Figure 14**). Looking at **Figure 16.D**, there is a general shift in connectivity towards the front of the brain. In terms of weighted degree, the highest parcels were the right superior temporal gyrus (beta weighted degree 26.72) and the left superior frontal cortex (beta weighted degree 22.50). The highest weighted connection here is between the left superior frontal parcel and the right superior-temporal parcel, this had a beta weight of 13.66 (percentile score of 98.5) and can be seen clearly in **Figure 16.D and E**. The higher weighted connections seem to be cross-hemispheric in this contrast.

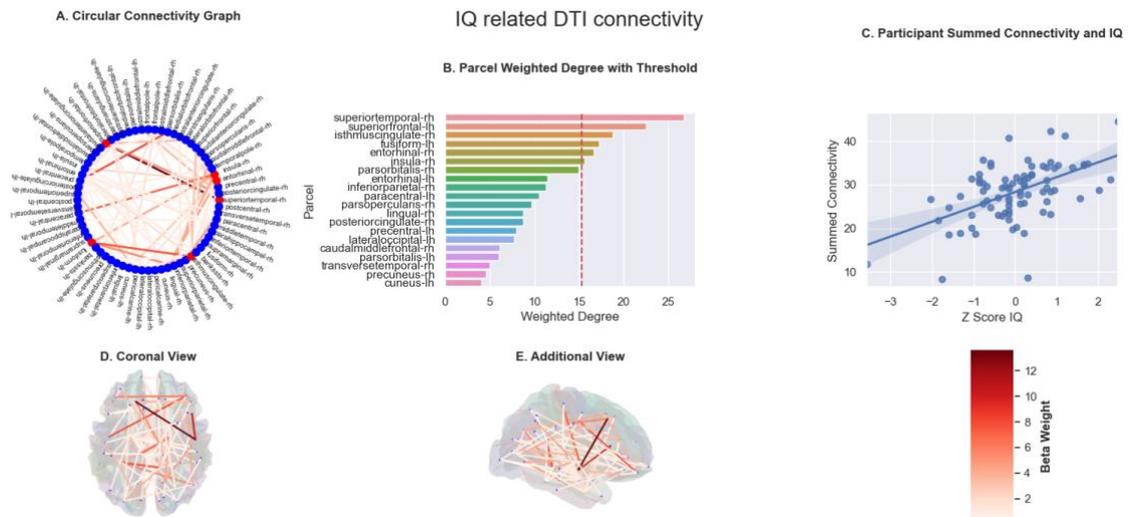


Figure 16. Summary of the IQ related connections in the DTI-connectome. **A)** A circular connectivity graph with parcel names, connections are coloured by beta weight (on the scale of CSD streamline count), the nodes are colored by those which cross the 90% threshold. **B)** The Weighted Degree of each parcel in the brain and the 90% threshold for node highlighting. **C)** average parcel weighted degree of these connections against Z-scored Age, at the level of each participant. **D)** and **E)** the connections plotted on the fsaverage glass brain.

Figure 17 represents the network edges related to the Objective SES factor. As mentioned earlier this factor weighted highly on household income, job title score and affluence of the local area. This contrast, and the SES contrasts in general, led to fewer significant connections in comparison to Age and IQ. The two higher degree parcels are the left lateral orbitofrontal cortex (beta weighted degree 21.52) and the right banks of the superior temporal sulcus (beta weighted degree 20.85). The largest value connection was between these two parcels, and has a beta weight of 16.71 (percentile score 99.16). The larger connections here appear to be mostly inter-hemispheric (**Figure 17.D**).

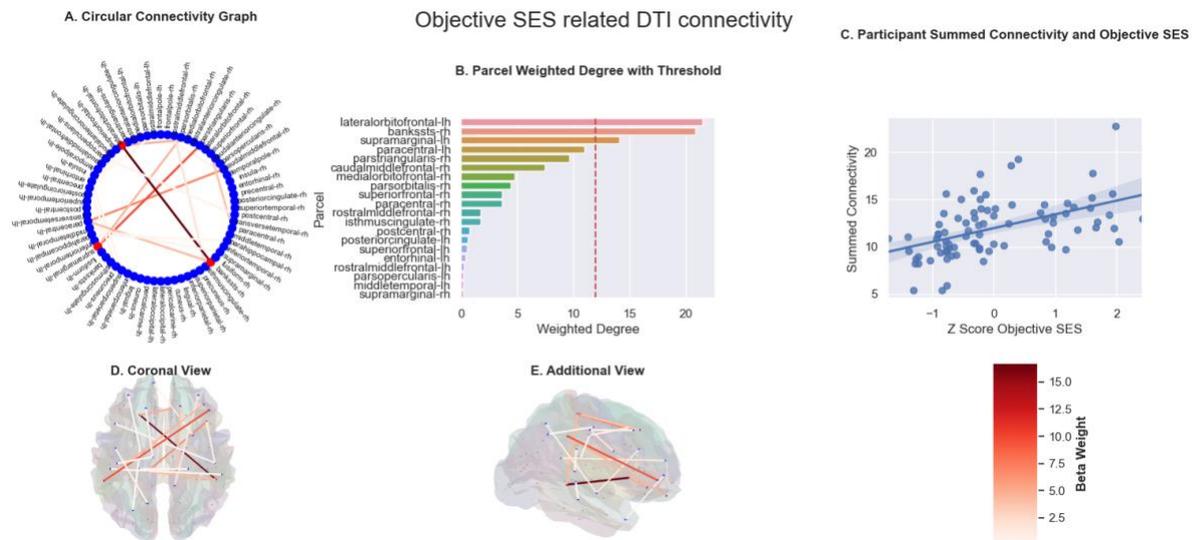


Figure 17. Summary of the Objective SES related connections in the DTI-connectome. **A)** A circular connectivity graph with parcel names, connections are coloured by beta weight (on the scale of CSD streamline count), the nodes are colored by those which cross the 90% threshold. **B)** The Weighted Degree of each parcel in the brain and the 90% threshold for node highlighting. **C)** average parcel weighted degree of these connections against Z-scored Age, at the level of each participant. **D)** and **E)** the connections plotted on the fsaverage glass brain.

Figure 18 shows the DTI connectome related to Subjective SES scores. This contrast had only a few low beta weight connections, which leads to the relatively low values visible in the beta degree histogram in **Figure 14**. This is also reflected in **Figure 18.B** where the maximum parcel degree is a small fraction of the other DTI contrasts. Due to the sparsity of these results it is difficult to delineate any global pattern. The largest connection is between the right pericalcarine cortex and the right supramarginal cortex, with a beta weight of 1.41 (percentile score of 63.16). This drives the largest degree parcel, which is the right pericalcarine cortex.

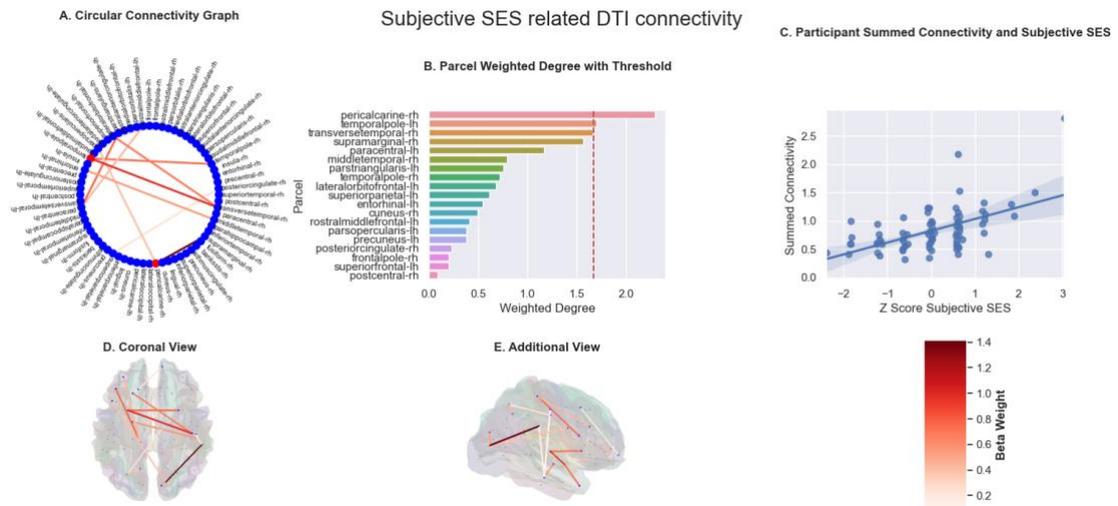


Figure 18. Summary of the Subjective SES related connections in the DTI-connectome. **A)** A circular connectivity graph with parcel names, connections are coloured by beta weight (on the scale of CSD streamline count), the nodes are colored by those which cross the 90% threshold. **B)** The Weighted Degree of each parcel in the brain and the 90% threshold for node highlighting. **C)** average parcel weighted degree of these connections against Z-scored Age, at the level of each participant. **D)** and **E)** the connections plotted on the fsaverage glass brain.

Figure 19 shows the DTI network associated with Household SES. Much like the Subjective SES contrast, this network has multiple relatively low weight connections (13 out of 17 are below a beta weight of 2). However, there is a strong connection between the left postcentral gyrus and the left posterior cingulate with a beta weight of 12.49 (percentile score of 98) — this again drives those parcels to a high relative weighted degree.

One possibility is that the recruitment strategy (two rounds of recruitment) may have impacted the Household SES related differences in connectomes. In short, this predictor differed between data collection runs, with the second run having a wider distribution. To explore this we bifurcated the regression plot in **Figure 19.C** and found the relationship the GLM picked out could not be explained by study differences (see Supplementary Figure 13).

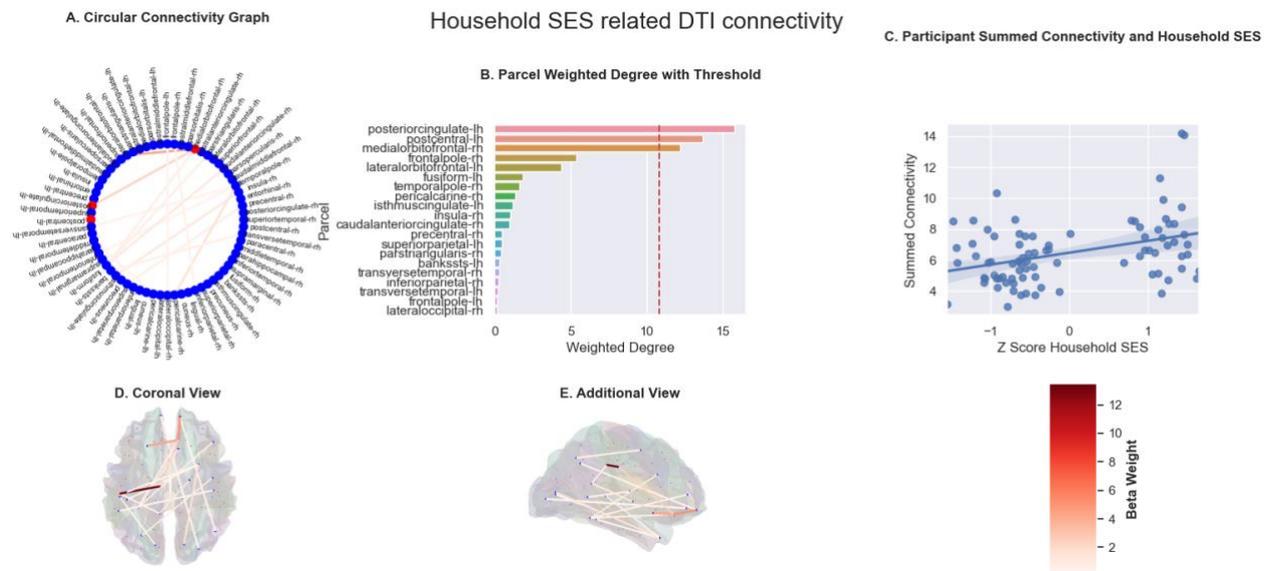


Figure 19. Summary of the Household SES related connections in the DTI-connectome. **A)** A circular connectivity graph with parcel names, connections are coloured by beta weight (on the scale of CSD streamline count), the nodes are colored by those which cross the 90% threshold. **B)** The Weighted Degree of each parcel in the brain and the 90% threshold for node highlighting. **C)** average parcel weighted degree of these connections against Z-scored Age, at the level of each participant. **D)** and **E)** the connections plotted on the fsaverage glass brain.

2.4.3 Interim Discussion

The above GLM analysis of the DTI connectomes outline five separate connectomes associated with each of the covariates. Looking at the distribution of t statistics, the DTI connectome seems to be less strongly associated with SES measures and more strongly related to Age and IQ. Subjective SES has notably lower correlation when contrasted with the MEG connectome (**Figure 13**). Rather fortunately, the sparseness and low dimensionality of the results avoided the need for a PCA reduction, or parcel selection.

The network related to the first SES factor — objective SES — displayed the strongest connection between the left orbito-frontal cortex and the right banks of the STS. This was a positive connection, so this *increases* in strength with increasing objective SES. These were also the parcels with the highest weighted degree in this contrast - so hub-ness increases with objective SES. The same right STS parcel came up as a hub node related to *subjective* SES in the MEG analysis. This association is consistent with the discussion above about the STS being an area involved in many processes. This involvement of a broadly involved area would also gel well with previous research

showing SES has a distributed effect on multiple networks (Brito & Noble, 2014; Johnson et al., 2021; Kim et al., 2019).

Subjective SES had the lowest predictive value of all the regressors by weight. One possibility is that the subjective opinion of the family reflects a broader environment, which impacted the electrical signals underlying functional processes, but had a lesser impact on the physical circuitry itself. This could be because objective measures of SES like income and household factors represent physical deprivation that can influence physical aspects of brain development (e.g. nutrition - Storrs, 2017; early life stress - White et al., 2020). Whereas the orthogonalised factor of subjective SES aligns with less absolute, and more social factors. The only strong network hub identified from this regressor was the right peri-calcarine sulcus, which deals with visual information, and was connected heavily to the right supra-marginal cortex. The supra-marginal cortex is commonly related to phonological processing (Ben-Shabat et al., 2015), and visual language (Stoeckel et al., 2009). This white matter pathway between an early visual area and a language area could facilitate differences between participants in reading, that in turn covaries with SES.

Household SES was the final SES related network outlined above. It comprised many lower weighted connections, the one that stands out (very clear from **Figure 19**) is between the left postcentral gyrus and the posterior cingulate. The posterior cingulate cortex (PCC) is a key node in the DMN connecting this network to others (Leech et al., 2012). Like other areas discussed in this chapter, it is unsurprising to see such a generally involved parcel's connectivity predicted by SES. Perhaps the connection from the post-central gyrus to the PCC could indicate that architecture involved in sensorimotor integration into higher level processes is less developed. The Household SES factor is most highly weighted onto whether the child has their own room or not (**Table 1** bottom row), so a tempting interpretation would be that the lack of personal space (and movement differences in this environment) could lead to this connectivity difference. However, this is just one amongst many possible interpretations.

Age-related hub areas in the DTI connectome (**Figure 15**) seem to be primarily in the insula and cingulate areas, with a relatively strong connection between the right insular cortex and the right isthmus of the cingulate. Previous diffusion tensor imaging has shown age-related changes in the insular cortex (Dennis et al., 2014) which also has connections to the nearby cingulate, both areas are implicated in socio-emotional

processes, awareness and interoception (Taylor et al., 2009). It is possible the age-related connectivity between these areas reflects rapid development of skills such as emotional regulation (Zeman et al., 2006). Contrasting the age-related hubs in the MEG and DTI results, these scan modalities are sensitive to different processes of development, and both should be considered in studies to provide a more complete insight into age-related processes.

In relation to fluid IQ, encouragingly, the higher beta weights were seen in the frontal lobe (**Figure 14**), which is expected given established work on frontal areas involvement in fluid IQ (Duncan et al., 2000; Kocevar et al., 2019b; Pineda-Pardo et al., 2016; Preusse et al., 2011; Roca et al., 2010; Tschentscher et al., 2017; Woolgar et al., 2010, 2018).

Overall, the structural network analysis reported here tells a complex story, but encouragingly shows some overlap in the SES component-related areas (STS and calcarine sulcus), whilst also hinting at important global differences in the predictive pattern of covariates (AGE-IQ => DTI vs SES=>MEG). To further delineate the overlap and differences between these connectomes the next section of this chapter deals with formal comparison of these networks.

2.5. Functional-Structural Comparison

As mentioned above, the benefit of carrying out the MVAR and DTI mass GLMs without the use of a clustering or dimension reduction step, was that the output statistics are comparable. This permits us to ask two novel questions:

1. Across the sample, do the networks derived from the resting state MEG scans match with the structural networks defined by the DTI scans?
2. How much shared variance does each connectome predict in the covariates, and how variance much is unique to each scan-type?

The first question can be addressed using graph theory, namely graph matching algorithms. The second question can be addressed using linear regressions within a dominance analysis, proving statistics on shared and unique variance for each connectome type.

2.5.1 Graph Matching

Various elements of graph theory have already been used throughout the thesis. For instance, in the MEG and DTI analyses ‘weighted degree’ of parcels in the network was a key measure. In this section I will define more concretely some of the key features of this approach to characterising networks. This is a necessary pre-requisite before describing the purpose and method of ‘graph matching’.

Graph theory represents a network as an abstract mathematical structure called a graph. This structure is formed from ‘nodes’ and ‘edges’. Nodes (sometimes called vertices or points) represent possible end-points and starting points, whilst ‘edges’ link these nodes together. Edges can be undirected and binary, or they can be directional and contain weight information. In our case nodes are cortical parcels defined by Desikan et al. (2006), however, in practice these can really be any region of interest within the brain (Dell’Acqua & Catani, 2012; Fornito et al., 2015). Connections between these nodes are represented as edges, in the present case these are either partial directed coherence values or values representing white matter fibres, the latter is the more common use of graph theory in neuroimaging (Bathelt et al., 2018; Qi et al., 2015).

An array of algorithms can be applied to these graphs to explore their organisational principles. These can be broadly categorised as global graph metrics, which characterise the whole graph, versus local graph metrics, which characterise subdivisions or individual nodes. An example of a local metric is *node degree*, which is a simple measure of the total number of edges to a given node. Our MVAR graphs are considered ‘weighted directional graphs’ because each edge has a weight and a direction, this means we can calculate a ‘weighted degree’ for each node which takes into account edge weight. Local metrics have been used to identify important areas within brain networks and how they relate to behaviour. Other graph algorithms have been used to investigate the developing brain. Bathelt et al. (2018) used several local and global metrics to establish relationships with academic attainment. This included clustering coefficients, which represent how nodes group together based on connections, and can be averaged into a global measure of modularity (Rubinov & Sporns, 2010), and global efficiency (derived from the inverse of path lengths in the network), which represents the integration of the network (Achard & Bullmore, 2007).

Graph matching is a potentially promising technique for my comparative analysis. I have characterised the two networks separately but integrating them is an important step towards understanding the association between SES and brain organisation. An obvious first step is to first identify whether the structure of the MEG and DTI networks relate to each other across participants, and graph matching does this. Previous work has matched functional and structural brain graphs. Osmanlioğlu et al. (2019) matched structural MRI derived networks with functional MRI networks, on a participant-by-participant basis. Euclidean distance (based on edges) is calculated between every DTI node, and every functional node. This distance is then used to choose pairs of closest nodes between the graphs, whilst also balancing this across the entire network. This local matching must happen with global consideration because several nodes may share a closest match. By looking at average matching distance for the whole connectome we can decide which option is globally optimal. This problem is known as the linear sum assignment problem (Burkard & Derigs, 1980) and is an optimisation problem where the total cost of assignment (i.e. the sum of linear distances) needs to be minimised. This problem can be resolved using the Kuhn-Munkres (or Hungarian) algorithm (Kuhn, 1955), which iteratively attempts different pairings until the total distances are as small as possible. We are left with a matching matrix with each node from the functional graph paired with the closest node on the structural graph.

If any pair of nodes are matched with their equivalent this is considered an accurate match. Group summaries then show the percentage of participants who have matches for each parcel. Osmanlioğlu et al. (2019) found 56-81% of the sample (depending on the area) showed accurate matching between structural and functional graphs across different nodes and systems, and that average matching accuracy decreases with age (between 8-23 years old), implying a lag between structural changes and their functional counterparts.

Given the success of previous applications in children of a similar age, this is a good candidate to investigate our structural and functional connectomes. Consistent with previous research, I approach the matching of participants' graphs as an inexact graph matching problem. The graphs are not suitable for exact matching because the DTI and MEG connectivity matrices contain differing numbers of zeroes (i.e. each vertex has a different number of edges).

There are some possible limitations that will apply. Unlike Osmanlioğlu et al. (2019) our parcellations are much coarser (68 areas vs 129-400 areas), but this is necessary given the spatial resolution of MEG. This may lead to two potential challenges. Firstly, we are less able to group areas into common networks with lots of parcellations (e.g., visual, limbic, Default Mode Network), so our approach is limited to individual areas. Secondly, the matching may not work as well, because each parcel has a reduced number of potential connections, thereby making the chance of a false positive match much higher.

2.5.2 GLM comparison

To address my second question regarding the unique versus shared variance explained by the connectomes, I first compared the explained variances (R^2) in the models. This will tell us how much variance in each scan type is explained by the predictors. However, this cannot establish if any of the variance explained by the connectomes is shared or unique. Given the size of the models and the permutations schemes involved, this is hard to assess.

An alternative is to form a set of models, but with the scan data themselves as the predictors. This can tell us the proportion of variance that the *scans* themselves explain in the SES, Age, and IQ measures. We can repurpose our OLS regressions, which provide us with explained variance. To give a concrete example, consider **Equation 3.1**, we have each subjective SES score, modeled as a linear combination of their MEG connectome reduced to a singular value, intercept and an error term. We can derive an explained variance value (R^2) which tells us how the variance across the sample's subjective SES scores is explained by our MEG scan. We repeat this with DTI (**Equation 3.2**), followed by a multiple regression with both (**Equation 3.3**).

$$\gamma_{\text{SubjectiveSES}} = \beta_{\text{intercept}} + \beta_{\text{meg}}X_{\text{meg}} + \epsilon \quad (1)$$

$$\gamma_{\text{SubjectiveSES}} = \beta_{\text{intercept}} + \beta_{\text{dti}}X_{\text{dti}} + \epsilon \quad (2)$$

$$\gamma_{\text{SubjectiveSES}} = \beta_{\text{intercept}} + \beta_{\text{dti}}X_{\text{dti}} + \beta_{\text{meg}}X_{\text{meg}} + \epsilon \quad (3)$$

Equation 3. Ordinary Least Squares formulae for scan comparisons of modelling subjective SES. 1: Subjective SES as a function of MEG scan value. 2: Subjective SES as a function of DTI scan value. 3: Multiple regression extension where Subjective SES is modelled as a combination of DTI and MEG scan values.

The three values R^2 can then be compared to each other in a series of incremental subtractions (in a procedure outlined in the methods section), to identify the shared and unique variance. This is called dominance analysis (Azen & Budescu, 2003; Budescu, 1993). A standard parametric t test applied to **Equation 3.3** can formally test the hypothesis that variance explained is unequal.

These two methods - graph matching and dominance analysis - allow me to compare not just the connectomes themselves, but the extent to which they are sensitive to SES.

2.5.3 Methods

Graph Matching

I was unable to obtain the MATLAB code used to run the graph matching algorithm in the previously cited literature. I therefore created a Python code library – ConnectomeMatch (Anwyl-Irvine & Dalmaijer, 2021) – that included all the preprocessing, matching and inferential tools needed to perform incomplete matching with the Hungarian algorithm. I will refer to each step in the analysis, and the functions used from this library. The code is hosted on Github at <https://github.com/u01ai11/ConnectomeMatch> and available to the wider python community on pypi at <https://pypi.org/project/ConnectomeMatch/> so can be installed on any Python installation with the command line command “pip install ConnectomeMatch”.

First, I reduced the 32 frequency MEG-MVAR graphs into four banded graphs per participant. I took the average peak frequency approach taken in the PCA reduction earlier in this chapter. As peak power for a given oscillation can vary between individuals (Haegens et al., 2014), and matching was done within each participant, I took a personalised approach to allow for this variability. A single 68x68 connectivity graph was taken at participant’s personal peak power within the Theta, Alpha, Beta and Gamma bands.

As the density of connections within the DTI-CSD & MEG-MVAR graphs are not the same, it is important to adjust them. The matching would simply fail at the group level because the linear distance between nodes with many edges, versus those

with very few, would be too great. To achieve this, I matched density within each participant's pairs. The MVAR connections are dropped below a threshold, which is adjusted iteratively, until the graph densities are matched. This takes place after we remove all self-connections (i.e. the diagonal of the connectivity matrix). The relevant function in the library is `match_densities()` and it takes a graph to drop connections from and a target graph whose density we need to match. Additionally it takes a starting density, a step-size and a maximum number of iterations before it accepts the nearest density (to avoid infinite loops). This can be done on the group level (every participant thresholded to the same value until group densities match) or the individual level (each participant has a personal threshold until their own densities are matched). I chose to take the individual approach, as this maximises the chance of finding a match between pairs of scans — and extends the individual-peak approach taken in the frequency reduction. The distributions of participant's densities are included in Supplementary Figure 15.

The next steps take place within the `match_graphs()` function. This takes two arrays containing all participant's graphs (in the same order), and optionally allows multi-threading (parallel processing) by specifying the number of jobs to batch, and a boolean flag to choose whether to provide a detailed log in the terminal. It splits each participant up and processes them separately. First it standardises the edge weights on the participant level. This is necessary for the euclidean distance calculation, to ensure scale has no impact. Again, this is done on a per-participant basis, by calculating z scores. Then a 2D matrix of euclidean distances between all nodes in graph 1 against all nodes in graph 2 is constructed (see **Equation 4**).

$$d(MEG_{node}, DTI_{node}) = \sqrt{(MEG_{e1} - DTI_{e1})^2 + (MEG_{e2} - DTI_{e2})^2 + \dots + (MEG_{e68} - DTI_{e68})^2}$$

Equation 4. Calculating the cost (d) of assigning a single node from MEG graph (MEG_{node}) to a node from DTI graph (DTI_{node}). This is the Euclidean distance between the feature vectors of each node (rows in connectivity matrix). In other words this is the square root of the sum of squared differences between each edge pair from the nodes. This equation is carried out for every possible pair of nodes, leading to a 2D (no. MEG nodes \times no. DTI nodes) matrix of distances.

These distances then are taken as the cost for assigning nodes to each other. The best matches are calculated by solving the linear sum assignment problem — i.e. given the whole matrix of distances which row is assigned to which column so that each column is assigned to at most one row (and vice versa). To solve this we use the Hungarian or Kuhn-Munkres algorithm (Kuhn, 1955). In practice, this forces each node into a closest match, with the reservation that all nodes must also match with exactly one other. After the function has looped through each participant, we now have an n-participant sized collection of binary (68x68) graphs that we can call the ‘matching matrices’. By averaging these matrices across participants, we get a value between zero and one representing how frequently each pair of nodes were matched — called ‘proportion matched’. The diagonals of these graphs show accurate matches (e.g. Lingual gyrus in MEG is matched to the Lingual gyrus in DTI), and the rest show inaccurate matches (e.g. Lingual gyrus in MEG matches to something else in DTI).

To assess whether any level of matching represents a significant pattern, I also implemented a permutation scheme. This approach needed to be slightly different from previous permutations, as a simple randomisation of all edges in the graph would violate the assumption of exchangeability (Winkler et al., 2015). Therefore, this permutation shuffled every participant’s two graphs whilst retaining the overall distribution of node degree per graph. This was repeated 1000 times, re-calculating the ‘proportion matched’ via the matching algorithm above each time. This null distribution was used to threshold the matrix to eliminate spurious matches.

Finally, to eliminate the possibility that decisions made in standardising or thresholding of either graph had eliminated possible relationships, the procedure was replicated: with CSA-DTI connectome, unthresholded MVAR connectomes, single-averaged (instead of peak frequency-banded) MVAR connectomes, and binarized matrices (removing weights by making all connections ‘1’ after thresholding).

As this is a relatively new implementation, I also ran a control analysis using the CDA and CSD DTI connectomes for each participant. These are both derived from the same scan, so they should match with minimal differences and act as reasonable sanity check.

Linear Model

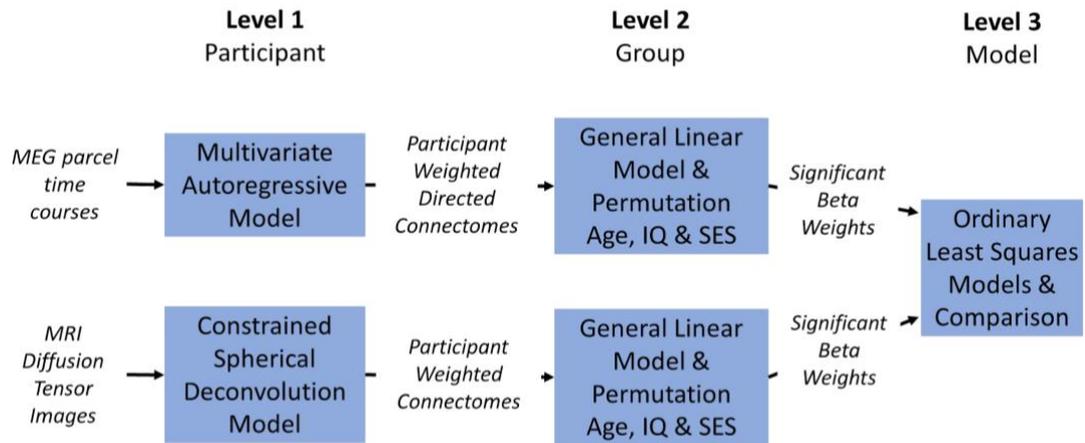


Figure 20. Summary of neuroimaging analysis pipeline for variance comparison. Arrows and labels represent data inputs and outputs, boxes represent analysis steps. Columns indicate the different levels of analysis.

Figure 20 presents an overview of how certain stages in earlier sections feed into this linear model. MEG and MRI are analysed in parallel, over the individual and group levels, then we compare the output models in a higher-level model comparison.

The first step to comparing explained variance can be achieved by calculating the coefficient of determination for each of our DTI and MVAR GLM models. We also adjust this figure for the number of extra predictors — as this can inflate the R squared estimates. I represent this in **Equation 5**. I calculate this metric for each connection in the graph, and then summarise it for each model by taking the mean and standard deviation.

$$R_{adj}^2 = 1 - \frac{SS_{residual}/df_e}{SS_{model}/df_t}$$

Equation 5. Adjusted R squared equation. Residual sum of squares is divided by degrees of freedom of the error (no. participants - no. regressors - 1) and is then divided by the model's sum of squared divided by the degrees of freedom for the population (no. participants - 1).

R squared values do not capture how much variance is shared or unique. To compare the relative variance explained by the DTI-GLM and the MEG-MVAR-GLM, I performed a series of ordinary least squares (OLS) regressions and contrasted the

resulting R^2 values. For each contrast (Age, IQ, Objective SES, Subjective SES, Household SES) we model individual participant's values using a single value each from their masked MEG-MVAR and MRI-DTI connectomes.

To obtain these single values, per contrast I took each participant's DTI connectome and their MEG-MVAR connectome (averaged across frequency bands) and masked them using the relevant significance maps obtained during permutation testing, then averaged the remaining connections. For example, with the Age contrast we used a mask for the DTI connectome that represents those connections significantly related to Age, calculated the mean, and then did the same for the MEG-MVAR connectome.

For each contrast I then established how much unique and shared variance could be explained by the scan types. This was achieved by comparing the R^2 values from several models: two models where the variable (e.g. SES) was explained by *just one* scan (**Equation 6.1** and **Equation 6.2**), and one model where it was explained by both (**Equation 6.3**). The combined R^2 value was then subtracted from the isolated R^2 values to produce unique variance for MEG (**Equation 6.4**) and DTI (**Equation 6.5**). Finally, these unique variances were summed and subtracted from the combined R^2 to ascertain shared variance (**Equation 6.6**). This approach to model comparison is detailed in (Darlington, 1968) and (Judd et al., 2011).

$$\text{DTI Regression} \quad \gamma_{\text{variable}} = \beta_{\text{intercept}} + \beta_{\text{DTI}} + \epsilon \quad (1)$$

$$\text{MEG Regression} \quad \gamma_{\text{variable}} = \beta_{\text{intercept}} + \beta_{\text{MEG}} + \epsilon \quad (2)$$

$$\text{Combined Regression} \quad \gamma_{\text{variable}} = \beta_{\text{intercept}} + \beta_{\text{DTI}} + \beta_{\text{MEG}} + \epsilon \quad (3)$$

$$\text{MEG Unique Variance} \quad \sigma_{\text{MEG}}^2 = R_{\text{combined}}^2 - R_{\text{DTI}}^2 \quad (4)$$

$$\text{DTI Unique Variance} \quad \sigma_{\text{DTI}}^2 = R_{\text{combined}}^2 - R_{\text{MEG}}^2 \quad (5)$$

$$\text{Shared Variance} \quad \sigma_{\text{DTI} \cap \text{MEG}}^2 = R_{\text{combined}}^2 - (\sigma_{\text{MEG}}^2 + \sigma_{\text{DTI}}^2) \quad (6)$$

Equation 6. Steps taken to establish unique and shared variance between MEG and DTI scans in explaining a given variable. Regression equations in 1, 2 and 3 are used to generate R^2 values which are then used to model explained variance (σ^2) unique to MEG (4), DTI (5) and jointly (\cap) between them (6).

In addition to the R^2 estimations, some formal hypothesis testing is also permitted with the OLS regressions including both the MRI and MEG connectomes. A simple t -test allows us to compare the t statistics from these regressions (formalized in **Equation 6.3**) and tell us if there's a difference in predicted signal between the two. As one is conducted for each variable, I correct for multiple comparisons by adjusting the critical alpha value for every test — 5 in our case leading to $\alpha = .01$ as our p-value threshold.

Alternative DTI Model

There are multiple ways to derive connectomes from diffusion tensor images. For later comparison I created connectomes using an alternate model. Constant Solid Angle (CSA) was used to reconstruct the fibre orientations (Aganj et al., 2010), this provides a sparser connectome. The streamline connectome was then also normalised, a symmetric intersection was used so that streamlines starting and ending in each ROI were averaged. This was then used in the final analysis to compare results.

2.5.4 Results

Graph Matching

Figure 21 shows the results of the matching process applied to the CSD and CSI derived DTI graphs. The algorithm indeed produced a reasonable level of matching across parcels (mean accuracy 84.49%, standard deviation 24.33%). It is very clear from this plot that this method works with a reasonable degree of accuracy. A few areas matched with areas other than their correct partner in the other connectome, but mostly they match correctly. This provides a welcome sanity check that the method works.

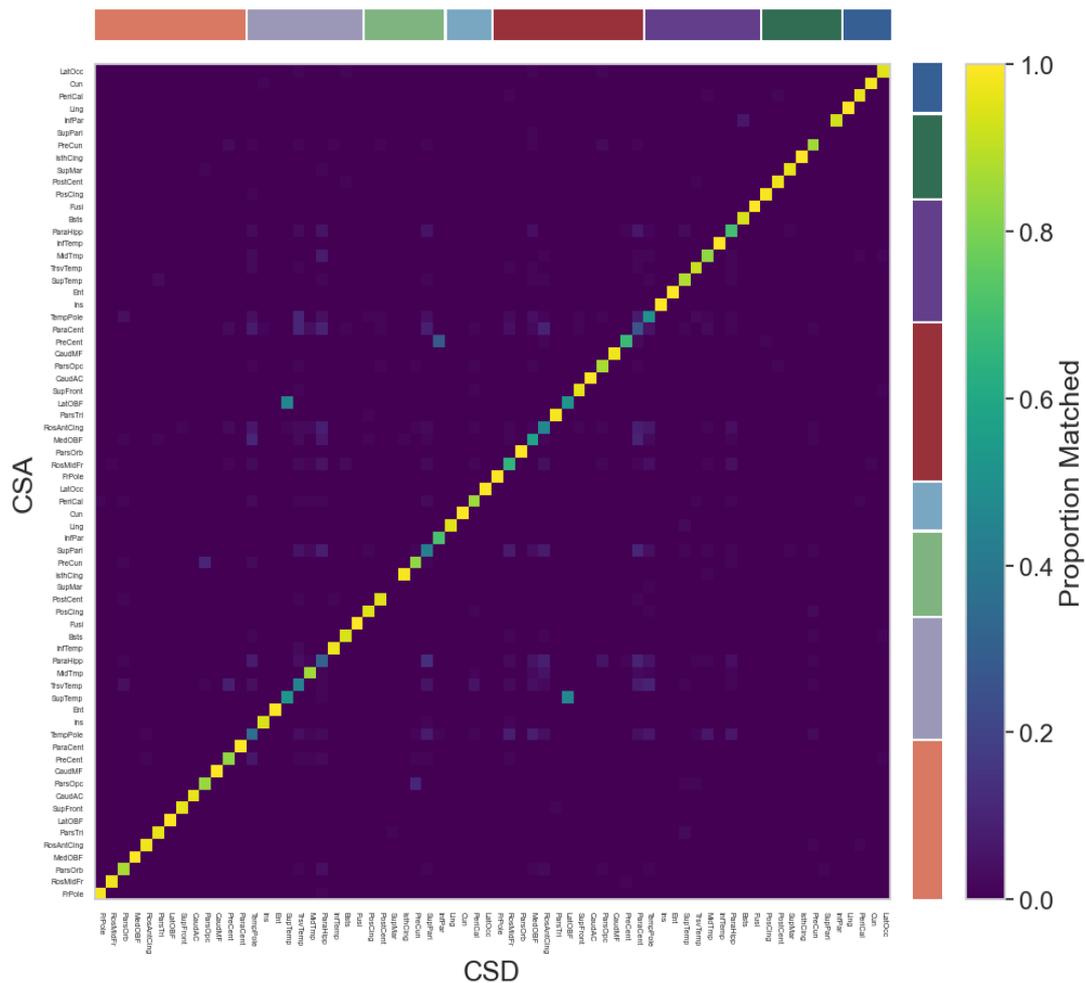


Figure 21. Matching matrix for CSD and CSA DTI graphs. Each voxel represents the percentage of participants who matched the area on the CSD axis to the area on the CSA axis. The diagonal represents ‘accurate’ matches (i.e. both parcels are the same). The matrix has been thresholded using the 99th percentile of a generated null distribution.

Figure 22 shows the results of the graph matching for each frequency band against the DTI (CSD) connectomes. After thresholding against a null distribution, they illustrate a lack of accurate matching. The matches that survive permutation correction are inconsistent across participants. The highest proportion matched for any pair is 0.2 - 20% of participants. In short, each of these parcels were just as likely (given the values and standard deviations in **Table 3**) to match another parcel as they were their analogue on the other graph.

	Accurate Matches Median (SD)	Inaccurate Matches (Median, SD)
Theta-MVAR \Leftrightarrow DTI	7.14% (1.48)	5.95% (3.48)
Alpha-MVAR \Leftrightarrow DTI	8.33% (4.23)	5.95% (4.04)
Beta-MVAR \Leftrightarrow DTI	7.14% (3.92)	4.76% (4.03)
Gamma-MVAR \Leftrightarrow DTI	7.14% (4.48)	5.95% (3.73)
Mean	7.44% (3.53)	5.65% (3.82)

Table 3. Matching accuracy across graphs in **Figure 22** averaged for accurate and inaccurate node matches. Accurate matches are those surviving permutation across the diagonals of the graph, inaccurate matches are the other voxels in the matrix. Median was used as the groups are not equally matched across graphs (due to differences in null distribution) and between diagonals and the remaining cells.

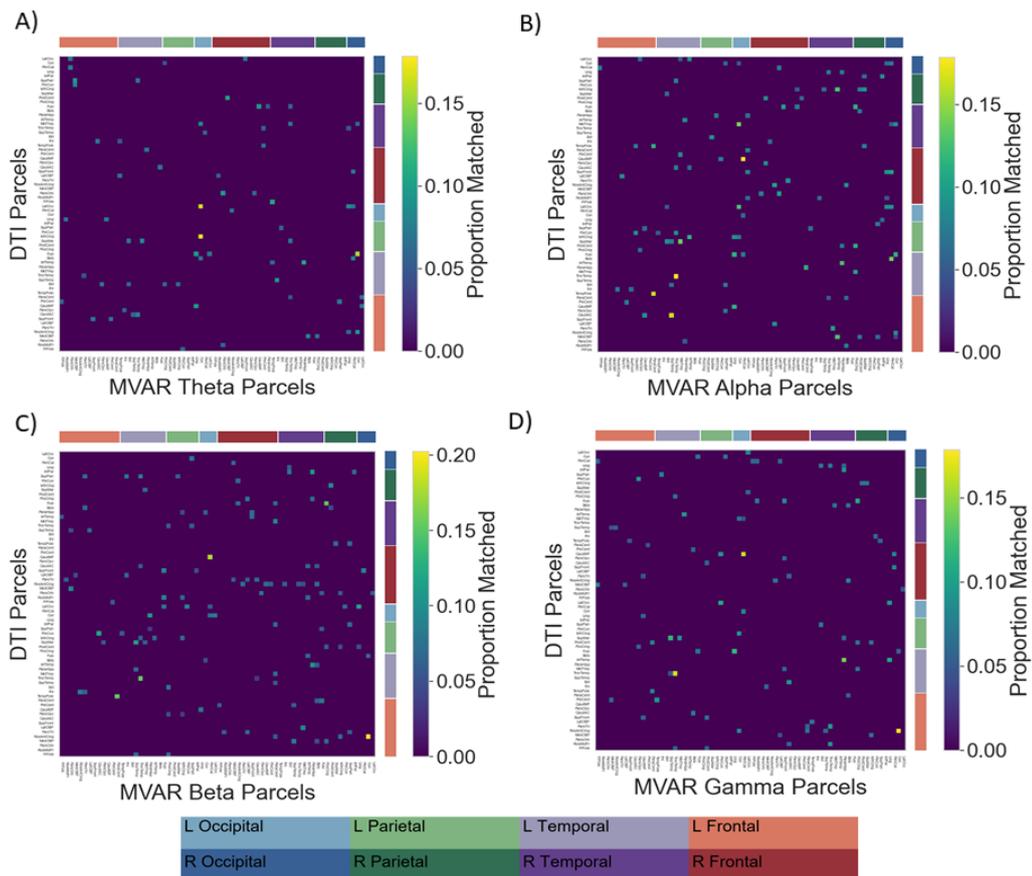


Figure 22. Matching matrices for DTI (CSD) against MVAR graphs. Each voxel represents the percentage of participants who matched the area on the DTI axis to the area on the MVAR axis. The diagonal represents 'accurate' matches (i.e. both parcels are the same). Each matrix has been thresholded using the 99th percentile of a generated null distribution. **A)** Represents the MVAR graphs with a individualised peak Theta frequency (1-7Hz), **B)** Represents the Alpha graphs (7-13Hz), **C)** Represents the Beta graphs (13-30Hz), and **D)** represents the Gamma graphs (30-75Hz).

Linear Model

The GLM models produced for MEG and DTI data indicate that the connections and areas related to children's age, IQ and SES differ between these structural and functional methods of imaging. This difference is best summarised in **Figure 23**, which shows the parcel-degree of betas for both models side-by-side.

The direction of the beta weights was the same for all contrasts, with an increase in the predictors leading to an increase in connectivity. The analysis revealed no connections or parcels that decreased with the effects.

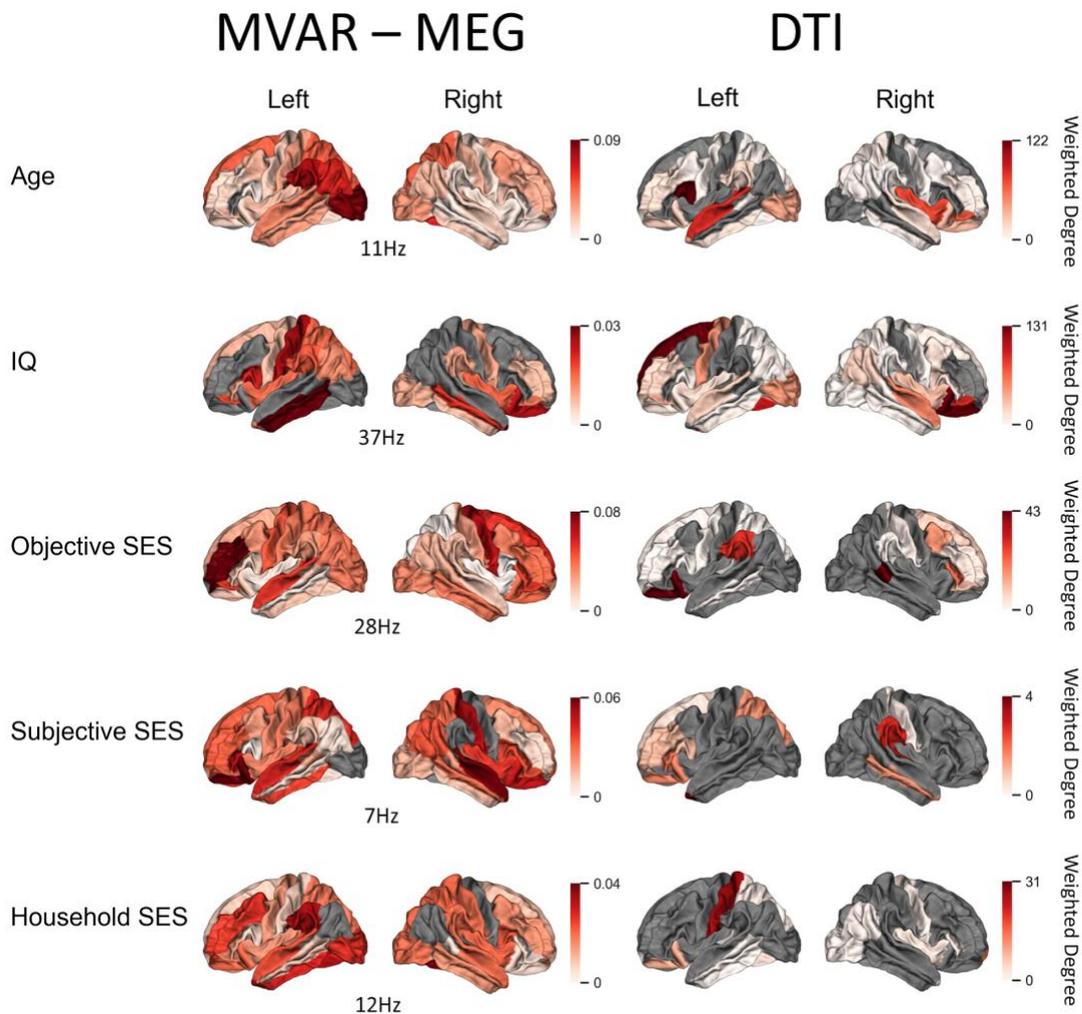


Figure 23. Comparison of MEG-MVAR and MRI GLM Models. Weighted degree is the sum of beta values connected to each parcel for each contrast in the model. Connectomes for the MEG-MVAR selected by peak frequency. Beta values for MVAR-MEG are on the scale of Partial Directed Coherence values, and values for DTI are on the scale of streamline count.

The adjusted R values for the MVAR model (i.e. how much variance in the MVAR connectome did all the combined predictors explain) had a mean of 0.764 and a standard deviation of .049. For the DTI model there was a mean of 0.281 with a standard deviation of 0.249.

The relative variance explained by the connectomes for each regressor is shown in **Table 4**. This shows that the MEG-MVAR connectomes account for the highest unique variance over all contrasts, and that the majority of variance explained by the MRI-DTI connectomes is shared with MEG-MVAR.

Contrast	<u>Unique Variance</u>		<u>Shared Variance</u>
	MEG-MVAR	MRI-DTI	
<i>Age</i>	57.06%	1.66%	18.62%
<i>IQ</i>	46.79%	1.26%	20.51%
<i>Objective SES</i>	34.24%	6.39%	17.7%
<i>Subjective SES</i>	42.88%	2.97%	27.92%
<i>Household SES</i>	47.35%	0.3%	13.64%
Mean	45.66%	2.51%	19.68%

Table 4. Unique vs shared variance comparison for MEG-MVAR and MRI-DTI connectomes. Values are calculated from contrasts of R^2 values from OLS models. Unique variance is the residual R^2 when R^2 value from other predictors are subtracted from the multiple regression model. Shared variance is the R^2 not accounted for by unique variance in the multiple regression model. These OLS models are constructed for the purpose of comparing scan types using output from a lower level GLM, as such these R^2 are only valid for comparing scans, not explaining total variance.

Table 5 contains the results of the formal comparison between the differences in each model type against each predictor. The MEG-MVAR variables were significantly greater explained by the predictors across all but the Subjective SES values. This is likely because the highest shared variance between DTI and MEG-MVAR occurred here.

One possibility is that the MEG-MVAR connectomes are less dense than the MRI-DTI connectomes, therefore offering artificially higher explanatory power by nature of connection count rather than the scan methods itself. To formally address this, I replicated the analysis reported in **Table 5** with density matched connectomes. For each participant I dropped connections in order of strength (starting with the

lowest) until the sample density matched between MEG and DTI. The rest of the analysis was identical. The outcome reported in **Supplementary Table 1**, that the results are extremely close (the average should be less than <1% difference), making this explanation of the difference unlikely.

As there are many ways you can create a DTI connectome (Petrov et al., 2017), I also investigated if the way of calculating DTI would change the variance explained. I replicated the entire analysis of DTI data (including GLM and permutation testing), but using the Q-ball Constant Solid Angle (CSA) method (Aganj et al., 2010) to generate the DTI connectome instead of the CSD method used before. I also mean-normalised each participant's connectome by parcel. This produced the figures **Supplementary Table 2**. Despite a slight decrease in DTI-explained variance, the general pattern remained the same. Suggesting different methods are unlikely to explain the differences in models reported here.

	<u>Total Explained Variance</u>		<u>T-test</u>	
	MEG-MVAR	DTI	T value	P value
<i>Age</i>	61.45%	20.29%	4.398	<.001 *
<i>IQ</i>	56.82%	21.7%	3.739	<.001 *
<i>Objective SES</i>	53.23%	24.08%	2.967	.004 *
<i>Subjective SES</i>	54.29%	30.89%	2.509	.014
<i>Household SES</i>	47.89%	13.94%	3.815	<.001 *

Table 5. Comparison of predictive ability for each predictor. T test indicates whether the difference in explained variance is significant. (*) indicates significant differences adjusted for multiple comparisons.

2.5.5 Interim Discussion

In a high-level model comparison, I found that the functional MEG connectomes explained more unique variance in every predictor than the structural DTI connectomes. The shared signal with the MEG connectomes explained the majority of DTI's explanatory power. These results are unchanged even when the density of the MEG connectomes is matched to the DTI connectomes, and when a different method

is used to process the diffusion images. This suggests that the combination of MEG and MVAR models have greater capability in representing variance in the Age, IQ, and SES of children, than structural DTI scans.

Despite the finding that MEG and DTI connectomes share explanatory variance, I did not find overlap in the topological structure of these networks in the graph matching attempts. This suggests that the networks formed by white matter produce electrophysiological activity in a non-linear way, with the structural hubs not necessarily mapping onto functional hubs. Or perhaps MEG is more susceptible to poor source localisation when we work with children, and whilst it captures the variance properly, the spatial domain is somewhat warped.

One potential reason for the matching failure could be the large parameter space in which we can tweak the scans before matching. Osmanlioğlu et al. (2020) investigated this systematically and found varying levels of consistency *in a single participant* depending on the methods used to generate the connectomes. It may simply be the case that I did not find the correct combination of parameters to optimise matching across participants. However, the procedure was repeated with different forms of connectomes, and different thresholding methods (including binarizing the network), and this produced very similar results. This suggests that there is very little linear relationship between electrophysiological connectivity at specific frequencies and white tracts across the brain.

Figure 23 shows the topographical comparison for each predictor in one figure and amplifies the point that this lack of matching likely extends to the patterns predicted in the GLMs. This was surprising, given the observations earlier in this chapter that areas like the right STS and calcarine sulcus appeared regularly. However, the matching algorithm's focus on global minimisation may mean that these effects are lost.

2.6. Discussion

For both MEG functional and DTI structural connectomes I found significant patterns of predictor-related connectivity for every regressor in each connectome type. I also report that the strongest hub areas in these patterns differ between connectome types, with little topological overlap between scanning modalities. When the MEG functional analysis was replicated with a dimension reduction step, the resulting global

networks also differed in their predictive ability from the areas identified earlier. Whilst I am the first to carry out a parallel connectomic analysis of this type in children, the findings are consistent with some aspects of previous research. An exhaustive list of connections with interpretations is unlikely to be the most fruitful way forward. Instead, of exploring these connections individually, I focus on potential explanations for the highly connected hub nodes, and the broad patterns identified in the PCA networks. As discussed, some of these interpretations are unfortunately tempered by the volume of significant connections and areas in the more granular approaches. Whilst the reduction techniques had some success in improving this, the issue is somewhat inherent to the approach. Readers will be pleased to know that the next two chapters use task-based analyses and are therefore far simpler to interpret. However, there are several important simple conclusions that we can draw from the current chapter, for example, the failure to statistically match the connectomes on global patterns, and that despite this failure, there is a reasonable proportion of shared predictive power.

2.6.1 MEG connectomes are more sensitive to SES associations than DTI connectomes

When comparing the different connectome properties. One of the interesting observations is in the relative difference in SES weightings between modalities. Previous research shows SES impacts cognition, mental health and school performance across the board (Dalmaijer et al., 2019). So, I was not surprised to find significant effects here. The MEG models were sensitive to Objective, Subjective, and Household SES scores — with **Figure 3** showing long tails with high t statistics. Whereas the DTI model furnished relatively low t statistics — with **Figure 13** having relatively shorter tails. This is surprising as there are several studies characterising the *structural* impact of poverty and SES on the brain (Brito & Noble, 2014; Kim et al., 2019; Piccolo et al., 2016; Romeo et al., 2018), and none I could find looking at topological connectomic patterns *in MEG*. Whilst this may reflect basic scanner availability, I did not predict this apparent difference in sensitivity. This relative efficacy in modelling SES suggests the MEG-GLM method has high untapped potential for researchers wishing to model the impact of the socioeconomic variables on the brain and makes an excellent method moving forward in this thesis.

Whilst results here seem consistent with some previous research, there are also patterns in the contrasts that conflict with previous research. For instance it would have been reasonable to expect frontal topology relating to IQ in the electrophysiological connectome (e.g. Luo & Zhou, 2020). However, there was no clear lobe-dominance in the weighted degree of parcels (**Figure 4**), and I found no hub-parcels that were in the top 10th percentile of contrasts. Similarly, the Gamma component network that was found to correlate with IQ had no lobe dominance. One potential reason for this, is that the participants were not performing any task in the scanner as it was a resting state study. It is possible to form task related MVAR connectomes, where I would expect to see IQ related activity. Despite this apparent lack of clear topological pattern, the MEG model did explain relatively more unique variance than the DTI model in the IQ domain, so perhaps it was sensitive to more distributed network activity that did not translate clearly to topology.

Beyond simply investigating the connectomic properties of these scans in relation to SES, another purpose of this thesis is to investigate task-based neurophysiological processes. It is clear from this data that MEG is an excellent scanning modality going forward, however resting state scans and structural data only tell part of the story. Whilst this type of data can be used to measure task-related networks (Beckmann et al., 2005; Smitha et al., 2017), measuring brain activity during tasks is much more compelling. In the following empirical chapters I present data on a passive phonological oddball task (Chapter 3) and an active visual working memory task (Chapter 4). These tasks roughly relate to two groups of areas that seemed to re-appear in the present analysis: those in the temporal lobe, and those showing occipital-frontal-parietal connections. I caution in the interim discussions about over-interpreting single connections; however, I have chosen these areas as they are consistent across analyses and have previously been observed in the literature. I expand on this below.

2.6.2 The superior temporal sulcus and SES

One parcel that appears in both the DTI connectomes (**Figure 17.B** - right banks STS) and the MEG connectomes (**Figure 6** - right banks STS and Beta) is the superior temporal sulcus. Specifically, the upper banks of the sulcus. DTI connections to this area increase with Objective SES, and with Subjective SES in MEG. As discussed above, this is entirely consistent with the broad engagement it has with various

functional networks (Hein & Knight, 2008). Most relevant of these functional networks to SES, are those supporting speech and audiovisual integration — relationships with the STS and language are commonly observed in MEG studies (Gutschalk et al., 2015; Maess et al., 2006; Nourski et al., 2021; Peretz & Lavidor, 2013; Scharinger et al., 2016). Furthering this connection between SES and language processing, the temporal lobe in general seems to reoccur in the data in relation to SES. The second subjective SES frontal node in the MEG results (**Figure 7**) has its highest weighted connection to the superior temporal gyrus - an area closely involved in phonetic encoding (Mesgarani et al., 2014) and phonological processing (Buchsbaum et al., 2001). This area's involvement in language processing, and the banks of STS involvement in integration between spoken and visual elements of language (e.g. Ethofer et al., 2013) makes the inclusion of some language processing MEG task promising. The inclusion of this task is also commensurate with the language route – outlined in Chapter 1 – through which SES impacts outcomes in children. This route specifically involves temporal areas (Brito & Noble, 2014).

2.6.3 Areas involved in visual attention and SES

Posterior networks around the temporal lobe and sensory cortices occurred frequently in 3/4 PC networks in the PCA section. These networks also seemed to be associated with the various SES measures. The Beta PC network, related to Subjective SES, had many connections originating, or ending in the occipital lobe (**Figure 10.D**). Beta frequency in the visual pathways (lateral geniculate nucleus => V1 => V2 => higher areas) has been established as a carrier for visual attention, where bursts of beta match with visual attention and enhance visual field representation in the visual cortex. This has been shown both in invasive animal models (Buschman & Miller, 2009; Wróbel, 2000) and in humans (Kamiński et al., 2012). By a considerable margin, the strongest weighted degree of any node-predictor grouping in the MEG analysis was the Occipital Lobe and Objective SES (**Figure 4**). In this chapter I also frequently observe reciprocal connections between frontal and occipital areas. In the Beta PC2 network there are several positive connections from the frontal lobes to the occipital lobes, particularly in the right hemisphere (**Figure 10.D**). In the earlier MEG analysis activity in the right frontal pole node relating to Subjective SES (**Figure 7**), we see clear two-way connectivity to the pericalcarine sulcus and lateral-occipital gyrus. In that same section the pericalcarine sulcus node related to Objective SES, we see incoming

connections from the bi-lateral orbitofrontal cortices (**Figure 9**). The frontal lobes are associated with *both* top-down and bottom up stimulus-driven attention (Corbetta & Shulman, 2002; Ridderinkhof et al., 2004; Wang et al., 2010). Taken together, the reciprocal connectivity between all these areas, associated with different SES metrics, implies some relationship between SES and the circuitry underlying visual attention and perhaps even working memory. Or perhaps the correlation between visual-attention networks activation and the SES measures could be partially explained by visual-imagery during the scan. Despite participant's being instructed to not focus on anything, it is possible some children were visualising something during rest. This propensity could also be correlation with SES. Yet this type of imagery is still likely to involve some visual-attention capacity, especially with the appearance of occipito-frontal connections.

The findings here could be consistent with research exploring the development of visual processes and SES. For instance preferential looking experiments in infants have found that SES predicts attention towards salient features (rather than just the object) (Werchan et al., 2019). Rosen et al., (2019) connect this attention relationship to pathways between the occipital visual association cortex and the prefrontal cortex. In an older sample, Leonard et al., (2015) have shown that low-SES correlates with poorer visual working memory in adolescents, and that this is not the case for other memory types. They also showed that the same low-SES children had lower pre-frontal cortex volumes. This body of research makes investigating visual attention and working memory a particularly promising area, something I follow up in Chapter 4.

Overall, I believe these results provide support for the use of whole-brain network construction models (MEG-MVAR) in developmental samples and the use of linear models to analyse these networks, in relation to demographic and cognitive covariance. It also evidences the strength of MEG scans in general for capturing interesting variance. Finally, the results reported here build upon previous research into topological associations between SES, fluid intelligence and age-related changes in the brain. Furthermore, they provide me with direction in next two empirical chapters, which explore the relationship between SES and task-related MEG activity, specifically in the context of phonological processing and visual working memory.

Chapter 3: Phonological Processing and Socioeconomic Status

3.1. Introduction

Chapter 2 focussed on the relationship between SES, the structural connectome, and the functional connectome at rest. In this next chapter I turn my attention to neurophysiological processing which reflects perceptual processing. Whilst the previous chapter explored the impact of SES at the granular network architectural level, this chapter moves more towards context on the middle level – passive processes (see **Figure 2** for a summary). I focus on the neurophysiological response associated with the passive mismatch negativity to changes in language stimuli. But why would this be important? The ability to decode sound structures within language – sometimes called phonological processing – is a key building block for language acquisition (Torgesen et al., 1994; Vihman, 1996; Wagner & Torgesen, 1987) and becoming a skilled reader (Wagner et al. 1997). Behavioural measures of language proficiency, reading ability, and phonological processing are all highly related to each other (Nation & Snowling, 2004). This broad category of phonological processing can be sub-divided into lower-level abilities: phonological awareness, phonological/verbal working memory, and phonological retrieval (Wagner & Torgesen, 1987). Here, I focus on the lowest level, *phonological awareness*, which describes the degree to which an individual can perceive, judge, and utilise constituent sounds of language (Hulme et al., 2005).

3.1.1 SES and language development

In terms of effect size, one of the strongest relationships between SES and cognition is present for language development (Bus et al., 1995; Pungello et al., 2009). Children who grow up in low-income households are more likely to have poorer language skills as an adult (Schoon et al., 2010), show poor reading ability (Buckingham

et al., 2014; Noble et al., 2006) and perform poorly on tasks that require phonological awareness (Noble et al., 2005, 2006, 2007; Whitehurst, 1997). A recent study by Dolean et al. (2019) drew on a sample of 322 children facing severe poverty in the Roma community and contrasted it with 178 non-Roma children. This study illustrated the core problem: low SES directly negatively impacts reading development, as well as all variables that contribute to it, such as school absence, rapid automatised naming, phonological awareness, letter knowledge, and non-verbal IQ.

As discussed in the General Introduction, Noble et al propose that SES impacts development through two parallel paths (Noble et al., 2012; Ursache & Noble, 2016). The first impacting a child's language skill through the linguistic environment at home. The second impacting a child's self-regulatory ability, memory, and socio-emotional skills. The approach taken in this chapter firmly falls within the first strand, and the next chapter will fall within the second strand.

In more recent work, Younger et al. (2019) reveal that greater maternal education (ME) (an element of SES) is associated with different patterns of brain lateralisation in 5-year-olds. Increased ME was related to higher brain lateralisation towards the left inferior frontal gyrus. Furthermore, this interacted with phonological awareness performance, such that performance was related to a leftward bias in the superior temporal gyrus in low ME children, but with a rightwards bias in high ME children. These results suggest that an SES factor (maternal education), is associated with actual neural recruitment during language processing – supporting the concept of an SES-moderated language developmental path in the brain.

Based on this prior work, it is therefore uncontroversial that phonological skill, and related processes, are influenced by a child's socio-economic status (SES) (Hoff-Ginsberg, 1998; Pungello et al., 2009). As alluded to above, there are many possible mechanisms by which a child's environment could influence this set of processes. One possibility is that SES is associated with the ability to discriminate word-like sounds. I test this in the present chapter, by measuring the neurophysiological response to passively perceived sound structures using Magnetoencephalography (MEG). Specifically, I look at the response to irregular word sound structures against frequent non-word sounds – representing sensitivity to the words. I investigated at which *time-points* and *locations* in the information processing stream this neurophysiological process is influenced by a child's SES. My whole brain/sensor analysis approach allows us to build

on the *a priori* area selection findings from work such as Noble et al. (2006) and Younger et al. (2019), by potentially revealing new areas that relate to SES. Furthermore, as SES captures such a variety of factors, I also split my measures into two aspects: one reflecting the absolute financial means available to the child's family, and another using a subjective rating of the family's means. Previous work has shown that subjective and objective measures of SES make independent contributions to children's executive functions, stress and cortisol (Ursache et al., 2015).

3.1.2 Phonological oddball paradigm

It is helpful to characterise the utility of the oddball paradigm for this type of research. An oddball tasks consist of sequences of repetitions of a "standard" stimulus, interspersed with infrequent deviant stimuli. Comparing the neural response of the subject's brain to frequent and infrequent stimuli provides a measure of whether and when those stimuli are detected as different by the brain (Dehaene-Lambertz & Gliga, 2004), independent of whether they were attended or consciously perceived (Schröger, 1997). The observed difference in response between standard and deviant stimuli ("mismatch signal") relies on networks of neurons adapting to a repetition of input by suppressing their activation, and then releasing from this adaptation when a change is detected (Naccache & Dehaene, 2001). In MEG and EEG, this signal leads to a negative peak at roughly 200ms, termed Mismatch Negativity (MMN), and later components such as the P300, which is associated with further semantic (Meador et al., 1987) and attentional processing (Bennington & Polich, 1999).

Oddball experiments have been deployed by researchers to investigate the underlying mechanisms of phonological awareness in both children (Cheour et al., 2001; Korpilahti et al., 2001; Linnavalli et al., 2017) and adults (Näätänen, 1990). Additionally, a large literature investigates specific conditions, for example: autism (Oram Cardy et al., 2005), dyslexia (Wehner, 2007), Developmental Language Disorder (Shafer et al., 2005), or community samples, such as poor readers (Bernal et al., 2000). In contrast, there is little research on the impact of SES on oddball-evoked responses, especially in typically developing children. One study utilised a visual oddball (i.e., a novel picture in a stream of standard shapes) in a group design, with 26 subjects aged 7-12 years, split between low-SES and high-SES groups. It found attenuated early mismatch responses, but no SES-related P300 differences (Kishiyama et al., 2009). The inclusion of only 13 children

in each group of this study potentially obscures any subtler relationships between the mismatch effect and SES. In fact, developmental auditory oddball studies often have smaller sample sizes and/or group designs that potentially limit sensitivity, for example: Korpilahti et al. (2001) N=10, Lovio et al. (2009) N=17, Cao et al. (2008) N=12 per group, Bakos et al. (2016) N=14 and N=15 in each group, Orinstein & Stevens (2014) N=18 and N=20 in each group.

In the current chapter I tested whether the neurophysiological mechanisms by which simple word-like sounds are distinguished varies according to a child's SES. I used a passive oddball task to test this. Children sat in the magnetoencephalography (MEG) scanner whilst watching cartoons. During their viewing they listened to a sequence of sounds containing carefully matched oddball words and non-words alongside fillers. The children also took part in a structural MRI scan, allowing attempted localisation of the MEG activity to a brain model created from their scan.

I used a GLM that included behavioural and demographic variables to predict evoked neural activity in three dimensions (time and 2D space) during the phonological oddball task. This tests how variance across the whole group predicts the underlying neural activity, as opposed to the limited single contrasts in group designs. This GLM allows for a data-driven approach, asking whether a child's SES is associated with their neurophysiological response to carefully matched words, and crucially, if so, *when* this influence occurs. One possibility is that SES will covary with the earliest neurophysiological response to an oddball Korpilahti et al. (2001). Alternatively, it may covary with a later processing stage more likely to reflect order, semantics or attentional processing (Bennington & Polich, 1999; Hill et al., 2004; Meador et al., 1987). My GLM will enable me to detect either, or both effects, if they exist.

As this Chapter's analysis was undertaken before the larger group reported in the preceding chapter was recruited, the approach to SES characterisation is slightly different. Rather than a PCA, SES was characterised using equivalised household income as an objective measure, and parent's self-reported SES as a subjective measure. Parental education level is another potential metric used within the literature, but it has relatively few levels (high school, university degree, higher education) by comparison with the other SES metrics. Relative to the whole sample, there was a wider array of behavioural data available: measures of educational attainment in reading and maths, and cognitive measures of working memory, verbal skills, and general IQ. These were

also incorporated within the GLM, to test whether these individual differences were also associated with the phonological processing of word oddballs, independent of socioeconomic status.

Based on the literature, and the data available in the previous chapter, I can ask some informed concrete questions:

- 1) Will the evoked response to words relative to non-words be predicted by SES?
- 2) Will this response be localised to temporal areas, in-line with MEG results in the network chapter?
- 3) Will there be a differential prediction between the two SES factors – Income and subjective SES?

3.2. Methods

3.2.1 Participants

A total of 82 participants took part in this study, conducted at the MRC Cognition and Brain Sciences Unit. This was a sub-set of the larger sample in this thesis, collected at an earlier time point. Due to technical problems with the scanner (4 children), attrition between sessions (2 children), and children opting out of either MRI or MEG (5 children) only 71 full datasets remain. There were two visits for each child, on the first, behavioural measures were collected and then a MEG scan took place. On the second (which was optional) the participants had a structural MRI. There was no more than a month between visits.

The mean age of the children was 9 years and 11 months (range: 6y 11.6m - 12y 9.3m). I computed the average net household equivalised income, which is income after tax deductions and benefit additions, weighted by number of children and adults using OECD equivalence scale (Anyaegbu, 2010). This was £24,313 on average, with a standard deviation of £12,261, ranging from £5,747 to £66,666. The sample was thus socio-economically diverse, but of lower means than the UK median at time of testing (£31,876), 2017/18. In fact, 26.8% (22 children) were living under the UK poverty line –classified as 60% of the median income or less (*Households below average income* 2018). All the families live in the Cambridge and East Anglia area, where the cost of living is high

by UK standards, so it is likely that this statistic underestimates the proportion living below the poverty line.

The age range was from just under 7 years old to just over 13 years – a wider range than previous studies such as Kishiyama et al. (2009). This may allow us to capture more developmental changes. Additionally, it expands on the phonological electrophysiology literature that focuses on earlier ages (<5 years) when these systems are just developing.

A questionnaire was given to parents to ascertain subjective SES, obtained by having caregivers place a cross on a ladder of 10 rungs, with the top representing those who were better off in the UK, and the bottom representing those the worse-off. This is a frequently used measure of subjective SES (e.g. Ostrove et al., 2000; Singh-Manoux et al., 2005).

3.2.2 Procedure

Volunteers and their families took part in all research sessions at the Medical Research Council Cognition and Brain Sciences Unit, University of Cambridge. Parents provided written informed consent, and children provided verbal assent. The study was approved by the Psychology Research Ethics Committee at the University of Cambridge (Reference: 2015.11).

3.2.3 Behavioural Measures

Children and their families visited the Unit for a battery of educational attainment and cognitive assessments. These included: Mathematics and Reading Fluency scales from The Woodcock-Johnson III Form B Tests of Achievement (Woodcock et al., 2001), the Matrix Reasoning and Vocabulary sub-tests of the Wechsler Abbreviated Scale of Intelligence (WASI-II) (McCrimmon & Smith, 2013), and the Automated Working Memory Assessment (AWMA) (Alloway et al., 2008), and the Phonological Assessment Battery (PhAB) (Gallagher & Frederickson, 1995).

3.2.4 Phonological Oddball

MEG Scan

During the first visit, neuroimaging data was acquired on a high-density VectorView MEG System (Elekta-Neuromag) with 102 magnetometers and 102 orthogonal pairs of planar gradiometers (306 sensors in total). Head Position Indicator (HPI) coils were attached to the child's head (one on each mastoid bone, two on the child's forehead, and one on the top of their head). A 3D digitiser was used to record the positions of each HPI coil, and a number of scalp points (50+) in order to assist in co-registration of MRI scans. To capture eye-movements and blinks, vertical and horizontal electrooculograms (EOG) were measured with a pair of electrodes to the side of each child's eyes, and another pair placed above and below the left eye. To record heart rate, an electrocardiogram (ECG) was taken with electrodes attached to each wrist. Audio was presented to the participants using in-ear earpieces attached to a long plastic tube that went outside the MEG's shielded room, where they were attached to the speaker and amplifier. This minimised the impact of any electrical signal from audio amplification and production.

MRI Scan

During separate visit, participants took part in an MRI scan, which yielded T1-weighted images from a Siemens 3T Tim Trio system. For these images, a Magnetisation Prepared Rapid Acquisition Gradient Echo (MP RAGE) sequence with 1mm isometric image resolution, 2.98ms echo time and 2250ms was used.

Task

Three auditory stimuli were used: a novel pseudo-word frequent ('boak'), a known word oddball ('boat') and a novel pseudo-word oddball ('boap'). The ratio between these stimuli was 6:1:1, i.e. one of each oddball for every six frequent stimuli. The task started with a train of 10 standard stimuli, so that participants could habituate to the frequent non-word. There were 1200 trials in total (900 non-word standard, 150 word oddball, 150 non-word oddball). In a pseudo-random manner, there were either 2, 3, 4, or 5 standard non-word stimuli between deviants. The inter-stimulus interval (ISI) was 800ms from the offset of one stimulus to the onset of the next.

The stimuli themselves were taken from (Hawkins et al. 2014). All words had identical first consonant-vowel, /boʊ/ ('boa'), which was spliced from natural spoken word taken from speaking the word /boʊt/ ('boat'). For each stimuli this sound was then cross-spliced with a voiceless-top consonant, that was either: /k/ to make standard non-word /boʊk/ ('boak'), /t/ to make oddball word /boʊt/ ('boat'), or /p/ to make oddball non-word /boʊp/ ('boap'). The first consonant-vowel was acoustically and coarticulatory identical until the final stop vowel, and peak sound energy was equated across all stimuli. This meant that the ability to perceive the sounds as different only happened at the last phoneme, which should target as exclusively as possible the systems underlying phonological awareness.

During the oddball task, all children watched a cartoon (Tom and Jerry: The Classic Selection Volume 1) (Takeda & Kimura, 2014), without any audio. This particular cartoon had the benefit of not having any moving mouths for speech – so visual speech cues would not confound or convolute signal from the auditory cortex (Sams et al., 1991). It also kept the children relatively entertained during the scanning session.

3.2.5 Analysis

Data was analysed primarily with the MNE-Python toolbox v0.19 (Gramfort et al., 2013) on CentOS Linux.

3.2.6 Preprocessing

Raw data underwent Signal Source Separation (SSS), Temporal Extension (SE), and movement compensation using Maxfilter 2.2. These data were loaded into MNE-Python and then high-pass filtered at 1Hz and low-pass filtered at 50hz. To remove noise associated with heart beats and blinks, a two-stage Independent Component Analysis (ICA) denoising procedure was used. An ICA was done using *fastica* with 25 components specified. Stage 1 involved automatic rejection of components that correlated with ECG or EOG electrodes more than 0.3. Stage 2 involved manual checking of excluded component topography, and selection of components to exclude for participants with insufficient ECG or EOG electrode signal. Data for each child was visually checked before and after to ensure the components were not present still.

Raw data were then epoched between 200ms before and 1000ms after the presentation of auditory stimuli. As participant data was split up into two runs, these were processed separately until epoching, where epochs were concatenated and treated as one after this.

3.2.7 Source Localisation

FreeSurfer (Fischl, 2012) was used to construct whole brain surface from MRI scans, using the recon-all command. A single layer Boundary Element Model (BEM) of the inner skull was constructed using the MNE watershed method. A source space was made using the cortical surface from the FreeSurfer output. The inverse model consisted of this one-layer BEM, and the method used to invert the evoked signals was the MNE toolbox's implementation of dynamic Statistical Parametrical Maps (dSPM), with empirical whitening done using a noise-covariance matrix taken from the baseline period, which I found to produce the most consistent results. Participants who lacked an MRI or moved too much during the MRI scan had models created using FreeSurfer's FSAVERAGE model.

3.2.8 Behavioural Statistical Analysis

There was a large number (12) of likely highly correlated behavioural measures. This multicollinearity makes using the predictors in the later GLM inappropriate. Consequently, these were reduced to separate components using Principal Component Analysis (PCA) with orthogonalisation through varimax rotation. Behavioural variables (Woodcock-Johnson III sub-tests, AWMA, and WASI-II) were reduced to 3 factors, which I labelled Working Memory & Executive, Classic IQ, Verbal Short-Term Memory (STM) & Working Memory (WM) – these were chosen as plausible factors based on previous work (Alloway et al., 2005) and explained 45.5% of total variance. Education (the Woodcock-Johnson III measures) was subject to a separate factor reduction. Parallel analysis revealed that in the best solution WJ Reading and Mathematics was a single factor solution, explaining 47.8% of variance in those scores. The factor weightings can be seen in **Table 6**. Even though the WJ were used to derive a single factor, I show correlations between all the components/factors and the scores. You can see that the WJ scores correlated with some of the other three factors, however they did not contribute to those factor scores.

We did not include scores from the PhAB alliteration measure, this task was too easy for children of this age, without phonological awareness difficulties. Fifty one out of 71 (70.4%) of the children answered all items correctly, so the measure showed little variance. I used age standardised (WASI t scores, AWMA & Woodcock-Johnson standard scores) scores in all of the analyses, with age in years then added as a covariate in the later GLM, such that age would be independent against all measures.

	Working Memory & Executive	Classic IQ	Verbal STM & WM	Attainment
AWMA Digit Recall	-0.05	0.23	0.71	0.24
AWMA Dot Matrix	0.62	0.02	0.00	0.00
AWMA Mr X	0.60	0.36	-0.03	0.02
AWMA Backward Digit	0.17	0.28	0.50	0.12
WASI Vocabulary	0.02	0.74	0.26	0.36
WASI Matrix Reasoning	0.42	0.59	0.19	0.28
WJ Reading	0.10	0.48	0.36	0.50
WJ Mathematics	0.24	0.33	0.34	0.45

Table 6. The factor weightings for each of the component scores extracted. This is shown as each component variables Pearson correlation with the factors. The WJ subtests were used to derive the 'Attainment' component, but excluded from the other components - correlations across all components and scores are still included for completeness.

3.2.9 MEG Statistical Analysis

Comparison of Word and Non-word contrasts

To investigate whether there was a significant difference between the word and non-word MMN a non-parametric, cluster corrected, two-tailed repeated measures permutation t-test was calculated using the difference field between the two. A connectivity matrix was computed over time and space, and a cluster forming threshold of $t=4$ was also used to calculate the clusters. This was much higher than the critical t of 2 calculated from an effect size (0.28) reported in a meta-analysis of oddball tasks in children (Cheng et al., 2016) with an error probability of .05 and a sample size of 71. The threshold is statistically arbitrary, since it is repeated in each permutation (Friston et

al., 1994) but having a narrower definition of clusters makes them far easier to interpret in terms of their spatial extent. The permutation test produces null-distributions of cluster t-statistics based on shuffling data, which is then compared to the actual observed cluster t-values. This is more computationally demanding than False Discovery Rate (FDR) methods, however it is also more conservative and has the benefit of directly controlling the Family-wise Error Rate, rather than the FDR statistic (Lage-Castellanos et al., 2010; T. Nichols & Hayasaka, 2003). I used a Monte-Carlo p -value of 0.05 to identify significant clusters over 5000 permutations –in other words, clusters identified were in the 95th percentile or higher.

General Linear Model

A mass multivariate General Linear Model (GLM) was constructed to analyse the three dimensional (2D sensor-space x time) average evoked responses for each individual in relation to the behavioural factor scores (in **Table 6**), along with age (in days), equivalised income and subjective SES. This allows us to test how individual's spatio-temporal responses predict their cognitive, attainment and demographic attributes. For the neurophysiological data I used only the Word contrast (i.e. word versus non-word fillers), as this represents the sensitivity to Word phonological forms, rather than the non-Word contrast which is concerned only with sensitivity to sounds unrelated to real words.

A design matrix was constructed with each row containing a continuous regressor of value 1, representing a single participant's word contrast (102 magnetometers in 2D space x 1200 ms time samples), and a single value regressor for each of: Working Memory & Executive Factor, Classic IQ Factor, Verbal STM & WM Factor, Attainment Factor, Age in Years, Equivalised Income, Subjective SES. All regressors were z-transformed (so they were normalised and centred around zero). The final design matrix was thus 71 x 8.

To find the best estimates of the model's betas, I used Ordinary Least Squares (OLS) to minimise the models error terms. This resulted in beta weights for each predictor at each point in time and space. These beta values (and statistics inferred from them) represent the relationship between regressor and evoked response for each timepoint. Larger values reflect a stronger relationship at that spatio-temporal measurement.

We then took a cluster permutation approach to establish inference from the model. The t-values were calculated for each beta value, and spatio-temporal clusters (2-tailed) were extracted from this (as in the previous analysis), and the mean t-value taken. I found that the cluster forming threshold of 4 yielded large numbers of small clusters, so reduced the value to create larger more interpretable clusters before permuting. This was a statistically arbitrary cluster forming threshold of 2.8. As before, 2.8 was higher than the critical t value for an expected effect size of 0.28, based on an oddball meta-analysis of children (Cheng et al. 2016), with a sample size of 71 and an alpha of 0.05.

We then permuted each of the 9 regressors in the model 5000 times (45,000 total permutations), where the rows of that regressor were randomly shuffled, whilst holding covariates constant (so they no longer matched the participant's data), spatio-temporal clusters were re-calculated, and the average t-value taken. This gave a Monte-Carlo distribution for each regressor that was centred at zero, which was compared to the original clusters. Any original (un-shuffled) cluster with a value in the 99th percentile of the Monte-Carlo distribution was kept as a significant cluster.

3.3. Results

3.3.1 Basic mismatch evoked signal

Evoked responses for the non-word frequent, non-word deviants, and word deviants can be seen for all magnetometers in **Figure 24**. This figure is purely illustrative, it shows the evoked signal for each trial-type before subtractions, on a handful of representative electrodes. For reference I identify the beginning of the sound, and the differentiation point (the final phoneme) on all points. Based on the topography of these responses, I selected right and left parietal sensors that showed the clearest apparent auditory evoked topography (the mean of these sensors is also illustrated in **Figure 1**).

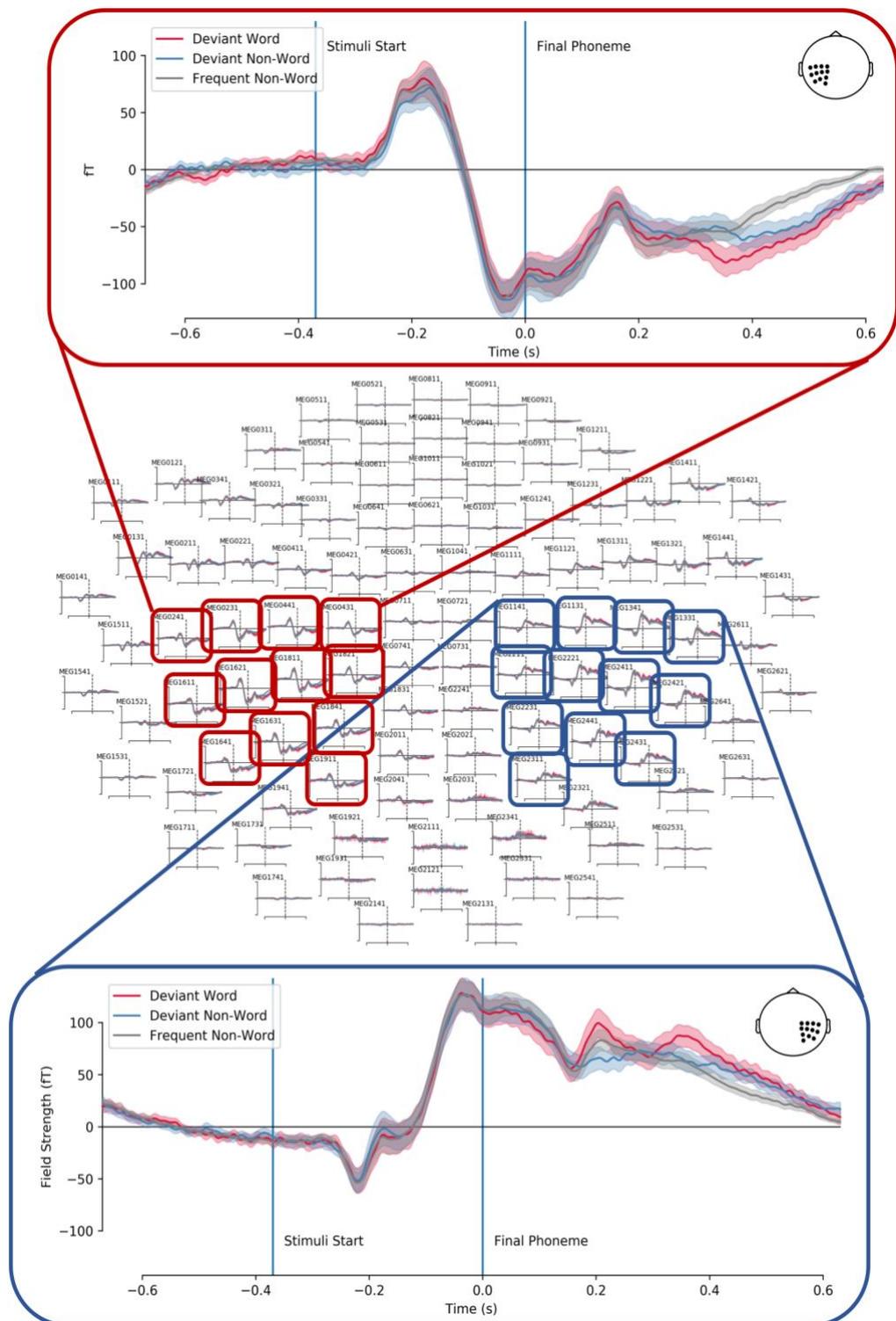


Figure 24. Illustrative topography and time course of the evoked responses for the frequent non-word and the word/non-word deviants. A sub-section of left and right sensors were selected and averaged to produce the time-courses above and below the helmet illustration.

There is a clear auditory evoked component at around 150 ms after the onset of the sound, the direction in power compared to baseline is positive on the right sensors and negative on the left sensors. There appears to be a difference in the evoked responses to the oddballs and the frequent stimuli that begins appearing around 200ms after the onset of the final phoneme, with more pronounced differences by 400ms. To test this statistically, I compared deviant minus frequent subtractions for the words and non-words. All sensors and timepoints were entered into a cluster-permuted t-test, as detailed in the Methods section.

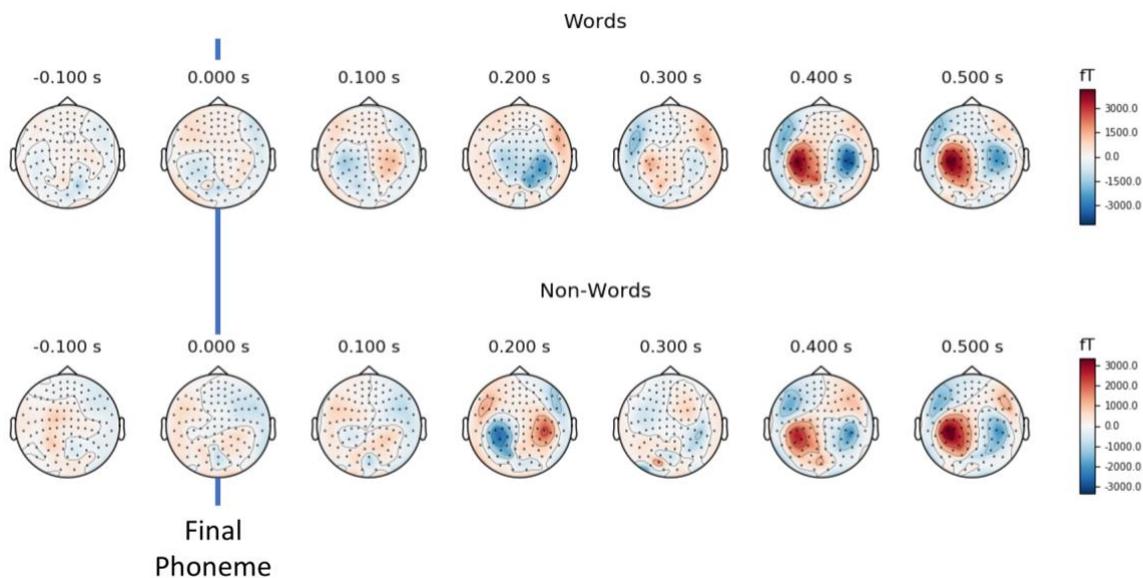


Figure 25. Field Strength topography of evoked contrasts for Words and Non-Words. Final Phoneme is marked with a blue line.

There were clear differences between the two different mismatch contrasts: words (i.e. Word deviants, relative to non-word frequent) and non-word (i.e. Non-Word deviants relative to non-word frequent). In sensor-space the evoked topography for these word and non-word contrasts is plotted in **Figure 25**. There is a clear pattern of left and right parietal activation at the 400ms and 500ms bins, where results are (qualitatively) similar between contrasts. At the 200ms bin, I see a unilateral decrease for the word contrast in the right parietal area, and this pattern is reversed in the non-word contrast.

The binned topography is a very coarse metric. Greater granularity is provided by looking at the spatio-temporal clusters from the cluster-permuted t-test. Four spatio-temporal (I.e. sensor-timepoint) clusters survived permutation testing, these are

illustrated in **Figure 26.a** shows a right-temporal topology with a higher response to word deviants vs non-word deviants at 177-243 ms, **Figure 26.b** shows a left-parietal response in the same direction (Word deviants higher than non-word deviants) higher later at 317-398ms, **Figure 26.c** shows a right-temporal topology with Non-word deviants responding higher in the same temporal pattern as **Figure 26.a** at 170-229ms, and **Figure 26.d** shows a very similar topology and relationship to **Figure 25.c** but later on at 335-401ms. As mentioned above these locations and times are a coarse indication of the ‘true’ effect as I have not permuted these dimensions. More detailed statistics on the clusters are available in **Table 7**.

	A	B	C	D
Mean t-value	0.1480	0.0776	0.0373	-0.1101
Monte Carlo p	0.0004	0.0002	0.0002	0.0002
Number of Sensors	5	13	8	8
Epoch Start Time (ms)	177	317	170	335
Temporal Extent (ms)	66	81	59	66

Table 7. Statistics for the evoked cluster. Mean T-value is calculated by averaging the observed T output from the test statistic at each timepoint and each sensor in the cluster.

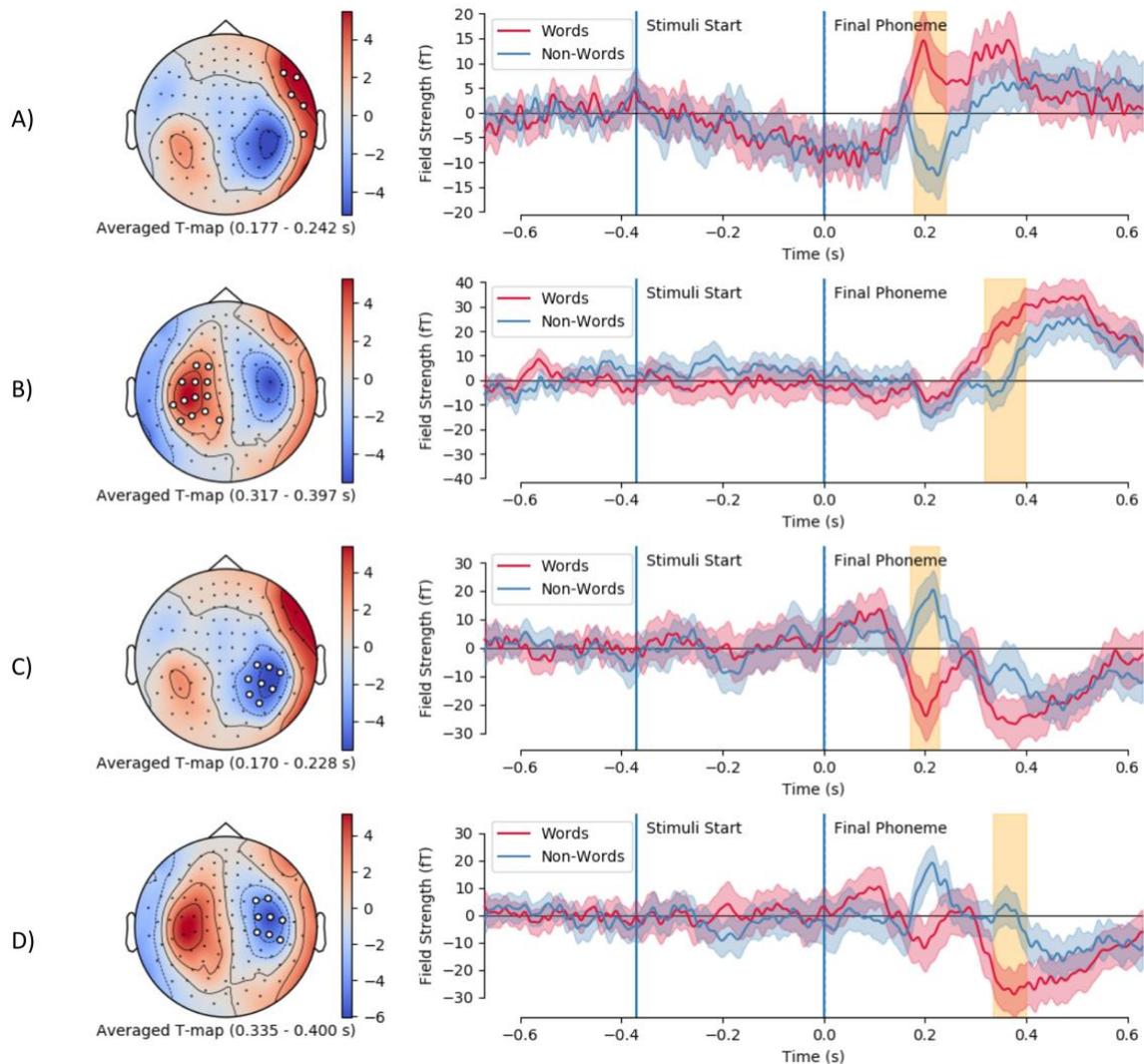


Figure 26. Evoked Field Cluster topography and time-courses for word and non-word mismatch subtractions. Mean T statistic maps are shown projected onto MEG helmet, significant sensors are marked in white. Time course showing Mean (line) and bootstrapped 95% confidence intervals (shaded area) field strength for each evoked contrast, stimuli start and final phoneme onset marked in blue, and cluster onset/offset shaded in yellow. **A)** shows MMN for Non-Word deviants and **C)** shows MMN for Word deviants; **B)** and **D)** show later difference in response.

Whilst not critical for the core research questions, I was interested in where these responses originated from. Quality source-reconstruction was possible for 47 of the participants – this was not high enough to go through with source analysis. However, I was able to show the average topology for these participants. Figure 27 illustrates the likely origins of the mismatch response. This replicated the sensor-level data, but also shows the word contrast more prominently localised to the left anterior temporal lobe at approximately 400 ms, compared to the non-word contrast.

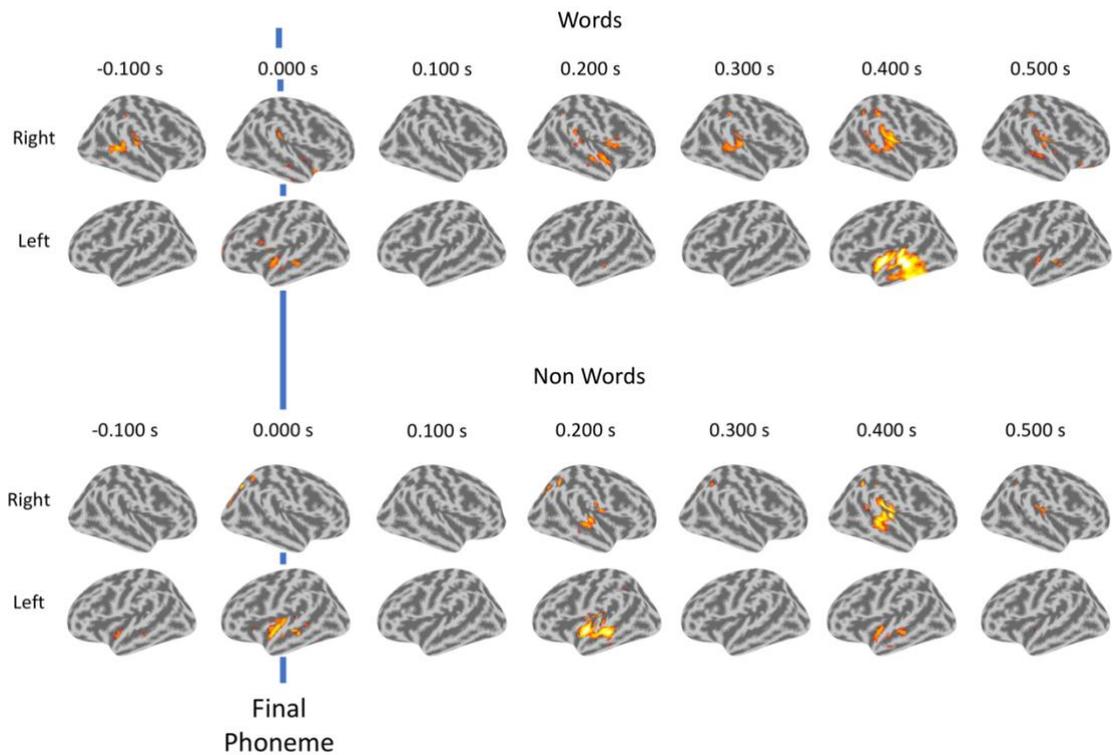


Figure 27. Average source-localised evoked contrasts for Words and Non-Words. Final phoneme is marked with a blue line. DSPM used to invert sensor-level data. For visualisation the estimates are binned into 100ms segments - so each image is a mean average across a bin.

3.3.2 Evoked Response and Covariates

The Attainment Factor, Age in Years and Subjective SES regressors all yielded clusters that were robust to the permutation testing (**Table 8**). The predictors Working Memory & Executive Factor, Classic IQ Factor, Verbal STM & WM Factor, and Equivalised Income did not survive this testing, and I found no evidence for a relationship between these variables and the MMN response.

	Attainment	Age in Years	Subjective SES #1	Subjective SES #2
Mean Beta	2.2929E-14	-1.5227E-14	-1.0352E-14	-1.9247E-14
Mean t-value	3.0505	-3.3638	-3.1600	-3.1044
Monte Carlo p	0.0222	0.0462	0.0460	0.0474
Number of Sensors	15	12	20	20
Epoch Start Time (ms)	463	516	3	340
Temporal Extent (ms)	185	106	72	77

Table 8. Summary of statistics for GLM clusters surviving permutation testing. T values and Beta values are the average from each cluster over sensors and time points. Beta values are in the scale of magnetometers field strength.

The topography of three of the clusters (**Figure 28.A, B & C**) showed clear overlap with the evoked response shown in the results above, whereas the third cluster (**Figure 28.C**) did not overlap with this temporally or spatially. The educational attainment cluster (**Figure 28.A**) had a right-parietal topography, started around 460 ms after the differentiation point, and predicted an increased response to word oddballs against non-word frequent. The Age cluster (**Figure 28.B**) showed a right-temporal topography, started around 500ms, and predicted a decreased response to word oddballs versus non-word frequent. The first Subjective SES cluster (**Figure 28.C**) had a fronto-central topography, an unexpected time-course that started at the differentiation point (with an onset just after differentiation) and predicted a more negative response to oddball words relative to frequent non-words. The second subjective SES cluster showed a more plausible time-course and topology, with a left-parietal topology starting around 350ms after the differentiation point and predicted a more negative response to oddball words versus frequent non-words. I report the temporal & spatial elements of these clusters roughly, as these dimensions of the clusters are estimates (Sassenhagen & Draschkow, 2019).

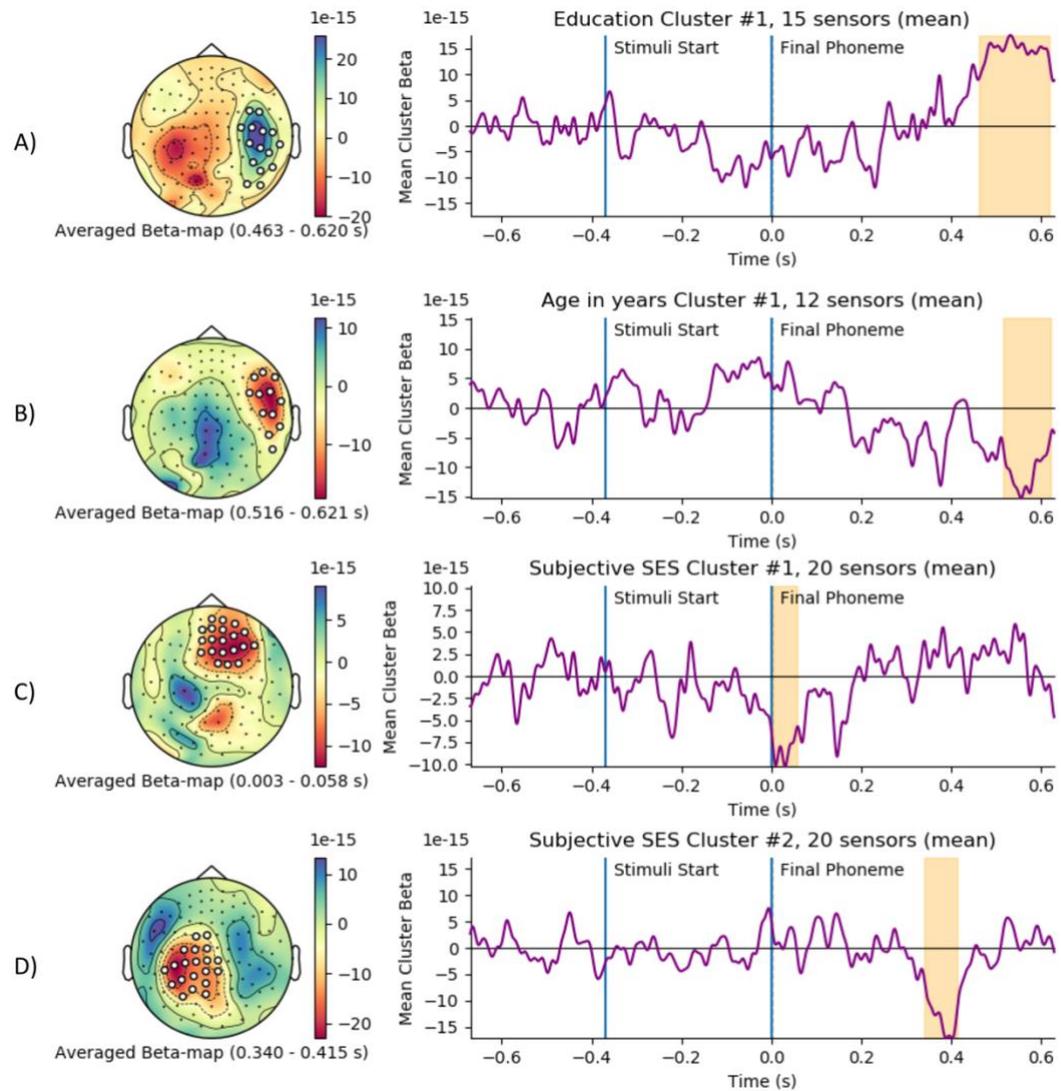


Figure 28. General Linear Model clusters for Attainment, Subjective SES and Age in Years. Topography of Beta-Weights with cluster sensors plotted shown on the left. Time-course of beta weights, with stimuli and final phoneme marked in blue, and cluster temporal extent shaded in yellow. It should be noted that spatial and temporal cluster extent are not cluster permuted, just the statistic - so this should be interpreted as an estimate of these dimensions. Beta values are in the scale of magnetometers field strength.

3.4. Discussion

I used an auditory oddball paradigm to explore the relationship between children's sensitivity to phonological deviations, and their subjective SES. Measures of cognition and educational attainment were also included in the model. I asked three questions: 1) will SES predict the evoked response difference between words and non-words. 2) Will this response be localised to temporal areas. 3) Will there be differences in these relationships between Income and Subjective SES. Children showed a robust and differential response to the final phoneme of word deviants versus non-word deviants.

The significant clusters of difference were at ~200ms, with two clusters showing opposing responses to words vs non-words – both on the right hemisphere, and then at ~350ms showing the same polar differences, but with a contralateral topography. Importantly, relating to the first question set out in the Introduction, a child's subjective SES is associated with their neurophysiological response to deviant words, and one cluster showed overlap with a later P300 response. Answering the second question, the topology of this later SES-related cluster is consistent with having a temporal source. Attainment and age also show statistically significant associations with the evoked response to word deviants, and these clusters occurred later, also consistent with a late P300 component. There was no evidence that these factors are associated with the earlier N200 response, and there was no evidence for cognitive measures or household income to be associated with the evoked response. This final point answers my last question, that I would find a difference between measures of SES in predicting neural response.

I report components that show a difference between the Word and Non-Word contrasts, a N200 and P300 component. The N200, or mismatch negativity, component implies that there is an early sensory detection between the processing of unexpected Word and Non-word phonemes – this replicates previous finding (Junge et al., 2012; Korpilahti et al., 2001; Maurer et al., 2003). The P300 component is commonly associated with conscious processing and attentional orienting (Bennington & Polich, 1999; Polich, 2007; Sommer & Matt, 1990). Despite the explicit instructions to ignore the stimuli and focus on the simultaneous cartoon playback, it is likely the irregular stimuli led to an involuntary orienting of attention (Lyytinen et al. 1992). The differences between word and non-word contrasts are therefore likely to reflect some degree of differing involuntary attentional shifting, or at least an increased demand on attention (Bennington & Polich, 1999), and the neural processing associated with this. Another strong possibility is that this component is associated with semantic processing (Meador et al., 1987) and phonological categorisation (Hill et al., 2004), perhaps indicating that this later difference could also reflect differing processing of semantics and categorization – which is likely given that the contrast of interest is between words and non-words.

A child's oddball response was not significantly associated with equalised family income, but it was significantly associated with parental rating of subjective SES. I

conclude from this that the economic situation *per se* is not the ingredient that drives SES-phonology associations, but instead that it is the wider environmental impact of SES, which the parent is uniquely placed to assess. Greater relative deprivation, which cannot be completely captured by standard measures like income, likely negatively impacts the development of phonological processes – the subjective SES effect may well reflect this. An alternative explanation is that lower subjective SES is associated with poorer parental mental health, which in turn leads to less support for language development and therefore phonological processing. Supporting this second explanation, lower subjective SES in adults is indeed associated with poorer mental health (Odgers & Adler, 2018; Scott et al., 2014), and poor parental mental health is negatively associated with early (1-2 years) language development (Lung et al., 2009; Paulson et al., 2009). I did not measure parental mental health, but this may be a potential mediating factor, and would provide a future direction for research.

Irrespective of the explanation, the results speak to the complex nature of socioeconomic status, which is often characterised as purely with income or occupation (Rubin et al., 2014). As income was included as a predictor in the GLM, it is likely that the subjective SES clusters represent variance independent of income. Indeed, this observation partly parallels research into children's executive functions where objective SES and subjective SES were shown to make independent contributions (Ursache et al., 2015). Across the literature, the way I conceptualise SES seems to be crucial. When maternal education is used to group children, differences in selective attention (Stevens, 2009) and auditory refractory periods (Stevens et al., 2015) are observed. By contrast, grouping by income alone does not always produce significant differences (Garcia-Sierra et al., 2011). Taken in concert with the results, this could also support one path of the theoretical model put forward by Noble et al. (2012) and Ursache & Noble (2016) – that language and phonological development are moderated by *some elements* of SES and impact later outcomes in children. In this case, it seems to be the subjective experience of SES, rather than income *per se*.

We found two SES-predictive clusters that survived permutation testing. One frontal-central cluster that starts very early (almost at the differentiation point), and a second more left-dorsal cluster that has an onset consistent with a P300 component. I am dubious about the first of these. Only the cluster statistics are permuted, not their spatial or temporal extent – meaning we cannot make statistical inferences about the

precise time and space (Sassenhagen & Draschkow, 2019). The shape and location of clusters are liable to display spreading. This limitation can explain the first SES cluster (**Figure 28.C**), which appears implausibly early. It is possible that the true effect has occurred later and by chance the original cluster had been formed in its current location. If this is the case, this may indicate an association with earlier sensory processing in reaction to the word oddballs, perhaps in relation to observations of auditory ventral stream processing reported in oddball tasks (Kim, 2014). However, due to its dubious time-course, this is unclear.

The second cluster (**Figure 28.D**) is more easily interpretable as the topology and timescale overlap highly with the left late P300 component shown in **Figure 26.B**. A reasonable interpretation is that subjective SES associated with the process of attentional orienting and/or semantic processing referred to above. In contrast with this finding, altered development of language systems – either through low SES or in children with neurodevelopmental conditions – have often been ascribed to early sensory differences. For instance, Stevens et al. (2009) reported that low SES children showed reduced evoked activity from selective attention to spoken stories at around 100ms post cue. The results do not replicate this type of early sensory finding. However, the subjects are relatively old, and it could be that we would see this kind of early effect in younger children, but that its timing is developmentally specific. The later effects that I observe are however consistent with some findings in the dyslexia literature. Dyslexia prevalence increases with lower SES, and dyslexic children and adults show altered P3 responses and long latency ERPs during reading and rhyming tasks (Taylor & Baldeweg, 2002). However, there may be many factors that explain this relationship between the later neurophysiological response and subjective SES, including important mediating factors that I did not measure. Identifying these factors could provide necessary information as to the mechanistic origins of this association.

From the behavioural measures, only the attainment factor (weighting primarily on the Mathematics and Reading WJ scores) was associated with MEG signal, rather than any of the factors that encompassed STM/Working Memory and IQ assessments. I think this is likely because I do not have good phonological awareness measures in the cognitive battery. I included the alliteration measure from the Phonological Awareness Battery (PHaB), however I discovered this contained many ceiling effects. These ceiling effects have also been reported in previous studies (Wheldall & Pogorzelski, 2003). This

is likely because of the age of the participants, as the PHaB measures are typically sensitive to individual differences earlier in development (Anthony et al., 2007; Cronin & Carver, 1998; Furnes & Samuelsson, 2011). One possibility is that the educational attainment measures are strongly associated because they in part reflect the longer-term outcome of these earlier differences. This is somewhat compatible with research showing that younger children's phonological abilities predicted their numerical competency and literacy (Krajewski & Schneider, 2009).

There are several limitations of the analysis. Firstly, as outlined above, cluster permutation testing permutes the test-statistic, but not the spatiotemporal aspects of the clusters themselves – thus the time-course and sensors in the cluster should be used as a general indication rather than a formal test of these attributes. A second limitation is the age of the participants. They are mid- primary school age to early secondary school, and arguably there could be strong relationships between phonological sensitivity and the factors earlier in development.

Lastly, my analysis approach – using a GLM – identifies how evoked brain data are associated with regressors. Whilst I select a wide range of regressors, these reported relationships could be explained by any number of unseen covariates, such as parental mental health as I mention earlier. However, this is broadly true for any model on this type of data – the regressors included are not exhaustive. Nonetheless, I believe these results are still important. The next step is to understand more precisely which elements of subjective SES may be the active ingredients in shaping the relationship with phonological detection skills.

3.4.1 Conclusion

Children have a differential neurophysiological response to word vs. non-word deviants in a phonological oddball task. These differences arise at both the N200 and P300 components, likely reflecting differences in early perceptual sensitivity, and later semantic processing and attentional orienting systems. The P300 components of the word condition were predicted by measures of age, attainment, and the family's ratings of their socio-economic status, but not by cognitive measures or household income. This shows that complex demographic measures like SES are predictive of the underlying mechanisms involved in phonological processing, and specifically associated

with (for the most part) the later stages, linked to semantic processing and involuntary attentional orienting.

Chapter 4: Visual Working Memory and Socioeconomic Status

4.1. Introduction

Chapter 2 showed that patterns of functional resting-state connectivity are significantly associated with a child's SES. This was followed by Chapter 3, showing that dynamic neurophysiological responses to phonological oddballs were also associated with SES. In this next chapter I focus on a different cognitive modality – visual attention and working memory. Like phonological processing, these skills are seen as foundational within many developmental accounts of cognition and learning (Alloway, 2006; Amso & Scerif, 2015; Scerif, 2010), but clearly reflect different underlying cognitive processes (Holmes et al., 2020), and a different configuration of underlying neural mechanisms (Buchsbaum et al., 2001; Casey et al., 1997). But are visual attention and working memory also associated with SES? I start by reviewing the literature on visual attention and working memory in childhood development, its relationship to SES, and the most promising paradigms for addressing this question.

4.1.1 Development of VWM

Our ability to extract meaning and regularities from a rich and complex sensory environment is central to building knowledge and interacting with the world in a goal-directed manner. Key to this functioning is the ability to allocate resources efficiently when presented with visual stimuli — *visual attention* — and then to maintain and

prioritise these items in memory — *visual short-term/working memory* (VSTM/VWM)³.

There are substantial variations in these cognitive skills across the population, in particular during childhood (Astle, Nobre, et al., 2012; Astle & Scerif, 2011; Koppenol-Gonzalez et al., 2018; Shimi et al., 2014).

Before we characterise why individual differences may arise, it is first helpful to understand the development of our visual attention and working memory. Within the first three months of life infants display modulations of cortical activity when switching attention between objects (Atkinson et al., 1992). Differences in this shifting skill, and associated brain activation, are sensitive markers of brain injury and atypical development (Atkinson & Braddick, 2012). Within neurotypical children we see developmentally stable individual differences in the allocation of attention – in other words a child’s ability early on predicts their ability later in life (Colombo et al., 1991; Colombo & Fagen, 2014; Rose & Feldman, 1987). These individual differences in early visual attention are correlated with child temperament and behavioural difficulties later in childhood (Papageorgiou et al., 2015). These skills develop further into school age (4 years onwards) with children showing the use of attention in more complex tasks, like searching for a target amongst distractors (Hommel et al., 2004), or detecting a target presented very quickly after another, also known as attentional blink (Shapiro & Garrad-Cole, 2003).

Although implicit attentional and short-term mnemonic processes can be indexed early in development, like preferential looking to a novel stimulus (e.g. Fantz, 1964) or occluded items (Káldy & Leslie, 2003), it is not until later (pre-school & school age – 3-7 years) that more complex *explicit* processing becomes measurable. For example, spatial recall tasks, in which locations must be remembered in sequence, become possible from around 4 years onwards (Buss et al., 2018; von Wright et al., 1978). Children show consistent improvements in precision in these tasks between 3-11 years old (Spencer & Hund, 2003), and by six years old largely overcome the bias towards overlaid

³There is some debate about where visual short-term memory (VSTM) ends and visual working memory (VWM) begins. Some researchers classify VSTM as a store and VWM as manipulation of this store, and draw very distinct boundaries between tasks, whilst others consider these processes to be highly overlapping and use them interchangeably. Burnett Heyes et al. (2012) use both terms to describe tasks that are likely to measure both to some degree. For simplicity I’ve opted to use VWM.

referencing axes that younger children show (Schutte & Spencer, 2009). Children also show improvements in tasks requiring prioritisation of the contents of memory. The developmental literature extends the work of Baddeley & Hitch (1974) and identifies VWM as distinct component using factor analysis of multiple tasks (Alloway et al., 2006; Gathercole et al., 2004). Alloway, Gathercole and colleagues showed that performance on tasks requiring children to remember sequences of spatially varying dots, mazes and blocks increase in a linear fashion between the ages 4 -11 (Alloway et al., 2006; Gathercole et al., 2004). The fact that these skills are still improving well into the age-range of our sample means that we are assessing developing systems, and differences between children indicates the progression of these skills, rather than static differences.

As children transition into early and middle childhood, VWM task performance starts to become more predictive of a wide number of factors in a child's life. Performance measures from VWM tasks start to correlate with measures that are directly relevant for school success. Mathematics skills in childhood and adulthood are predicted by working memory ability — including VWM tasks — even after accounting for other abilities like fluid reasoning (Raghubar et al., 2010). Tsubomi & Watanabe (2017) studied a range of academic abilities in relation to performance on a VWM task and showed that VWM without distractors predicted performance in school mathematics, science and literacy.

4.1.2 Memory Precision

Most studies of developmental change in memory performance focus heavily on either accuracy (correct or incorrect, or span) or reaction time, but there are other ways to capture memory ability. We can also estimate the resolution or fidelity of items held in memory, using a concept called *precision*. Instead of characterising memory with capacity *per se* or timeliness, precision captures the certainty or resolution of these items in memory. This can be ascertained through the modelling the variability of responses for recalling an aspect of a given item – colour, location, or angle – over repeated trials (Bays & Husain, 2008). A strength of precision is that it taps a more direct process than the span of correct items recalled. It is also a more fine-grained measure, as we are assessing the *quality* of a given representation, beyond the binary.

Burnett Heyes et al. (2012) investigated the precision with which children aged 7–11 years-old could retrieve items. Various angled and coloured bars were presented, with

children replicating a target item in several experiments: firstly, a single item sensory-motor task, duplicating the angle of an item whilst it was still on screen; secondly, recalling a single item after a delay; lastly, recalling an item from three possible candidates. The modelling approach extended the VWM precision (the fidelity of any given item in memory) estimation methods of Bays & Husain (2008) and Zhang & Luck (2008), permitting the authors to model the *precision* of those items (i.e. how close was the angle reproduced) independently of *visual-motor ability* (i.e. the angle replication whilst still on screen). Increases in precision continued throughout the age range. The precision improvements included the single item condition, despite capacity research showing children at ceiling. These precision improvements were also not fully explained by a simple improvement in motor performance. Furthermore, Burnett Heyes et al. (2012) showed that precision of children's recall, specifically in the multi-item condition, increased in-line with their IQ score. Ultimately, this revealed that VWM skill is modelled well by the precision of children's responses, and this measure is more sensitive to changes than capacity alone. Sarigiannidis et al. (2016) also found that precision was a superior measure of individual differences. The authors separated guessing rates and precision using a mixture model and found individual differences in both predicted performance on standardised STM and VW assessments.

4.1.3 Orienting attention within VWM

In addition to performance metrics of VWM tasks, there is also variation in how we can indicate which item to attend to and commit to memory. This is achieved with the use of a cue, which can come in many forms. Cues can consist of sounds (Botta et al., 2011), written words (Pearson & Wilbiks, 2021), a centrally presented arrow (LaBar et al., 1999), or a cue in the location of the item (Zhang & Zhang, 2011). Cues can also be presented before, during or after the items have been presented. Presenting the cue after the items have been encoded is known as a retro-cue (Gazzaley & Nobre, 2012; Griffin & Nobre, 2003). If a participant has improved performance with a retro-cue, there are multiple possible interpretations, including that they have used the cue to prioritise the search process, selectively enhance the representation of the cued item, or to allow uncued items to degrade within VWM (Astle, Summerfield, et al., 2012). Regardless of the specific theoretical interpretation, the retro-cue benefit allows us to distinguish between general memory maintenance (i.e., performance on all trials

regardless of cues), and the ability to orient one's attention during maintenance (i.e., retro-cue performance benefit) (Kuo et al., 2012).

Retro-cues have been more recently utilized in the developmental literature – notably in work by Shimi and colleagues. Shimi et al. (2014) found the ability to use retro-cues to prioritise information during memory was significantly improved with older ages and into adulthood. The authors also showed that this ability was closely predicted by individual differences in VWM span, implying that this cueing effect reflects these underlying skills. In a second experiment Shimi et al. (2014) confirmed that these age-related changes were likely the result of *voluntary* orienting with the retro-cue, rather than an automatic process. Benefits were reduced, and age effects eliminated, when uninformative cues were produced – if the cue-benefit was automatic they would expect increased costs of uninformative cues relative to age. Later work demonstrated this benefit increased if the children were familiar with the remembered items, and that this familiarity effect increased with Age (Shimi & Scerif, 2015). More recently, this design was used to explore the constraints of VWM (Shimi & Scerif, 2017). Shimi et al manipulated delay, attentional bias, and memory load differentially over several iterations. Load and temporal limits in the orienting of attention within memory in load and time were evident, and these improved with age. This body of work outlines the strength of retro-cue designs in delineating developmental changes in VWM, and that there are multiple interacting systems which the design partially measures.

4.1.4 Neural Correlates of Developing VWM

So far, I have discussed the development of performance on VWM, but now turn my focus to the development of the neural circuitry that underlies these behavioural effects. The neural mechanisms underpinning both selective visual attention and VWM are distributed amongst various brain areas. There is a well-established distinction here between stimulus driven attention (i.e. bottom up), which happens automatically and involves visual cortices and temporal areas, and attentional *control* (i.e. top down) which overlaps these areas with additional activity in frontal areas (e.g. frontal eye fields, prefrontal cortex) (Desimone & Duncan, 1995). We also know that retaining objects in VWM is accompanied by contralateral activity in the occipital and parietal cortices, and that this scales with the load in memory (Vogel & Machizawa, 2004). This increased activity is also accompanied by a suppression of distracting visual information that may

have been retained in memory (Todd et al., 2005). Some of the same mechanisms which underlie selective visual attention are also recruited when participants are asked to prioritise items in memory -- which can be measured with the retro-cue design mentioned above. The idea that top-down attentional processes are recruited is further supported by the finding that retro-cues induce retinotopic-type activity in visual areas (Kastner et al., 1999), and at the same time recruit pre-frontal and parietal areas (Gazzaley & Nobre, 2012; Kuo et al., 2012; Nobre et al., 2004). A popular theoretical interpretation is that a highly overlapping neural architecture is used both to select sensory representations (visual attention), and to maintain those representations over brief delays (VWM).

There is also a growing literature outlining changes in these VWM-associated brain regions in children across development, and in relation to task improvement. Whilst showing the development of visual attention in infants as following a distributed pattern across the brain, Reynolds (2015) also found several best-fitting current dipoles during EEG on different VWM tasks within the inferior prefrontal regions. In their review, Buss et al. (2018) describe evidence from multiple studies which show that VWM tasks consistently recruit similar brain areas (frontal and parietal) from childhood into adulthood. Task evoked activity in frontal regions specifically increases with age and task-demands, and this pattern likely reflects improvement in an ability of localised networks to increase activation whilst inhibiting connections far away – named Dynamic Field Theory (Schutte & Spencer, 2009). Astle et al. (2014) investigated contralateral delay activity, which is event related activity contra-lateral to where stimuli are presented, which scales with number of items retained in memory. Astle et al replicated this effect in children, showing contra-lateral activity in posterior electrodes during memory maintenance, which increased for target items in memory and predicted performance.

In a more general sense (i.e. not just in the visual modality), children completing working memory training have shown increases in the coupling between the dorsolateral prefrontal cortex inferior temporal cortex at resting state (Astle et al., 2015). In another study, phase-amplitude coupling was also found to increase between the same frontal areas and various task specific regions (Barnes et al., 2016). This suggests that whilst the primary visual areas play an important role in reflecting spatial attention, the key developmental and task-based activity occurs in networks around the frontal regions.

4.1.5 The present study

There is a growing body of research demonstrating that VWM and visual attention improve substantially across the course of development (see Astle & Scerif, 2011 and Fitch et al., 2016 for a review). Whilst it is likely that these developmental processes are associated with SES, remarkably few studies have tested this. This has been explored in auditory attention, for example D'Angiulli et al. (2008) have shown that the electrophysiological evoked responses for attended stimuli are higher in children from higher SES backgrounds, which has been replicated by others (Isbell et al., 2016; Stevens et al., 2009). Kishiyama et al. (2008) outline associations between SES and ERPs related to attentional control in a target detection task, and a reduced response to novel stimuli for low SES children. Very recently Wijekumar et al. (2019) utilised a preferential looking change detection task and fNIRS (Functional near-infrared spectroscopy) in a sample of rural Indian children aged 4 months – 4 years. Behaviourally, lower SES children showed lower detection of changes. The fNIRS data revealed activity in the inferior frontal gyrus and the dorsolateral pre-frontal cortex that scaled with maternal education and family income. Taken together, this suggests that there is every reason to suspect that frontal networks linked to VWM would also be associated with SES, but it remains to be tested whether this would be present in our sample, who are substantially older, and in our task, which is far more active. I could find no studies which assess VWM in older children, and with an active engagement. This chapter will shed some light on this question.

For the present study, I constructed a VWM task that allows us to estimate precision, rather than simple capacity. As discussed above precision estimates a more direct process than span measures and it continues to improve within the age-range of our sample. Whereas capacity (as measured by span) is less sensitive (Zokaei et al., 2015). Precision has also been shown to be predictive of IQ and Age (Astle, Nobre, et al., 2012; Burnett Heyes et al., 2012). I have also chosen to use a retro-cue design, giving children the opportunity to orient attention to the cued memory item. Not only does this engage working memory *and* attentional processes at the same time, but it also allows us to tease apart the general impact of memory from the ability to orient attention within memory.

Based on the literature to date, here are my predictions:

- 1) Informative retro-cues should improve precision and accuracy. Perhaps also improved reaction times.
- 2) General measures of performance (precision, error, reaction time) and cue benefit will increase along with IQ and Age.
- 3) A lateralised evoked pattern of brain activity should be observed after the retro-cue is presented. The degree of this activation should predict performance (Mok et al., 2016).
- 4) Lower SES will negatively impact the behavioural measures of performance, including the retro-cue benefit. Additionally, the magnitude of the neural evoked activity related to the task will be increase with higher SES.

4.2. Methods

4.2.1 Participants

Participants completed two visits with a caregiver: an MRI session during which the structural scan was acquired, and an MEG session including several tasks and a resting state scan. Unfortunately, this VWM task experienced a high rate of non-completion. Overall, 90 children took part in the RED study, of which 88 took part in the MEG session, 5 dropped out before this task, 11 then did not produce sufficient trials (>50%, 60 trials) to be included in the behavioural analysis. This cut-off was chosen as this would provide sufficient trials to balance the conditions with a minimum number of 20 trials per condition. This left 72 participants with a mean age of 8 years 6.47 months, with a standard deviation of 10.49 months. Ranging from 6 years 9 months to 11 years 1 months.

Neuro-imaging wise, out of 72 children who had sufficient trials in the VWM task, 27 participants had extremely noisy-data due to MaxFilter failure. Likely due to too much movement. This left 45 children with usable imaging data. Out of those 42 had sufficient epochs (3 had to be dropped due to trigger errors which gave them less than

20 trials per condition), and finally 33 of these were suitable for source localisation (i.e. a good fitting freesurfer source-model was successfully constructed).

Some children displayed more movement in this task than others, and this caused serious issues in the tSSS Maxwell filtering step of the preprocessing pipeline, causing a propagation of noise — re-filtering and trying several different toolboxes did not improve these results. Unfortunately, this noise propagation lasted throughout the entire recording, so if this occurred no trials could be used in the analysis.

To summarise: behavioural analysis includes 72 children, sensor space results include 42, and source-localised images are based on 33.

Of the 72 children analysed to some degree. Equivalised household income was £22,313 on average, with a standard deviation of £14,261, ranging from £7,747 to £61,248. 18 Children were below the poverty line (25%).

4.2.2 Visual Working Memory Task

I used a VWM retro-cue task. In this task, children had to recall the orientation of coloured bars presented on the screen. They were aided in this with a potentially informative cue, indicating which side would be probed at the end of the trial — giving them the opportunity to orient attention to one in memory. An illustration of a typical trial is given in **Figure 29**.

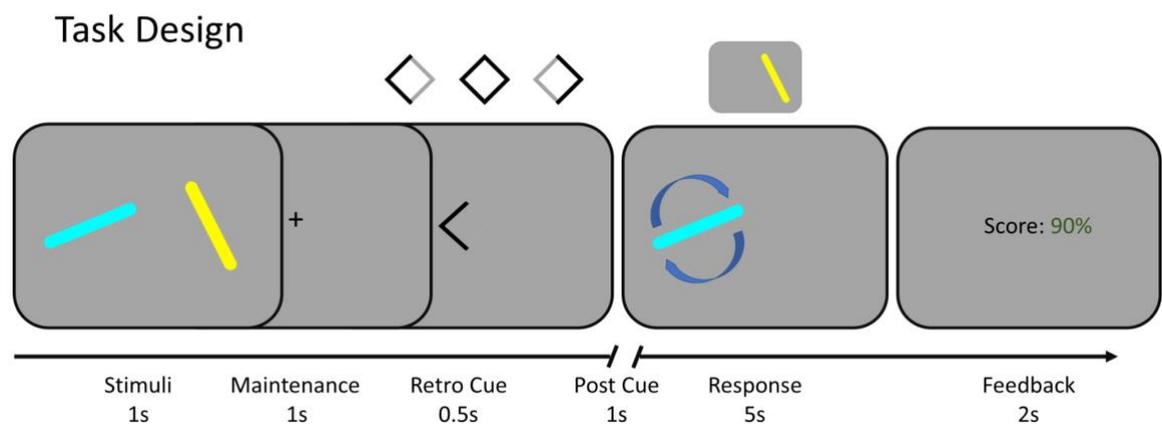


Figure 29. Illustration of the retro-cue task design. Timings are in seconds and interval frames have been left out for conciseness. These are cartoon representations and are not screenshots.

Task instructions were delivered in a series of screens and a tutorial. The coloured bars were characterised as ‘worms’ whose orientations needed to be remembered. The full detail of these screens is included in **Supplementary Table 3**. After the instructions and tutorial, participants were given a practice of 10 trials.

A standard trial consists of the following sequence: participants were first shown two blue and yellow-coloured bars at different orientations, for 1 second. A maintenance period of one second followed with a fixation cross. Then a centrally presented informative retro-cue, which either indicated the left or right bar would be probed (with 100% validity), or an uninformative cue indicating nothing (presented by a fully shaded diamond). A post-cue period of another second followed, again with a fixation cross. Finally, the probed bar was shown alone, in the same location but in a new orientation, and participants had to use two buttons on a button box to orient the bar within 5 seconds. There was then a 2 second feedback frame, which gave a score out of 100% for the distance between their response angle and the actual target angle. Finally, between each trial there was an inter-trial-interval (ITI) that was jittered between 1.25 and 1.75 seconds. This was jittered to reduce any potential temporal expectation impacting the patterns of activation (Wolff et al., 2015). A break was given every 10 trials, which gave participants feedback on the previous block’s total score. At the end of the game each participant was shown their total score (sum of percentages across the whole experiment).

Excluding the 10 practice trials, there were 120 trials in total. This includes 40 trials with uninformative cues, 40 with left cues, and 40 with right cues. For a given participant the coloured bars always appeared on the same side, but this was randomised across the sample. E.g. the yellow bar was always on the left for some participants, and on the right for other participants. This was to maximise the lateralised signal. The orientations of the bars were randomly selected from a uniform distribution between 0-180 degrees, and the jittered ITI was generated in the same way. The order of the trials was then randomly shuffled.

The stimuli were presented using a PC running Windows 10. A single optical button box with four buttons sent triggers to the stimulus computer via a National Instruments I/O box. The code also sent triggers denoting all events (screen onsets, offsets and button presses) in the trial to the Neuromag acquisition computer, allowing alignment of MEG and behavioural data. The code used to configure and present the

task is publicly available at <https://github.com/u01ai11/gotWorms>. The Nidaqmx python library (National Instruments, v.0.5.7) was used to receive and send triggers, PyGaze (Dalmaijer et al., 2014) and PsychoPy2 (Peirce et al., 2019) libraries were used to present the stimuli.

The scanner was identical to that used in the MEG data in Chapter 2. During the task participants sat upright in an Elekta Neuromag MEG scanner, with 102 magnetometers and 204 planar gradiometers. Pairs of horizontal and vertical electrodes were placed above and to the side of the child's eyes to detect blinks, and a pair of electrodes were connected to the wrists to monitor heart rate. A screen displayed the stimuli from a projector outside the magnetically shielded room. This was placed 68cm from the participant. The size of each coloured bar was 19.85cm giving a visual angle of 16.61°.

4.2.3 MRI Scan

Participant's structural MRI scans were used for source localisation of the MEG data in this task. These are identical to those used for source localisation in Chapter 2.

4.2.4 Behavioural Analysis

Error and Precision

Trial-wise error was calculated as the absolute angular deviation of the response from the target orientation in radians. The response angle was wrapped at 180 degrees (3.14159 radians), as the stimuli are symmetrical, and an orientation of 181 degrees would therefore be equivalent to 1 degree. This absolute error was then mean averaged within trial types (Left, Right and Uninformative), and on average (regardless of cue) for each participant.

Precision was also calculated, which is the consistency/fidelity of these responses when retained in memory. I calculated precision using methods used previously in the literature (Bays & Husain, 2008; Burnett Heyes et al., 2012; Zokaei et al., 2015). Specifically, precision was derived from the error scores, and is the reciprocal of the standard deviation (SD) of these angular errors across trials. The circular definition of standard deviation (Best & Fisher, 1979) was used, as the angular error data is circular

(Fisher, 1993). As above, separate precision metrics were calculated for each trial type (Left, Right and Uninformative), and overall, for each participant.

Response Onset and Duration

Response onset time (i.e. reaction time) was calculated for each trial, this was the time in milliseconds from the probe appearing and a response to be given. Duration time was then calculated from the onset of response to the last button press. Again, these were averaged for overall each participant and for each trial type within participant (Left, Right and Uninformative).

Impact of cue type

The main effect of cue on Error, Precision, and Onset & Duration times, was assessed using separate repeated measures ANOVAs, followed by post hoc *t*-tests, with critical alpha level adjusted for multiple comparisons.

Associations with SES, Age and IQ

A multiple, multivariate regression approach using Ordinary Least Squares (OLS) was taken to determine any association between the measured covariates and the outcome metrics. Significance testing was undertaken using a Conditional Monte Carlo (CMC) permutation test.

The metrics outlined above were used for each subject as outcome measures in the regression: Precision (1/Circular Standard Deviation), Error (Radians), Onset Time (milliseconds), Duration Time (milliseconds). Each was an average across trials for each participant. I also calculated the effect of cue for each participant across each of these metrics. Precision Cue Effect was the average precision for informative cues minus the same metric for uninformative cues - higher indicating an improved score for informative cues. Error, Onset Time and Duration Time were treated similarly, but with these metrics a lower number indicates an improved effect of cue information. These scores for each participant were assembled into a data vector with a row for each participant and eight columns for each metric.

The predictors used in the regression model were: Age, Wechsler Abbreviated Scale of Intelligence second edition (WASI) Matrix Reasoning Scores (McCrimmon &

Smith, 2013), Total Strength and Difficulties Questionnaire (SDQ) Score (Goodman, 2006), Objective SES Factor Score, Subjective SES Factor Score and Household Factor Score. The SES factor scores are the same as those used in Chapter 2 and are discussed in more detail there. The WASI matrix reasoning sub-test is covered in Chapter 3, it estimates fluid IQ using abstract pattern completion tasks. The SDQ is a parental ratings scale, which aims to capture the behavioural problems and general well-being as a child. It is often used as a screening tool for mental health and behavioural problems in children. I included this to detect and potential relationship between VWM and behavioural issues in this sample.

The z-scored covariates for each participant, along with a vector of ‘1’s (for an intercept) was assembled into a design matrix. A single contrast was evaluated for each predictor. The design matrix and contrasts are illustrated in **Figure 30**.

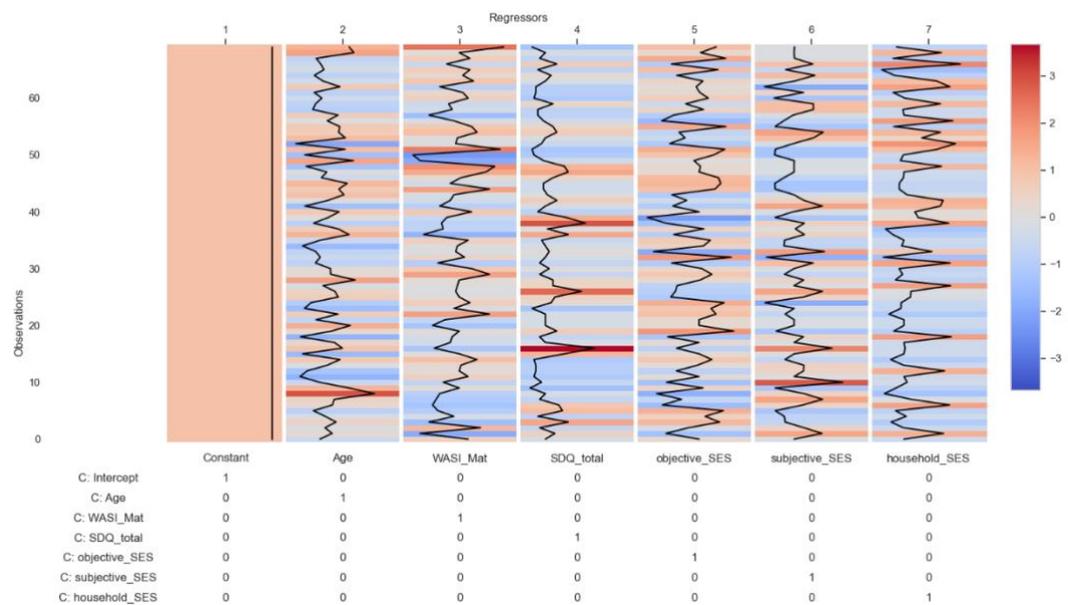


Figure 30. Design matrix illustration for the behavioral GLM. Regressors and their pattern across participants are represented at the top. The contrast matrix within the GLM is represented by the table at the bottom.

The GLM produced beta coefficients, which represent the strength of association between each predictor and each outcome metric. To establish which of these weights was statistically significant, each contrast was permuted by shuffling the rows of the design matrix for that contrast (whilst all other contrast’s rows remained the same) 100,000 times. This was repeated for each of the seven predictors - for a total of 700,000 permutations. The permutations used here are higher than in neuroimaging

chapters, as this GLM required less computational power. The benefit of this is a more precise estimation of the null distribution, allowing us to generate a Monte-Carlo p value that is precise to $1e-5$.

4.2.5 MEG Analysis

Pre-processing

The MEG data was pre-processed and cleaned using the procedure detailed in Chapter Two. To recap briefly: tSSS with movement compensation using Maxfilter v2.2 was applied, then blink and heart artefacts were removed using ICA, the results of which were manually checked to identify artifactual components in the case of electrodes with a broken connection. The data was bandpass filtered using a Finite Impulse Response (FIR) filter between 1-200Hz. A notch filter was used to remove power line noise at 50Hz and its harmonics of 100Hz, 150Hz and 200Hz (FIR zero-phase and a length equal to 6.6 times the reciprocal of the shortest transition band). After filtering the data was down-sampled to 250Hz. The continuous time-courses for each participant were next split into trial epochs. These ran from 0.5 seconds before the onset of the initial stimuli, until the end of the trial at 4.5 seconds. Noisy epochs were then rejected using a generalised Extreme Studentized Deviate procedure. After rejection, segments across trial-types were equalised by randomly dropping the over-represented trials. Epochs were then aligned with the behavioural meta-data. Unfortunately, due to an intermittent malfunction in the trigger recording, around 10-15% of trials did not have matching epochs.

Gradiometer Noise

As in the previous chapter, the gradiometers were discarded, due to excessive noise and spatial disruption, likely from larger movements which then propagated into noise during the tSSS preprocessing step. This should not be an issue as previous research has shown that results from each sensor type are broadly equivalent (Garcés et al., 2017). Regardless I carried out one of the analyses below (the permutation t -test between informative cues and uninformative cues) on gradiometer data to illustrate the extent of the impact of the spatial noise on the results had I used the gradiometers (**Supplementary Figure 16**). It is clear from this, that whilst there is some signal, it is largely uninformative to conduct the analysis on these sensors.

Trial Evoked Response

The evoked responses over the trials were calculated by subtracting the activity of the 0.5 seconds before the stimuli from the remaining time course. These epochs were then averaged across all trials for each participant, creating one average time-course across sensors for each participant.

This simple evoked response was then used as outcome data in two separate cluster permuted GLMs. The first with the performance metrics (Overall Error, Overall Precision, Onset Time, Duration Time) entered as normalised predictors and simple contrasts. The second with SES scores, Age and WASI Matrix reasoning as normalised predictors and simple contrasts. Each GLM permuted each contrast 5000 times, with cluster values compared to these null distributions.

Cue Effect

One analytical approach commonly used in this type of design is to collapse trials and sensors into ipsilateral and contralateral to presented informative cues (e.g. Mok et al., 2016). This has the advantage of combining the power of all informative trials, whilst avoiding the averaging out of lateralised activity. This is often conducted with EEG, where head position is irrelevant, or MEG in adults where positioning can easily be accounted for. I attempted this approach here, however differences in child-head position led to vast differences between participants in identifying appropriate ipsi- and contra- lateral sensors, and often eliminated signal all together. As such I have chosen to take the following approach.

A cue impact difference wave was created by calculating the evoked averages described above for Left, Right, Uninformative and combined cued conditions, for each participant. These were then cropped from the stimuli's offset until the end probe onset (1 - 3.5 seconds). Three separate cluster permuted t-tests were conducted comparing the difference between: Left minus Uninformative; Right minus Uninformative; Combined Cues minus Uninformative.

As explained further in the results, I also undertook a more simplistic analysis aimed at characterising lateralised activity in response to the cue, by comparing the evoked averages of left and right cues (without subtracting uninformative). This was to

answer the hypothesis that informative cues would lead to lateralised activity in the post-cue period.

To investigate potential relationships between the neural underpinnings of cue-utilisation, the mean value of the difference cluster for each participant was calculated. This was the mean evoked activation of the informative minus the uninformative trials, taken at the sensors and times belonging to the cluster. These single values were then used as outcomes to be predicted in the same GLM scheme used to model the evoked response (task metrics and SES, Age, WASI analysed separately). This masking approach is a departure from other sections of MEG analysis in this thesis. As discussed below, and observed in Chapter 3, this sample's difference waves tend to be excessively noisy and therefore not particularly sensitive in mass multivariate GLMs with our sample size. For reference, this noise is illustrated in **Supplementary Figure 17**. So, rather than a mass multivariate GLM, this targeted approach is used instead. The t -values in the linear regression were permuted using the same scheme as mentioned before (100,000 permutations per contrast for each GLM).

Source Localisation

Source localisation was attempted using the methods described in Chapter 2 & 3, for each participant's initial evoked responses the inverse models were used to create localised time-courses using the minimum norm estimation method. Time-courses of the difference wave were also generated. The significant cluster time dimensions were then used to bin the localisation for illustration purposes. As in Chapter 3, I was not able to create a sufficient number of localisations to allow statistical analysis (only 33 participants). Source localisation with just magnetometers failed, as the minimum norm estimation model fit explained around 8% of variance in activity, whereas this increased to >85% with both sensor types. Because of the time-constraints of completing the thesis, the source estimations are presented with the caveat that they should be interpreted with caution.

4.3. Results

4.3.1 Behavioural results

Error and Precision

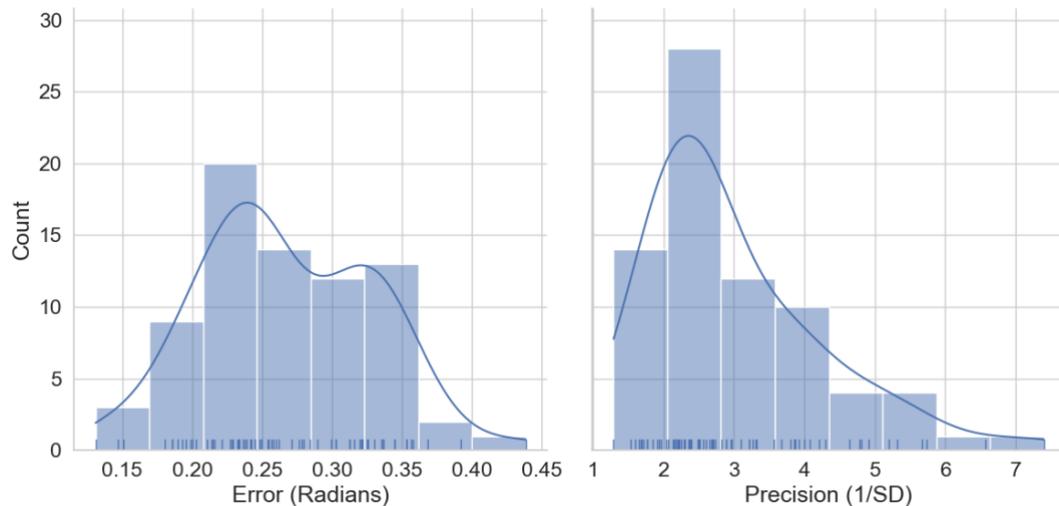


Figure 31. Distributions of error and precision metrics across participants. Error is in radians from the desired target, precision is the reciprocal circular standard deviation of these responses. The histogram bin widths are set automatically using the seaborn histplot function. The rug plot on the x axis represents individual participants. A kernel density estimation (KDE) curve shows the distribution without binning. The y Count represents density as the number of participants.

Participants showed variability in their precision and error scores across the task.

Figure 31 illustrates this. Error had a higher variability across participants.

Error and precision scores were compared for each of the three cue types: Left, Right and Uninformative. A repeated measures ANOVA was used for the main effect of cue direction on error, the results of which are illustrated in **Figure 32.A**. This first ANOVA revealed a significant effect ($F(2, 73) = 4.292, p < .05$) with a weak effect size ($\eta_p^2 = .056$). Post hoc Holm corrected t-tests revealed this effect was driven by a significant increase in error between the uninformative (0.281 radians error) and right facing cues (0.258 radians error), $t=2.75, p < .05$, cohen's $d=0.320$. There was no significant difference between the left and right cues, and a borderline, but ultimately non-significant, difference between the Uninformative and Left cues ($t=2.25, p=.052$, cohen's $d=0.326$).

A similar repeated measures ANOVA was carried out on the precision metrics, with the results shown in **Figure 32.B**. The precision data are not spherical (Mauchly's $W=0.825$, $p<.05$), which violates the assumption of this form of ANOVA, so a Greenhouse-Geisser correction was applied, this was the only difference between the two behavioural ANOVAs. The main effects of cue direction on precision were also significant ($F(1.703, 62.15) = 5.826$, $p <.01$) with a weak effect size ($\eta_p^2=.074$). Post hoc Holm corrected t tests revealed a significant difference between the right and uninformative cues ($t=3.28$, $p<.01$, cohen's $d=0.382$) and between the right and left cues ($t=2.43$, $p<.05$, cohen's $d=0.283$). On visual inspection it appears as if the non-sphericity violation and the differences were greatly influenced by some participants with much higher precision in the right-ward condition. These are 3 standard deviations away from the mean, but are chosen to stay within the analysis, as this performance was genuine – consistent responding *within* that participant – rather than being driven by anomalous measurement.

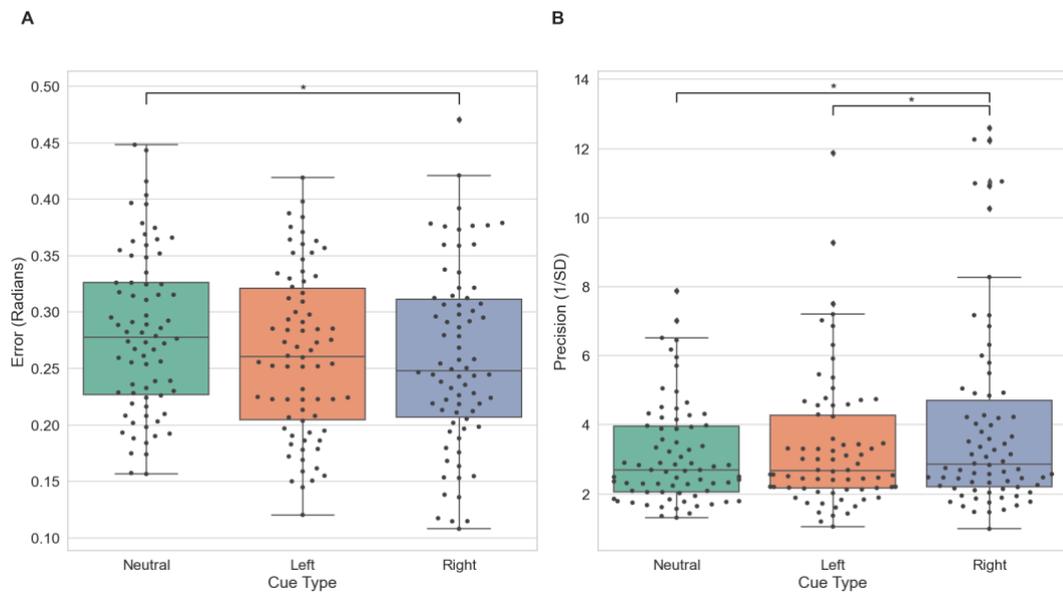


Figure 32. Boxplot contrast of precision and error split by cue types across participants. Boxes edges represent quartiles of distribution, the line the mean, and the whiskers the standard deviation. Individual points are placed over the graphs with a random x offset if many are close together. Horizontal lines with * denotes significant differences revealed by each ANOVA and post hoc tests. Both plots have the cue type along the x axis. **A)** shows Error in radians on the y axis. **B)** Shows precision in circular standard deviations on the y axis.

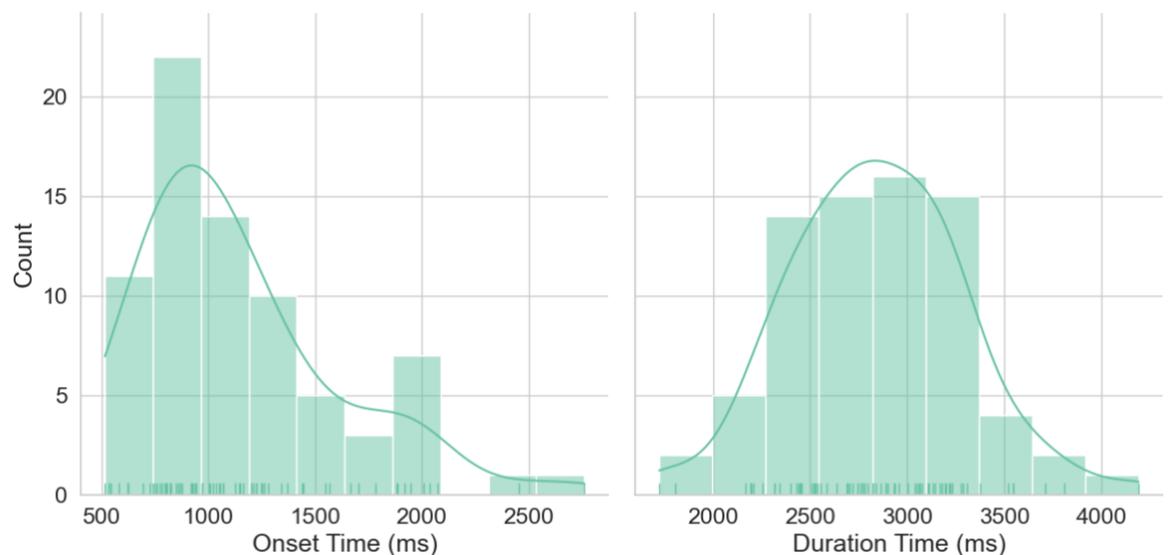


Figure 33. Distributions of Onset and Duration times in milliseconds across participants. The histogram bin widths are set automatically using the seaborn histplot function. The rug plot on the x axis represents individual participants. A kernel density estimation (KDE) curve shows the distribution without binning. The y Count represents density as the number of participants

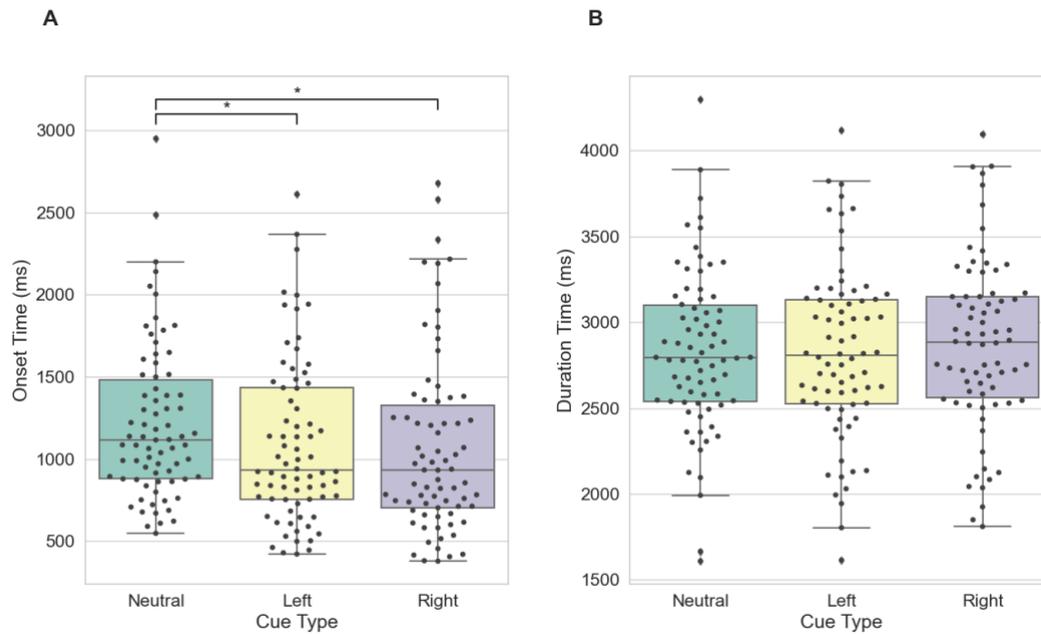


Figure 34. Boxplot contrast of onset (**A**) and duration (**B**) times in milliseconds split by cue types across participants. Boxes edges represent quartiles of distribution, the line the mean, and the whiskers the standard deviation. Individual points are placed over the graphs with a random x offset if many are close together. Horizontal lines with * denotes significant differences revealed by each ANOVA and post hoc tests.

Onset and Duration

The key temporal metrics from the responses were the onset and duration times of the trials. **Figure 33** shows the distribution of both times across participants.

I also tested for differences between cue directions and informativeness. A repeated measures ANOVA was conducted on the onset times (**Figure 34.A**) revealed a significant main effect of cue on onset time (reaction time) ($F(2, 73) = 10.911, p < .001$) and a small effect size ($\eta_p^2 = .130$). Post hoc Holm corrected t-test revealed that this was driven by significantly faster onset times for left cues against uninformative cues (124ms faster, $t=3.651, p < .001$, cohen's $d = 0.424$), and right cues and uninformative cues (148ms faster, $t=4.39, p < .001$, cohen's $d = 0.506$). There was no significant difference between left and right cues.

For the duration of the response, a repeated-measures ANOVA provided no evidence for a significant main effect of cue on the duration of participant's responses ($F(2, 73) = 0.877, p = .48$). These results are illustrated in (**Figure 34.B**). In short, there is good evidence for the impact of the informative cue on the speed with which

participants started to enter their response, but no evidence that this cueing effect impacted the overall time taken to input that response.

Covariates

After establishing the basic differences between task conditions, I tested for correlations between each metric and the covariates of interest. This was achieved using the Ordinary Least Squares Multivariate GLM procedure described above.

In total eight covariate-outcome metric associations survived the permutation procedure. These are all illustrated in **Figure 35**. All these significant associations were in metrics relating to Error and Precision, rather than reaction time. In decreasing order of beta weight Overall Precision (i.e. consistency of response) increased with Age (**Figure 35.A**), Objective SES (**Figure 35.E**) and Household SES (**Figure 35.G**), and WASI Matrix Reasoning score (**Figure 35.B**). The cue effect on precision — i.e. whether the child utilised the informative cues to improve precision — increased with Objective SES (**Figure 35.F**), WASI Matrix Reasoning (**Figure 35.C**), and Household SES (**Figure 35.H**). Overall Error was only predicted by each child's Strengths and z scores.

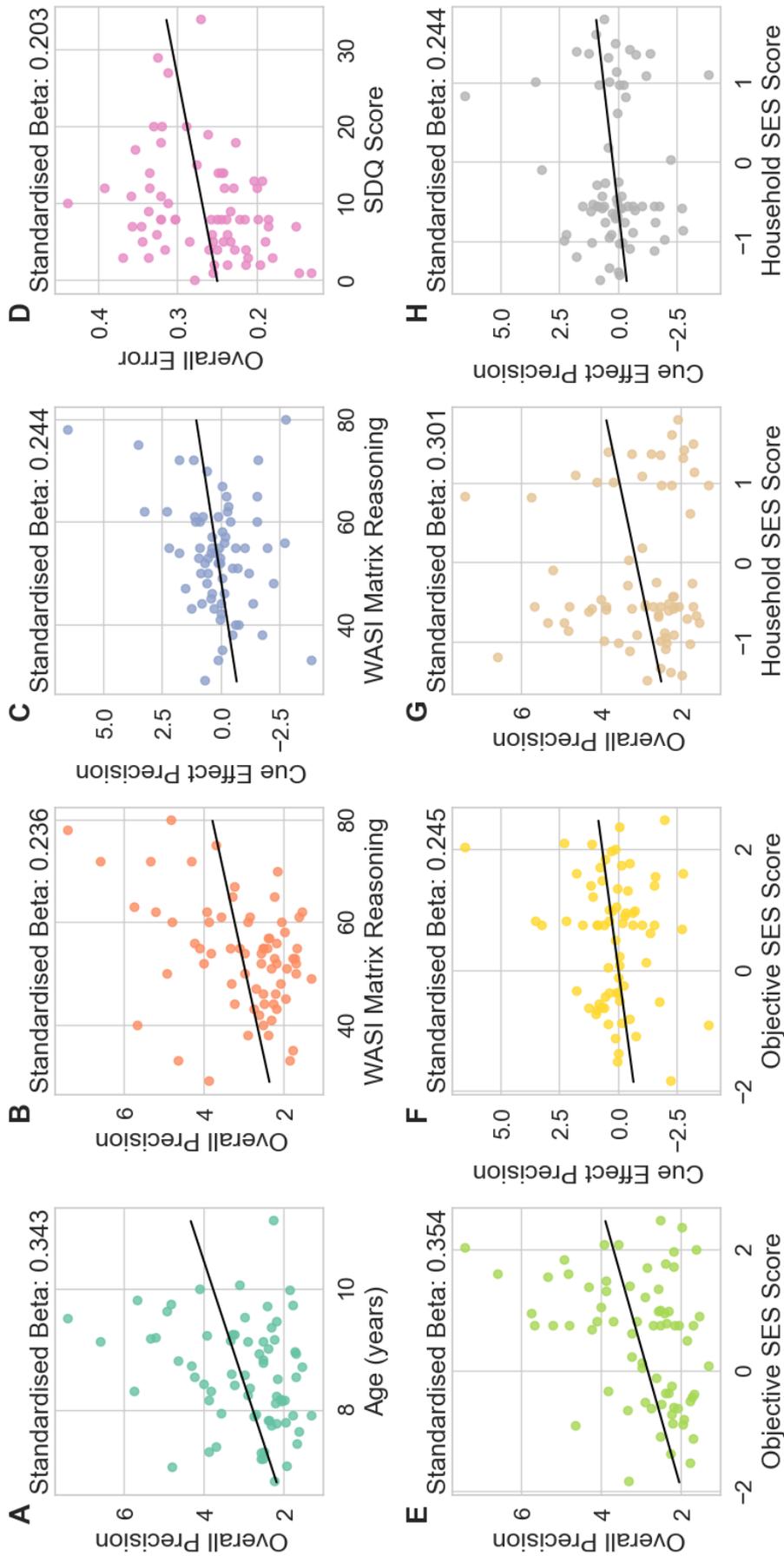


Figure 35. Significant relationships identified by the permuted general linear model (GLM). The coefficient line for each predictor is overlaid over individual points in each graph, the standardised beta weight of each is written above. **A)** Age in Years on the x axis and Overall Precision in circular SD on the y axis. **B)** WASI Matrix Reasoning in standised score and Overall Precision. **C)** WASI Matrix Reasoning in standardised score and the impact of cue on precision. **D)** Strengths and Difficulties Score (SDQ) and Error (in radians). **E)** Objective SES component score and

4.3.2 MEG Results

Evoked Response

The first MEG analysis sought to characterise the basic evoked response across the whole trial. First, a grand median across all participants was calculated this is included in **Figure 36.A**. The participant median signal was then used in two separate GLMs, the first with all the task-based metrics used in the behavioural section above. This revealed a ‘precision cluster’ in response to the cue at around 2.28 to 2.78 seconds (**Figure 36.B**), with a mean t value of 2.99 (min 2.01 - max 5.13) and a Monte-Carlo p of .04 (i.e. in the 96th percentile of the null distribution). This cluster’s topology was a broad topology of 20 sensors on the left side of the head. The timeframe of this cluster was used to bin of the source-reconstructed evoked time course and is shown in **Figure 37.A**.

The second of the GLMs with the predictors (Age, IQ and three SES scores) revealed a single cluster related to Subjective SES during the retention interval (before the cue, after the stimulus had disappeared) at around 1.42 to 1.73 seconds (**Figure 36.C**). This was across 26 right, frontal sensors, with a mean t value of 2.835 (min 2.000 - max 4.804) and a Monte-Carlo p of <.001 (i.e. above 99.99th percentile of the null distribution). The time-frame binned source estimate for this cluster is shown in **Figure 37.B**.

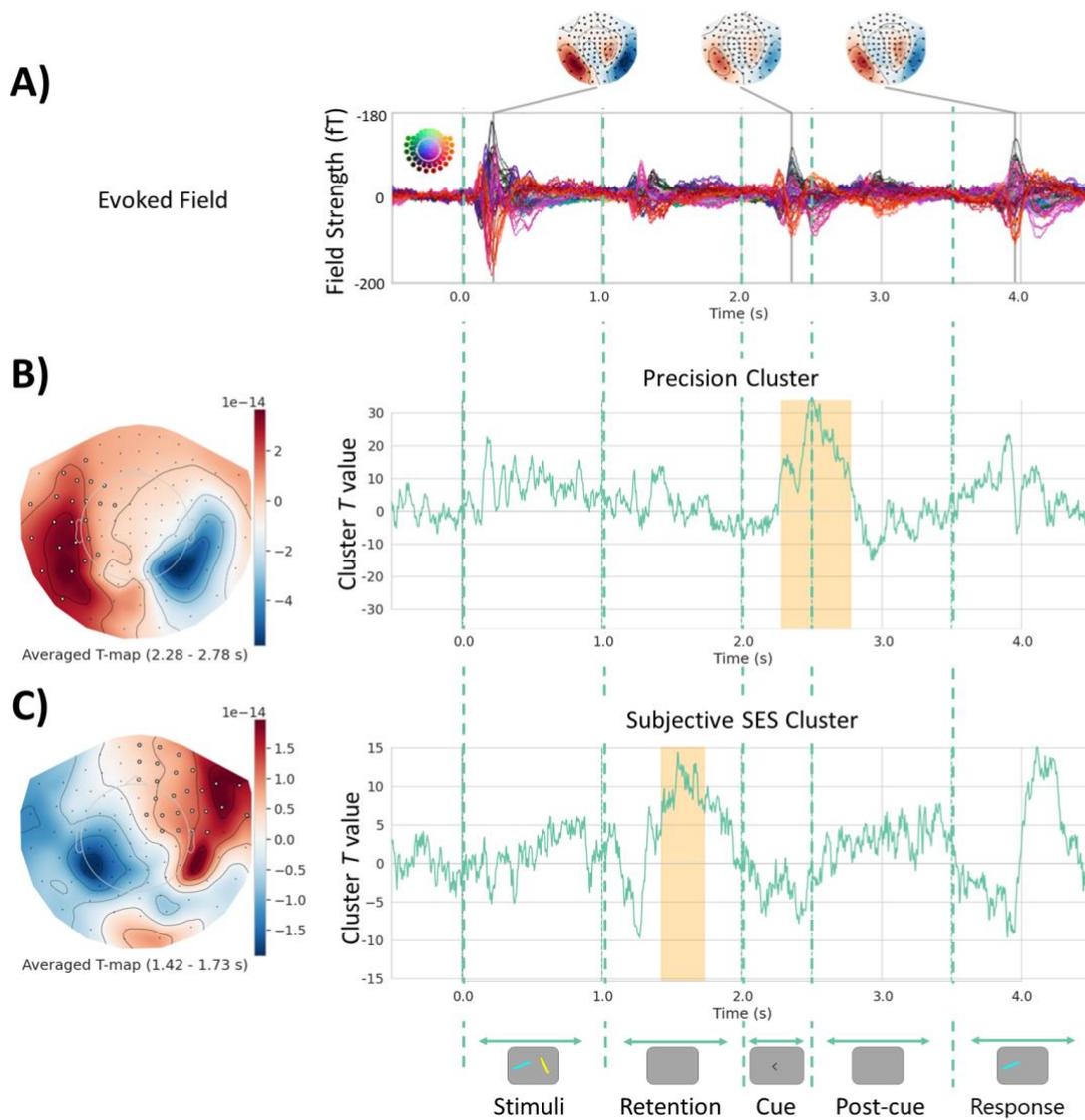


Figure 36. Summary of the average trial evoked analysis, with key trial events overlaid and aligned at the bottom **A)** Shows the average evoked field for magnetometers across all participants, baseline corrected from 0.5s before stimuli onset. Topographs are chosen at the average strongest global field strength peaks. **B)** Shows the topography and T value timecourse for the Precision GLM cluster. **C)** Shows the same for the Subjective SES cluster. All times are in seconds.

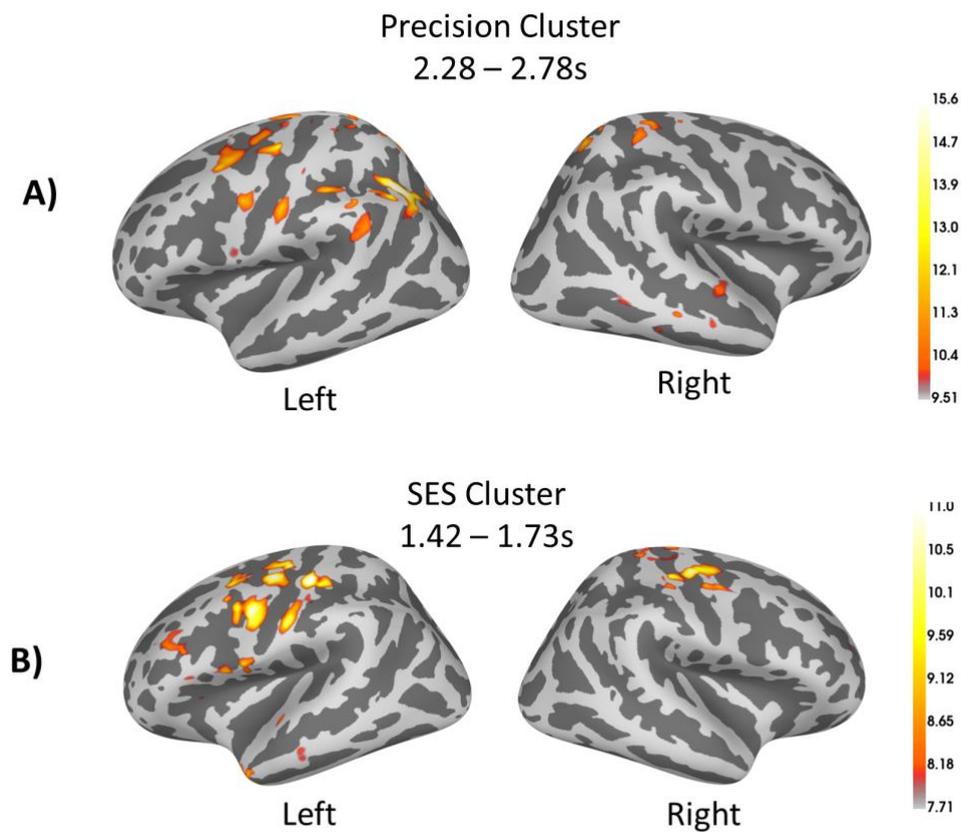


Figure 37. Average evoked response in source space. Constructed using minimum norm estimation. Bins represent the temporal dimension of significant clusters in sensor space, rather than clusters from a source space analysis. **A)** shows the mean activity at the same time as the Precision sensor space cluster. **B)** shows the same but relating to the Subjective SES cluster.

Cue Utilisation

A simple contrast of time courses, between informative cues and uninformative cues, was conducted using a cluster permuted t-test. This analysis revealed a significant cluster from 3.36-2.38 seconds across six right fronto-temporal temporal sensors. The cluster had a mean t value of 4.49 (4.06 - 5.61), and its Monte-Carlo p value was .034 (i.e. 96.6th percentile of the null distribution). This is illustrated in **Figure 38**. The corresponding times were also used to bin the source-localised difference wave, creating a source map of the difference wave, illustrated in **Figure 39**, which shows a clear frontal topography with a slight bias to the right hemisphere.



Figure 38. Illustration of the significant difference cluster between evoked response for informative cues and uninformative cues. The orange line represents average evoked field strength for Uninformative cue trials, with a shaded standard deviation, and the green line represents the same but for informative cue trials. The topology of the cluster t-values, mean taken across the time dimensions, is represented on the right, the cluster’s sensors are denoted by white marks, and the bar indicates the t-value-color mapping.

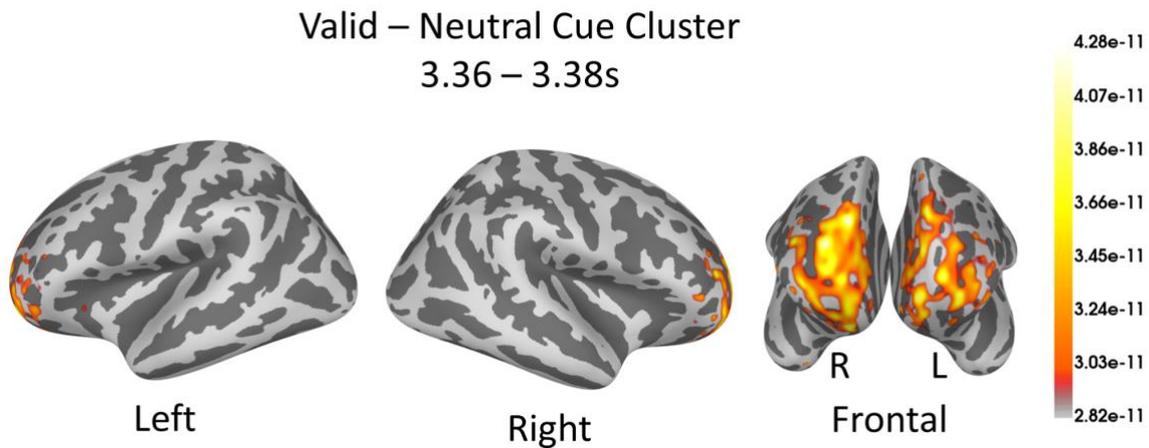


Figure 39. Source localised difference wave between informative and uninformative clusters. A higher value is denoted by a lighter coloration, and indicates that activity in that area was greater for informative cues than uninformative ones. Activity is averaged over the time duration. This binning represents the temporal dimension of significant clusters in sensor space, rather than clusters from a source space analysis.

To identify any potential lateralized activity, the time-courses of the left-cued and right-cued trials were also compared separately against the uninformative-cued trials. These two cluster-permuted t-tests failed to identify any significant clusters. I also applied the mass multivariate GLM to the difference signal between cued and uninformative-cued time courses, however it yielded no significant effects. This was unsurprising given the noise-level of this difference signal (illustrated in **Supplementary Figure 17** and discussed in the methods above). In a further attempt to identify lateralized activity, I tried a simple contrast of the left and right cue trials, baseline corrected to the onset of the cue, and without a subtraction of the uninformative condition — this maximises the possibility of detecting a difference in lateralised activity. This did reveal a single lateralised cluster illustrated in **Figure 40**. The time course of the difference wave was similarly localised and masked off by the cluster time-course, as can be seen in **Figure 41**. This shows us that the presentation of a cue did lead to some form of lateralised activity, just not strong enough to show up against uninformative cues.

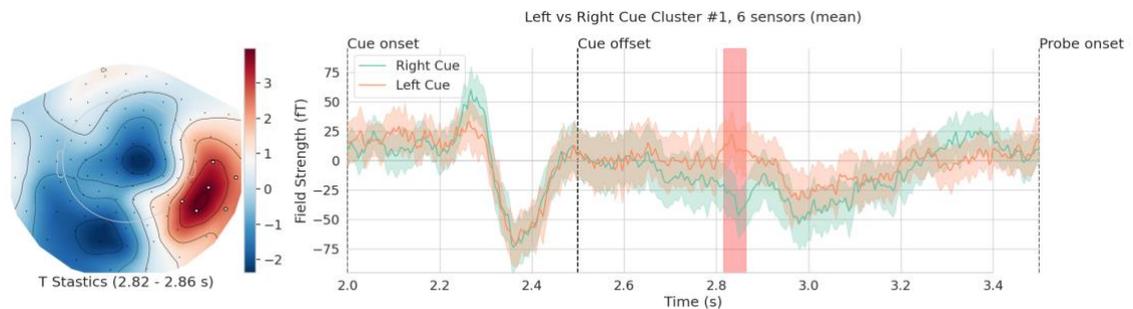


Figure 40. Lateralised cluster in the evoked response to the cue, difference between left facing and right facing cues. Green time course is the average evoked response of right cues, and the orange is the left cues. The cluster is highlighted in red, and the plot on the left illustrates the t statistics.

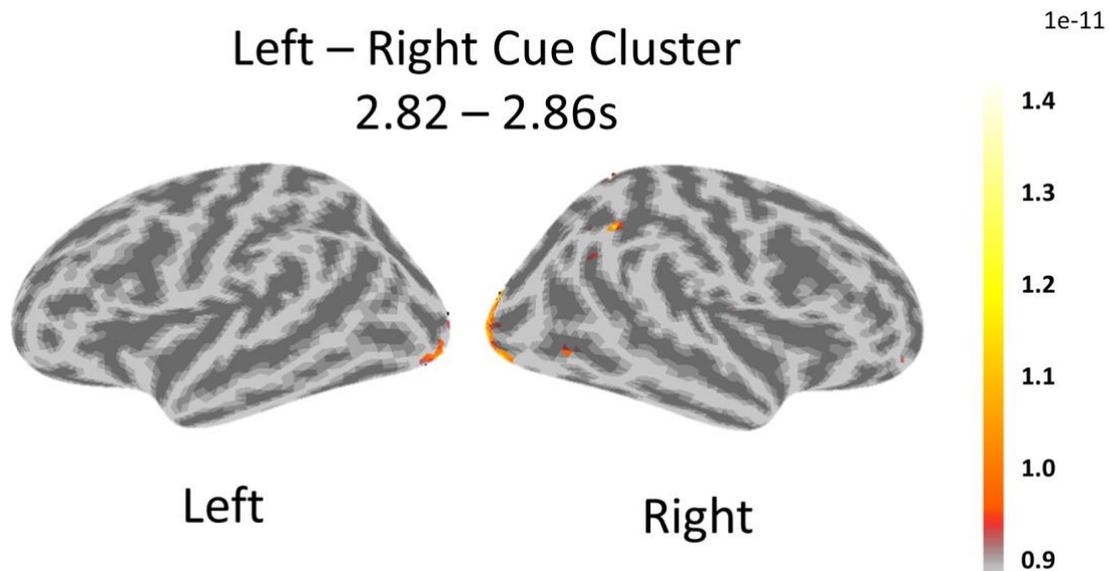


Figure 41. Source localised difference wave between left and right cues. A higher value is denoted by a lighter coloration, and indicates that activity in that area was greater for left facing cues than right ones. Activity is averaged over the time duration. This binning represents the temporal dimension of significant clusters in sensor space, rather than clusters from a source space analysis.

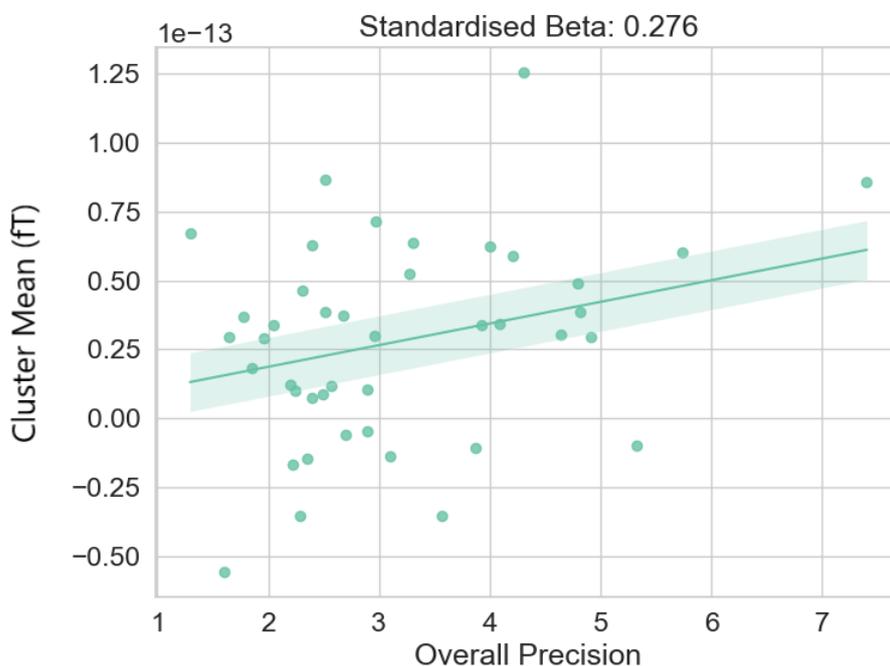


Figure 42. Single result from performance-cue cluster GLM. Overall Precision against Cue difference cluster activity. Precision is in radians and cluster value is the mean-masked difference in fT. Points represent individual participants, solid line represents the coefficient line, and the shaded area the standard error. The coefficient (beta) is represented above in standardised form.

To investigate the relationship to the evoked activity of the cue relative to uninformative trials, I masked the significant difference cluster and used the mean difference between cued and uninformative-cued values as a single value data point in two separate GLMs (for performance metrics, and SES, Age and WASI). For the performance metrics, only Overall Precision predicted the cluster activation significantly, with a higher precision being associated with higher activation for cued versus uninformative cued trials (**Figure 42**).

This procedure was repeated for the left-right cluster, however there were no significant associations which survived the permutation procedure.

Figure 43 illustrates the results from the SES, Age and WASI GLM. Two effects survived the permutation scheme. Age, showing the activity in the cluster increases with age in years (**Figure 43.A**). Household SES showing that the activity in this cluster increases with a higher Household SES standardised score (**Figure 43.B**).

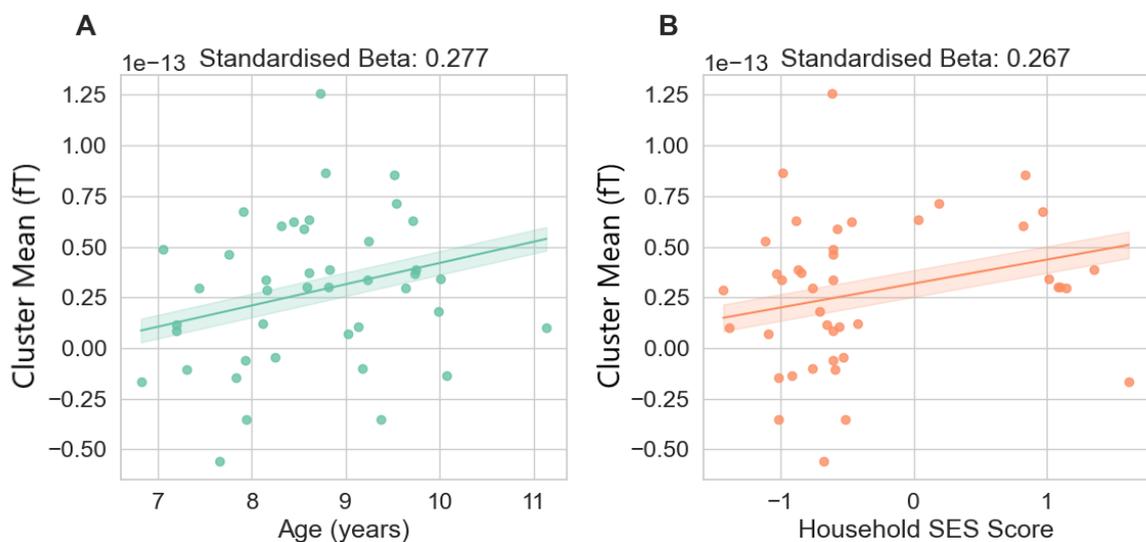


Figure 43. Results from performance-cue cluster GLM. Overall Precision against Cue difference cluster activity. Points represent individual participants, solid line represents the coefficient line, and the shaded area the standard error. The coefficient (beta) is represented above in standardised form. **A)** Shows Age in years and cluster value is the mean-masked difference in fT. **B)** Shows Household SES in standardised score and cluster value is the mean-masked difference in fT.

4.4. Discussion

Children performed a simple VWM task, with a retro-cue design. My first prediction, that informative cues should improve precision, accuracy and timed performance was confirmed, the retro-cue conferred a benefit in terms of participants' precision, error, and onset times. Children were able to orient attention within memory to improve performance, and the benefit of this was apparent in the accuracy with which the item was recalled and the speed with which that recall process started. The second prediction, that general measures of task performance would increase with IQ and Age, was also confirmed. Precision and error were significantly predicted by Age and IQ scores, the cue benefit for precision also predicted IQ scores. Put simply, the older the participant, and the higher their IQ score, the more they benefited from the retro-cue. The third prediction, that I would see lateralisation after the retro-cue is presented, was only partially confirmed. Left and right cues did evoke a lateralised difference, but it was not predictive of performance. However, the non-lateralised informative vs uninformative cue cluster did predict overall precision. Moving onto the fourth prediction, that lower impact of SES would negatively impact retro-cue benefit, general performance and magnitude of evoked responses. I showed that Objective and Household SES negatively correlated with overall precision and the benefit of the cue. The magnitude of the evoked activity from informative cues over uninformative cues was also negatively associated with Household SES. The task presented here therefore replicates previous research on VWM retro-cue and precision designs in children. Beyond my initial predictions I find that error in responses increases with poorer scores on a parental behavioural wellbeing questionnaire, indicating that this task is partially sensitive to behavioural difficulties in children. Importantly it also extends that understanding by showing that absolute affluence SES (Objective and Household factors) predicts the resolution of VWM memory, and the orienting of attention during memory maintenance. I further extend this neurophysiologically, showing a dissociation between activity related to cue processing, which is predicted by the absolute measure of Household SES, and activity during un-cued memory maintenance, which is predicted by the subjective rating of SES.

4.4.1 Behavioural Effects and Previous work

Before further exploring the implication of the impact of SES on this task, it is worth discussing the basic effects we observed, as these are of interest in themselves. The behavioural results give us a measure of the ability to retain items in VWM (average precision) and a measure of the ability to attentionally orient within these representations (the impact of cue). This integrates different elements of the previous literature. Firstly, precision in this type of task improves as children age – observed by Burnett Heyes et al. (2012) and Sarigiannidis et al. (2016). This acts as a sanity check, indicating our task is likely picking up on the development of VWM skills. Secondly, I observed an informative retro-cue effect, increasing both general performance (Error) and precision of the recalled bars. This extends the retro-cue work of Shimi and colleagues (Shimi et al., 2014; Shimi & Scerif, 2015, 2017) into a measure of precision. In fact Shimi & Scerif (2017) found that a 2-item memory array showed no benefit of retro-cue, whereas in the present work we do. The authors explain their results by suggesting 7-year old's have sufficient storage capabilities to simply rely on storage capacity without the need to use the cue. I suspect that the present task's requirement to recall a continuous feature (angle), places additional load on memory, leading to our observed cue-effect. This illustrates the benefit of modelling precision of representations rather binary recall; it is likely more sensitive to performance differences and therefore possibly more sensitive to potential associations with SES. A compelling next step would be to compare these two measures in a larger array, where participants had to identify the correct target *and* recall the precision, in order to compare the relative sensitivity more directly.

The timing metrics here seemed to be less important. The time before participants initiated a response was significantly shorter for cued items. Indicating that the attention orienting improved not only the precision of responses, but the processing time in initiating a motor response. This replicates work with adults (Nobre et al., 2004). However, these timing effects didn't seem to predict any covariates, which I discuss in the section below. The duration of the response had no relationship with the cueing, or any covariates. I suspect this is likely diluted by the fact that random differences between the target orientation and the probe presented orientation, lead to differences in duration. In future this could be explored using a joystick – where time to reach the response orientation does not scale with distance.

One thing that I did not predict, is that the accuracy metric of error only revealed a significant effect of right informative cues, rather than left. This is most likely due to the low effect sizes we are dealing with, where a small amount of noise could be the difference between significance – the effect sizes for left and right-ward cue benefits are almost identical, falling just either side of the arbitrary significance threshold. Alternatively, there is a literature on hemi-field biases. This phenomenon is known as pseudoneglect (Bowers & Heilman, 1980), and reflects the subtle effect of hemispheric dominance for various systems of spatial attention - usually a leftward bias in line-bisection tasks. However the direction of this bias can change depending on the task — (Sheremata & Shomstein, 2014) used a spatial VWM task and demonstrated a spatial bias towards the left for a single item, but a reversal if more than one item was encoded. However, I think it is more likely the former explanation, that noise levels and a small effect size are responsible.

4.4.2 Behavioural Effects and SES

As with the preceding two empirical chapters, the results of this experiment paint a complex picture of how SES relates to the neural and behavioural measures. Particularly that the constituent components of SES differentially predict neural and behavioural aspects of our VWM task. Unlike the phonological task in Chapter 3, here we see multiple factors of the SES score predict metrics. The two factors related to empirical affluence (household and objective) both predict behavioural precision. Improved income and household facilities could promote a greater ability to store visual information and use those skills for precise responding. This may well reflect the already established association between SES and attentional control. Attentional control is required to perceive and maintain angular information in memory (Barrett & Zobay, 2014). The allocation of attention in the encoding phase can be conceptualised as a gateway to forming precise memory representation – you cannot remember what you do not attend to. Attentional control has an established and clear link with objective measures of income (Noble et al., 2007; Spruijt et al., 2020). In typically developing children, out of many executive function measures, attentional control was shown to be predicted by household income more than maternal education, SES composite scores or home-environment (Dilworth-Bart, 2012). This may provide an explanation for the associations I identified here.

Household and Objective SES also predicted the benefit of cue on precision, with children rating higher on this score performing better on these metrics. The cue benefit represents an ability to orient one's attention to items maintained in memory (Griffin & Nobre, 2003; Nobre et al., 2004). The mechanism behind this is likely a combination of two things. The increased representation of the cued item in memory, and the downregulation and forgetting of information related to the un-cued item. Whilst my design cannot parse these apart, it seems likely that SES could co-vary with these mechanisms. Household SES for example, is closely related to the levels of noise and unpredictability in a home (Coldwell et al., 2006; Lecheile et al., 2020). As mentioned, attending to the cued item involves the inhibition of the other item. Growing up in an unpredictable environment leads to certain strengths – like improved attentional switching – but also a lack of ability to inhibit distracting information (Mittal et al., 2015). Animal models show that exposure to stressful & unpredictable environments during development impair neural sensory gating mechanisms (Baisley et al., 2011; Cilia et al., 2005; Sutherland & Conti, 2011). This likely involves a mechanism where stress related hormones like corticosterone impact receptors related to this gating (Cymerblit-Sabba et al., 2013a). Given this information, one could imagine a situation where children from low SES backgrounds become exposed to less predictable environments. In turn, this leads to a lower ability to inhibit distracting and irrelevant information, *even when* that distracting information is held in memory. This is another candidate mechanism for the results I report here.

Whilst the precision and error metrics show a relationship with both the neural measures (explored below) and covariates, I did not find any-such relationship with the onset and duration time. I included timing in my predictions above, as previous work had shown a relationship between slow reaction times and low SES (St. John et al., 2019). I think this relationship may not have occurred because the working memory load was only ever two items (reducing to one on an informative cue), which is well within the capacity (2 items, 2 features) of the age of children in our sample (Oakes et al., 2006). St. John et al., (2019) may show a RT effect because participant's find the task much harder, therefore making a trade-off against time. An alternative explanation is that the present task did not reward speed or limit the response time for fast responses. This lack of motivation may have led to a lack of speed-accuracy trading off (Jiang et al., 2000). Meaning the responses represented precision of memory representations, rather than the fast motor skills needed to quickly reproduce under time pressure. I did not

include more items, as this may have reduced the power further (due to the need to counterbalance conditions over a limited scanning session), but perhaps if the load was increased, we would start to see an impact of SES on response times.

4.4.3 Neurophysiological Patterns

Within the MEG data, the basic visual evoked response to the retro-cue was revealed as a clear lateralised cluster predicting the precision of individual participants. At an earlier time-point, during the maintenance period prior to cue onset, a cluster of activity in the right-frontal area was significantly predicted by the subjective SES rating of the child's family. Comparison of informative against uninformative cues revealed a right-frontal cluster around 800ms after the cue was removed. A comparison of left and right cues revealed significant lateralised activity around 300ms after cue removal, indicating a degree of lateralised visual-cortex localised activity. When both entire difference time courses were used in a cluster permuted GLM, it was not related to any of the covariates, however inspection of these difference waves revealed a high noise level. An alternative masking approach revealed that the mean activity of the frontal cue cluster was significantly positively predicted by precision — indicating that individuals who displayed stronger evoked response to the retro-cue had better performance. Activity within this cluster also increased with Age and Household SES, indicating that the activation of neural mechanisms underlying informative cue processing increased with age, and in children from a higher SES household. The masking approach revealed no such relationship with the occipital left vs right cue difference, implying that this association is with a more general non-spatial attentional process, rather than the specific orienting of spatial attention

There are some encouraging consistencies on the topology of activity seen here and previous work in this thesis. In Chapter 2, the connectomic analyses revealed that the various SES factors were predictive of hub nodes in occipital and frontal areas, and their reciprocal connections. Here, I show that overlapping areas are implicated in a VWM task. The cue difference cluster, which is predicted by Household SES, shows a right-frontal topography, and this is complimented by source-localisation of the

matching time-course showing a prefrontal pattern⁴. This is consistent with the Household SES related structural connectome, which has a highly connected hub node in the right orbito-frontal cortex (**Figure 19.C**). However, there are observations here that are also inconsistent. Firstly, no occipital activity was related to any of the SES factors in the analysis, which is surprising given the consistent patterns in the posterior sensors, and the occipital lateralisation when comparing left and right cues — so lack of sensitivity to this area is unlikely to be an explanation. This is inconsistent with the results in Chapter 2, which found highly connected SES network nodes in both modalities with topology in the occipital lobe. This implies that not all components of VWM are associated with SES. With only two memory items it could be that the lower-level processes in occipital areas are not scaling to the extent that they would associate with SES, whereas activity within prefrontal cortex, which presumably reflects different components of VWM, does.

Another interesting and unexpected pattern of effects was the finding that Subjective SES did not predict any behavioural metrics, but it did predict visual evoked activity during the maintenance period before the cue. This was across right-frontal sensors, and positive, so a higher subjective rating of the family predicted greater activity during this time. This seems to be entirely a function of strength and is unrelated to relative cue processing or a cluster which also predicts behaviour. It was also in the period where there is no benefit to prioritising, so both items are being held in short-term memory without systematic bias. Evoked activation related to memory load in the frontal sensors has been shown before - both inhibitory and excitatory – in VWM maintenance periods (Hsieh & Ranganath, 2014; Scheeringa et al., 2009). The fact that this SES factor is not related to task metrics also suggests that this is affecting the underlying physiological activation on a processing, perceptual level, rather than effortful engagement. This aligns with the finding of Subjective SES impacting the evoked responses in the previous phonological chapter, as this was a passive task explicitly avoiding attentional control. Taken together these findings hint at some relationship between subjective status (irrespective of income) on the development of

⁴ I must point out that the source-localisation does not stand on its own, as there is no formal analysis. However, presented with the sensor-space analysis, it still represents an informative pattern.

basic perceptual mechanisms — both visual and auditory, and a lesser potential impact on attentional control and precision of memory.

Household SES was the only SES factor which predicted the participant's evoked activation in response to informative cues over uninformative cues. This suggests that the household environment is an important factor in the development of the ability to hold items in memory and manipulate them, as well as the underlying processes. The Household SES factor weighs highly (0.66) onto whether a child has their own bedroom. Quality of sleep is one practical outcome from this factor, which could plausibly impact attention and VWM. Sharing a bedroom has been shown to decrease a child's sleep efficiency, duration and increase variability, even after accounting for household income (Buckhalt et al., 2007). Sleep quality and duration have a well-established impact on working memory — with children showing more errors in both auditory and visual WM tasks with poorer sleep (Steenari et al., 2003). This impact is so marked that researchers can explain day-to-day variation in working memory performance by fluctuations in sleep-quality (Könen et al., 2015). A sleep-based explanation of at least some proportion of the SES attainment gap has already been suggested by Buckhalt et al. (2007). The authors argue that poor sleep is part of a multi-systemic dynamic of multiple health disparities (such as access to healthcare, household chaos and more), which compound to negatively impact cognitive functioning. One possibility is that this is what we are observing here: Household SES impacting functioning through lack of sleep, which influences how likely children are to pay attention to internal memory representations, or process cues to improve precision.

4.4.4 Limitations

There are some limitations that need to be acknowledged. Firstly, the high-level of scanner noise seen in the phonological oddball was also present in this task. This meant that only a subset of the children could be included in the sensor space analysis, and even fewer could be source localised. This severely limited the source-localised data to basic visual depiction, rather than statistical inference, and means that the study was underpowered to detect subtle differences in SES. As such I had to adjust one of the analytical processes to use a masked-cluster analysis, which departs from the data-driven ethos of this thesis.

4.4.5 Conclusion

This chapter demonstrates the use of a novel VWM precision task in 72 children, identifying significant effects of retro-cue use, as well as associations with age and IQ. In a subset of these children, I was able to show that differences in *frontal* activity in response to different cue types relate to the overall accuracy of children. I have also shown that objective measures of SES show a negative association with both the maintenance of items in memory, and the ability to orient attention within these representations. At the neural level, I show that Subjective SES is related to evoked responses, likely representing passive perceptual systems, whereas Household SES predicts the activity underlying the attentional orienting in response to a cue

Chapter 5: General Discussion

I put forward several questions at the beginning of this thesis. Firstly, how would the different contributors to SES impact of neuro-cognitive processes? Secondly, which processes would be most related to SES & would this replicate Noble et al.'s dual model? Lastly, would neuroimaging modalities differ in their sensitivity to SES influences? After a very brief recap of the results, I review whether I have answered these questions.

5.1. Summary of Empirical Chapters

The purpose of this thesis was to explore the potential relationship between SES and neurocognitive processes, at multiple different levels of explanation. Across the three empirical chapters, I present five analyses on two samples of children totaling 200 individuals and their families. These analyses succeeded in establishing how SES predicts brain network architecture, activation patterns, and task-based activity. These results summarised in **Table 9**. Taken as a whole, the results in this thesis demonstrate both distributed and focused covariance between brain structure and function with objective, subjective and household related elements of SES. Brain networks yielded broad and complex SES-related activity (Chapter 2). The MEG functional networks reflected all the dimensions of SES. The structural networks varied more with the objective dimensions of SES, particularly in the Frontal and Parietal lobes, but were generally less predictive relative to MEG. Electrophysiological processes during a passive phonological oddball were specifically sensitive to Subjective SES, yielding lateralised temporal and frontal clusters. Whereas evoked activity from informative cues during a VWM task yielded a cue-evoked cluster which was significantly predicted by Household SES, and task-related activity.

Analysis	Areas	Lateralised	SES Impact
Structural	Distributed – Frontal, Parietal	None	Objective & Household
Functional	Distributed – Occipital, Frontal & Temporal	None	Objective, Subjective and Household
Phonological	Specific – Temporal & Frontal	Left – Temporal Right – Frontal	Subjective
Visual Working Memory	Specific – Frontal	Right	Household Subjective

Table 9. High-level summary of how different elements of SES impact different levels of analysis, and the topological properties of this.

5.2. Differences in the dimensions of socioeconomic status

Personally, one of the most exciting features of my analysis approach was the use of different orthogonal SES-related factors across chapters. Distinguishing between variability related to household factors, income & education, and self-identified status. This allowed me to parse potentially independent relationships within our data, when previous research often collapses these together. This became a great strength, as there is real nuance in the brain-SES relationship that would have been lost in a compound measure.

Below, I explore a potential explanation for each of these sets of associations. As will become clear, there is no single harmonious relationship that links all my findings together. There are likely hundreds, if not thousands, of potential SES-related factors at play, all contributing to the variation in the imaging data. However, I have chosen candidate explanations based on the results and the literature, which I feel provide the most compelling explanations significant common threads.

5.2.1 Subjective SES

Subjective SES was the most persistent brain covariate throughout the chapters of this thesis. In the phonological chapter it was the sole SES association; in the PCA resting state analysis, it was the only SES factor related to a PC network; and, in other sections, it was present and sat with other measures in predicting variance. What is it about this factor that explains its consistent relationship across MEG-derived neural measures? Whilst touched-upon in the discussion of Chapter 3, this is worthy of deeper exploration.

What does this SES measure represent? The key contributor to this factor was a parental ranking from worse- to best-off in the UK, called the MacArthur scale of subjective social status (Adler et al., 2000). This was a more abstract and personal question than straightforward reporting of income, education, household factors or postcode. It was the only SES question that taps how the caregiver *feels* about their socioeconomic standing. In the General Introduction I categorised absolute and relative measures of deprivation. Subjective SES firmly falls into the latter. It is a relative judgement, so not only does it reflect the affordances of the household, but it also effects the place that parent feels they fit into in the national community. In other words, variation in scores can come from two sources: the first is a more individualised assessment of affluence, the second is a personal judgement on how well *others* are doing around them. Let's consider how each might impact a child's cognitive development.

In the UK, like many countries, there is a class-system. This is a codified and stratified system, where individuals are categorised based on their family, education, income level, use of language and cultural values. Historically this has been viewed as three hierarchical levels: working class, middle class, and upper class. More recent evidence suggests these concepts have drifted into more atomic structures – culminating in the Office for National Statistics's socioeconomic classification (NS-SEC) with 8 analytical classes with 17 further categories (Chandola & Jenkinson, 2000). Despite these classification changes, many people in Britain still identify themselves along the lines of traditional class. In 2013, over a third of people self-identified as 'working class', and surprisingly more than half of those in professional and managerial occupations (i.e. not typically working class) identified in this category (Park et al., 2013). In fact, class identity can stay static across generations, being relatively unaffected by an individual's

current social and economic state (Rubin et al., 2014). This outlines two things. Firstly, that class identity is still important to people in the UK. Secondly, that self-identification does not necessarily reflect the current occupation or wealth of the individual and can often reflect family history and birthplace (Heath et al., 2009). In schools, being a member of a perceived lower social class can have a negative impact on attainment through un-intentional discrimination. Uniform codes, accent correction, and social exclusion from extra-curricular activities, all have an impact beyond simple objective affluence (Adair, 2009; Langhout et al., 2009; Ostrove & Cole, 2003; Rubin et al., 2014). Class has long been thought to contribute towards the difference between the stated objectives of a school education, and the extra skills which support social success, called the 'hidden curriculum' (Anyon, 1980; Portelli, 1993).

Most importantly, class-membership, even when self-identified, is likely to influence multiple factors proximal to child development, like attitude to healthcare (Blacksher, 2008) and parenting styles (Sherman & Harris, 2012). Via these mediating factors, this relatively crude, but remarkably explanatory, measure of SES could have a general impact on the cognitive and brain development of children and could account for the distributed effect we see in the MEG connectome. One candidate route for these impacts, and a key domain in how social class manifests, is language. A key indicator of social class in language is the pronunciation of words. For example, 'Received pronunciation' is historically associated with the upper-class, and became the de-facto accent for teaching in schools well into the late 20th century (Honey, 1988), later 'normalising' a standard accent. Deviating from culturally 'standard' accents have been shown to illicit negative judgement on professional competence (Levon et al., 2021) and trustworthiness (Fuertes et al., 2012), even detectable on the electrophysiological level (Pélissier & Ferragne, 2021). This bias starts early. School children have been shown to judge accents as more or less 'smart' or 'nice', independent of their own accent, and without demonstrating any stereotype knowledge (Kinzler & DeJesus, 2013). It's reasonable to assume that pronunciation varies with subjective SES, and the impact of social class and language this represents will play some role in cognitive development and educational outcomes. It is likely this occurs through peer and teacher judgements (Ahn & Moore, 2011; Loban, 1968; Peterson, 1994). This would likely lead to a general impact and explain why we see a broad relationship between subjective SES and resting state, phonological, and VWM processing. Unfortunately,

this hypothesis assumes accent, class and subjective SES ratings are linked in our sample. In hindsight I would have included some accent assessment and class questionnaire with the parents.

Beyond accent, there may be a deeper and more specific role language plays in our results. This is explored in Chapter 3, where I speak about linguistic environments. Self-Ratings of low SES may be particularly sensitive to the quality of linguistic environment during a child's development. Highly cited work by Hart & Risley (1995) outlined that children in low SES families were exposed to threefold fewer words at home before kindergarten, and this translated into poorer language skills during pre-school years. This occurs because higher-SES caregivers have a greater vocabulary (Hoff, 2003), and are able to spend more time with their children paying them direct attention (Tamis-LeMonda et al., 2001). This relationship is also reflected on the electrophysiological level. Brito et al. (2020) studied infants and confirmed the association between SES and language input reported above and conducted an analysis with resting state EEG. The authors reported reduced beta power in relation to language input, but this was only the case for children who lived in homes with high levels of unpredictability and noise. In my PCA analysis, the beta PC network also consists of parietal connections which decrease with higher subjective SES (**Figure 10**). This language impact, is a key pathway in how SES impacts the developing brain set out by Noble et al (2012). The convergence of my data here – the phonological task associations, the beta PC network similarities with Brito et al. (2020) – lend support to this hypothesis, but narrow it specifically to subjective aspects of SES.

In addition to identity, I also believe that subjective SES represents a more sensitive assessment of the environment and means of a household. The only other measure that weighs any meaningful amount onto the subjective SES factor is the families Index of Multiple Deprivation (IMD) score. This reflects the affluence of the family's postcode, representing the area's relative ranking in terms of income, employment, education, health, crime, living environment, and access to housing services (Noble et al., 2006). This implies that the care-givers judgement reflects the level of surroundings to some extent. It's also interesting to consider what subjective SES does not relate to. It was very notable the seeming lack of structural association in the first empirical chapter (**Figure 14**) - even amongst the relatively low scores of other factors. To me, this suggests that subjective SES may not overlap with absolute

deprivation – which *would* lead to things like white matter differences in the brain (Hanson et al., 2013). I think the shared variance between subjective SES and the IMD represents the community aspects of the local area, rather than lack of resources. Combining all this together, I think the correlations with subjective SES reflect a combination of family social-identity, and the impact of relative affluence, on the developing brain. As far as I could ascertain, this thesis represents the broadest exploration of subjective SES and electrophysiology, with these potential influences being separated from objective factors. This next step is a thorough investigation of this interesting construct, using both qualitative and quantitative approaches, to disentangle its potential constituent processes.

5.2.2 Household SES

The remaining two factors – Household and Objective SES – are tied together in that they both describe measurable objective factors. Household SES maps closely onto whether a child shares a bedroom, and slightly less upon how many books are in the house. Whereas Objective SES maps onto income, education, postcode, and occupation. Unlike Subjective SES, they do not consider the parent’s own judgement of affluence. I think associations with these directly measurable constructs reflect the impact of more absolute factors in the child’s life – like the quality of their sleep, diet, and general home-environment. Whilst general SES association was low in Chapter 2’s DTI analysis, Household SES and Objective SES had seemingly specific peaks in the frontal and parietal lobes respectively (**Figure 14**). As alluded to above, this may suggest that these absolute factors reflect actual deprivation, large enough to have an impact on the structural organisation of the brain.

First, let’s consider Household SES. There could be several contributors to associations with this factor. But, in my opinion, one solid candidate is sleep quality. This is first outlined in Chapter 4; the quality of a child’s sleep is reduced when sharing a room. I am not suggesting all children who share a room will have poor sleep, it simply means it is more *probable*. There is precedent for this: Buckhalt et al. (2007)’s study on SES, sleep and cognitive function found that the *only* factor related to Household SES in their sample was the probability of sharing a bedroom or not. They also showed that SES moderated the impact of poor sleep on cognitive performance – higher SES children were less impacted by poor sleep. This demonstrates a clear link

between SES, bedroom sharing and cognitive development. Sleep hygiene describes the use of multiple behaviours to promote good sleep. This might include avoiding daytime napping, winding down mentally before bed, restricting caffeine intake, and avoiding technology use before sleep (Carskadon, 1993). Whilst I've already outlined the potential impact on VWM, the consequence of poor sleep hygiene extends further. Poor sleep in children and adolescents results in issues with emotional self-regulation (Baum et al., 2014) and resulting behavioural issues (Wiater et al., 2005), weight-gain (Fatima et al., 2015), cardiovascular health (Quist et al., 2016), executive functioning, reasoning and problem solving (Spruyt, 2019). Sharing a bedroom has repeatedly been associated with poorer sleep quality, duration and hygiene in children and adolescents (Jenni et al., 2005; Mindell et al., 2009). This sharing has also been identified as a contributory factor to poor sleep in low SES households (Buckhalt et al., 2007; Marco et al., 2012).

What are the mechanisms by which poor sleep may affect the brain? Sleep disruption due to apnea (where oxygen supply is impaired) leads to hypoxic damage, slowing the grey matter volume in children (Beebe & Gozal, 2002; Philby et al., 2017). However, the disruptions we describe here are externally generated, causing fragmented and shortened sleep. Similar grey matter volume reductions have been reported in non-apnea children – particularly in areas like the dorsolateral pre-frontal cortex (Kocevska et al., 2017). A candidate for this association is that sleep allows synaptogenesis, and that disruptions in sleep quality can limit this process, causing macro-architectural differences in the brain. This is supported by animal work, which shows that sleep deprivation induces expression of stress-response genes, which then limit cellular growth (Cirelli, 2006). Sleep could also impact brain processes via altering homeostatic plasticity mechanisms like synaptic pruning and potentiation (Cirelli & Tononi, 2015; Kocevska et al., 2017). Supporting this explanation, slow-wave activity during deep sleep between 8-19 years old is tightly coupled with the development of area and thickness of various brain regions (Buchmann et al., 2011). Slow-wave sleep has an established association with plasticity, established in human and animal models (Miyamoto et al., 2003; Tononi, 2009). The strongest sleep related decreases in cortical thickness as children aged occurred in the parietal lobes, where slow-wave activity was most localised (Buchmann et al., 2011). This theory is consistent with data presented here, with the strongest structural associations of Household SES – by quite a distance – localised to the parietal lobe (**Figure 14**).

5.2.3 Objective SES

Objective SES is the last environmental factor I consider. This factor bundles together: equivalised household income, parental occupation, parental education, IMD, and free school meals status. This is the closest thing to the ‘classic SES’ measure that our data-driven decomposition produces. That these different measures load onto a shared factor speaks to the high covariance between education, work, postcode, and salary, which is uncontroversial. An alternative label for all these things could be ‘affluence’. This objective factor is the one most directly comparable to how previous research has measured SES. Despite this, I found no evidence of its *neural* involvement in either of the task-based chapters. This really underscores the importance of my factor-based approach and implies that other studies may have been conflating household income & education with subjective factors and household attributes. However, it is important to remember that our sample is geographically restricted, which is very likely to reflect the SES diversity of East Anglia. The importance of this factor might change had we sampled a more extreme SES spectrum.

First let’s consider what is potentially different about this sample demographically from previous studies, and how these differences may be reflected in my findings. The fact education levels, and income here are connected tightly, suggests they do not have a differential impact. This contradicts the narrative in previous research, that the impact of income differs in predictive degree from education (Akhlaghipour & Assari, 2020; Noble et al., 2015; Zill, 1996). For example, Lawson et al. (2013) reported that parental income but *not* education predicted developmental changes in anterior cingulate gyrus and left superior frontal thickness. In the present sample there was no evidence for these differences. Beyond the sampling issues spoken about, a key difference in our study that may account for this lack of differentiation, is the healthcare system in the UK. The studies cited above are all based in the U.S., where access to medical care is mostly with private health insurance and income (Papanicolas et al., 2019), this means that U.S. families treatment availability is paired with their income more than in the UK (Schoen et al., 2010). As access to healthcare closely predicts outcomes for children from relatively early on (Brooks-Gunn & Duncan, 1997; G. J. Duncan et al., 1998), one might expect income to predict outcomes more than parental education, in a country with an income-related healthcare provision.

Given that there are no links between Objective SES and neural activity during either of my tasks (Chapters 3 and 4), I will focus on interpreting the network results in Chapter 2. The functional connectome seemed to show a broad pattern, but with a big peak in the Occipital lobe. When I used the PCA analysis to make the results more digestible, no PC network was associated with Objective SES. The structural connectome showed its strongest Objective SES-related connections in the frontal and temporal lobes, with two big peaks in the left orbitofrontal cortex (OFC) and right superior temporal cortex (STS). This converges with Lawson et al. (2013), who found a specific interaction effect between Age, parental education, and the left OFC – education decreased the impact of SES-related thickening over age. Rolls et al. (2020) review decades of research into the OFC’s role and make a case for it as a hub-node in reward processing across multiple modalities and levels. That the affluence of a child’s environment influences reward processing is a tempting interpretation of our findings. However, in the absence of any direct measure of reward processing, this is impossible to confirm. Similarly, the association between the right STS and Objective SES is consistent with links between SES and language processing (Biazoli et al., 2020). However, I then failed to confirm this effect in the MEG phonological oddball task in Chapter 3 – there was a potential temporal effect, but it was on the left, and it related to Subjective SES. There is however a lot more to skilled language use than phonological processing, so it would be important to conduct a more thorough exploration of active language processing in future.

Despite the absence of significant associations between task-related neural activity and Objective SES, I did find a behavioural relationship in the VWM task. Higher Objective SES predicted increased precision, and an increased benefit of cueing. This suggests that Objective SES is significantly associated with working memory precision, and the ability to orient attention within memory. But this poses an interesting question – why is there a behavioural impact without significant neural correlates? This could simply be a difference in noise levels between behavioural and neural data. The neural correlates in my active chapters were particularly noisy, so it’s entirely possible there *was* underlying activity, and it was not detected. Still, the other covariates – household and subjective SES – *were* strong enough, and that itself tells us something. It fits the narrative that when we separate material affluence from subjective identity and household factors, the former relates to brain activity less. As explored above when

discussing Subjective SES, economic and parental measures may be less sensitive to the day-to-day environment children *experience*. To put this into an anecdote - a child having a poor-night's sleep, in a chaotic household, would intuitively be less able to focus on a WM task – but what independent variance would their salary or education level explain? Probably not much. This may explain why Objective SES is a much weaker correlated of neural activity during task performance.

5.3. Implications for existing theories

The work in this thesis adds to a large and growing literature. Specifically, Noble et al.'s theory, suggesting dual routes for SES' impact on the brain and cognition. The first is linguistic environment impacting language through the left hemisphere language cortex (mostly temporal regions) (Noble et al., 2012; Ursache & Noble, 2016). The second is a stress route, negatively impacting inhibition through the hippocampus, amygdala, and pre-frontal cortex. How well do the findings of this thesis align with this theoretical framework?

Let's consider the first route. Most relevant here is Chapter 3 – the phonological processing chapter. I report a cluster related to Subjective SES at approximately 400ms after the final phoneme. This is contingent with the later ERP components, associated with semantic and attentional mechanisms during oddball tasks (Bennington & Polich, 1999; Meador et al., 1987). This effect, and the passive nature of our task, are consistent with previous EEG language work reviewed by Ursache & Noble (2016). They state specifically, that whilst there may be equivalent behavioural competencies between SES groups, the underlying mechanisms in the brain differ. This makes the passive oddball design particularly appropriate. Furthermore, the clear topology of this phonological cluster effect is also consistent with Noble et al's characterisation of the impact on left-hemisphere language networks. We also see language related areas, like the left temporal lobe re-appear in network analysis in Chapter 2, on a structural and resting state level. Based on both chapters, I think the findings of this thesis are broadly consistent with the presence of a language-related pathway via which SES impacts cognitive and brain development.

There is less substantial evidence in this thesis for a second, stress-inhibition, pathway. But this may reflect the absence of a task directly assessing inhibition. The

closest is the VWM task in Chapter 4. As discussed in the chapter, it is probable a portion of behavioural and neural differences in relation to cue-processing, partially tap into inhibition, as there is substantial evidence from elsewhere that cue use recruits inhibitory processes (Facoetti & Molteni, 2000; Händel et al., 2010; Houghton & Tipper, 1994; van Moorselaar & Slagter, 2020). Children with lower SES measures do indeed show reduced cue benefits for precision. The evoked cue response was also correlated with Household SES. Interestingly, the topology of this was firmly in the pre-frontal cortex, which is consistent with the cortical area described by Noble et al. The authors reference a review by Arnsten (2009), which suggests pre-frontal activity is sensitive to even mild stress, because the PFC has a relatively high proportion of receptors that are sensitive to small changes in stress hormones. This subtler stress-axis may explain these VWM-associated prefrontal and behavioural effects. The range of SES in the sample here is large but not likely to contain a significant group suffering serious poverty. Another observation supporting this stress-inhibition pathway, is the presence of the late component in phonological analysis. In Chapter 3 I mentioned this could have an attentional component to it, as the timing of the later SES cluster was consistent with attentional orienting and semantic processing (Bennington & Polich, 1999). All this considered, I think some evidence for the Noble et al.'s second pathway, but in the absence of a direct inhibition assessment this remains tentative.

Finally, it is also worth considering the findings in this thesis which clearly do not align with this theoretical perspective. For instance, whilst we find a pattern consistent with the language and memory impacts of SES, there is no evidence here for differences in emotion processing. This is unexpected, as it plays a key role in Ursache & Noble (2016)'s framework. In fact, there is much evidence for such an association in previous work, in both emotion recognition (Edwards et al., 1984) and regulation (Cymerblit-Sabba et al., 2013b; Edwards et al., 1984; Kim et al., 2013b; Liberzon et al., 2015). One potential explanation for this, is the use of cortical parcellations, excluding the sub-cortical hippocampus and the amygdala. These are key areas in the literature which SES is proposed to impact. I still would have expected to see more consistent patterns of SES related connectivity in DTI or MEG in hippocampal adjacent cortical areas or with connectivity to the amygdala, but this was not the case. I suspect the cause of this could again be due to the restricted range of SES in the sample. That more severe poverty is needed to see this effect, rather than contradicting existing literature. In a more general

sense, in Chapter 2, both the structural and functional connectomes exhibit an overwhelming range of connections (in the scale of 1000s) between all parcellations. This cannot be dismissed as simply noise, as the robust permutation procedure would have eliminated this. This is instead evidence of a distributed, and complex, set of associations with SES in the brain. This problem is analogous to the system-blindness in the GWAS genetic studies I described in the introduction. Simply put, we can explain a lot of variances in these complex systems, and at the same time extremely impaired in the identification of mechanisms. It is probable the mechanisms and theories promoted within the literature so far explain just a proportion of this variance. This still leaves a large amount unaccounted for. The use of evoked activity in Chapter 3 and Chapter 4 – where a baseline is subtracted – ensures that this ‘unrelated’ variance is partialled out. So, by the nature of the technique, we find specific associations. This could give a false sense of parsimony, but if we were to repeat this with different tasks, other areas would likely be associated with SES. In the end I think identifying the process through which SES reflects upon brain activity needs to be a cumulative scientific endeavour, and we should avoid making system-level claims until more aspects (genetic, hormonal, neural, functional, behavioural and social) have been investigated. Key to this is more multi-level investigations, using multiple modalities and tasks within the same sample, such as this thesis and Tarullo et al. (2020). This approach permits the tying together of empirical observations to provide a more complete picture. That said, we must consider the representativeness of those samples - there are simply too many social differences between individual countries to ignore.

5.4. Functional networks more sensitive to SES than structural networks

Functional networks – characterised by MEG modelling – demonstrate a much stronger predictive value than structural networks when it comes to SES. This is highly relevant to a large swathe of the present literature, as it is more common for researchers to look at structural markers of SES, deprivation, and related developmental trajectories. For example, highly cited articles examine the trajectory of cortical thickness and SES (Lawson et al., 2013; Piccolo et al., 2016). But my work shows that functional markers are much more sensitive to covariates like SES. Much of the existing theoretical frameworks draw from structural brain imaging, or restricted contrasts in fMRI studies.

Here I show that these approaches reveal only a portion of the mosaic. It is possible, and likely, that a greater deal of the impact of SES takes place in overlooked functional networks

One explanation for the sensitivity of functional networks to a child's environment, relative to that of structural networks, is simply that impact of socioeconomic disadvantage on the brain extends less into physical architectural brain changes. Alternately, there could be differences in the measurement properties of these two techniques. SES could still impact the physical architecture of the brain, but the DTI connectomic measure does not capture this. Deciding between these explanations do not change the suggestion I make – that MEG is more appropriate than DTI for studying SES – but they do affect the *interpretation* of the results on a systems level.

First, let us explore the idea that SES somehow has a greater impact on functional networks. There is nothing in the existing literature which compares the SES-predictive strength of a functional connectome against a structural one. However, there is work that explores *which* brain networks show stronger or weaker structure-function coupling. Horn et al. (2014) used simple correlations to compare exactly *where* resting state fMRI and DTI connectomes matched. Ares in the Default Mode Network (DMN) showed a stronger inter-connectome coupling than other brain areas. This tells us that some networks exhibit a stronger convergence of structure and function than others.

Therefore, it is possible that SES happens to impact networks that have a weaker structure-function association, like the DMN. Using the example of the DMN, researchers have repeatedly found evidence for its sensitivity to SES factors, such as: neighbourhood affluence (Lawson et al., 2013; Rakesh, Seguin, et al., 2021), household income (Rakesh, Zalesky, et al., 2021), and childhood poverty (Sripada et al., 2014). I found DMN hub-areas in both MEG and DTI analyses which had high degree associations with SES. For example, one of the few areas with a high relation to Household SES in the structural connectome was the posterior cingulate cortex – a pivotal area in the DMN (Fransson & Marrelec, 2008). Work by Gu et al. (2021) show that the parcels with the lowest coupling are in the temporal lobe. Consistent with this, temporal areas in our DTI connectome show relatively little relationship with SES in contrast to the MEG connectome. Put simply, it may be that SES happens to impact

networks that are less well defined by anatomical connections, and therefore these associations are more easily identified with functional imaging.

What about other explanations for this apparent functional versus structural sensitivity difference? Our data are cross-sectional, with each child scanned at one point. It is possible that structural changes will happen after this scan, being preceded by functional changes. This function-to-structure pathway is well-established in the mental health literature. That negative functional changes related to a psychopathology like depression, eventually impact on structure, and support the ongoing maintenance and re-occurrence of symptoms (Bremner, 2002). This is usually interpreted as reflecting Hebbian plasticity – neurons which fire together, wire together. Altered neural activity related to psychopathology leads to structural changes, but this takes time. In addition to this, the coupling of structural and functional networks is not static across development, but itself changes. Baum et al. (2020) characterised the degree of association between DTI networks and fMRI networks during an N-back task, between the ages of 8 and 26 y/o. Multiple areas show changes over development in structure-function coupling. Specifically, decreased correlation in areas specialised to one function (like sensory cortices), and increased coupling in trans-modal areas, like those in the DMN. Had we scanned our participants a couple of years later, we might see a different relationship between my MEG and DTI connectomes. The additional developmental time may enhance the sensitivity of the DTI connectomes to SES influences. Longitudinal data collection for this sample are indeed underway, so this is a hypothesis that can be tested in future.

Another explanation for this functional-structural discrepancy is the inherent difference in what each connectome represents. Structural architecture underlies a good deal of neurophysiological communication in the brain. That is, physical connections in the form of neurons, myelinated fibres, and so on, provide a substrate for electrical signals to carry communications between regions (Sporns et al., 2005). But we also know that functional connections are not directly constrained and can be routed through many potential non-direct pathways. For instance, we can measure functional coupling between areas without a direct anatomical link. An example of this is polysynaptic pathways – routes of communication which jump through synapses. It has even been proposed that cortical neurons can communicate extra-cellularly (i.e., not through synaptic connections). This is achieved through processes like ephaptic

coupling, wherein neighbouring neurons influence each other through extracellular electrical fields (Anastassiou et al., 2011; Martinez-Banaclocha, 2018). Or global neuromodulation through large scale magnetic fields (Jones, 2017; Marshall et al., 2006; Tiganj et al., 2014). The role these mechanisms play in the scale of networks here is unquantified in the context of global connectomics, and some elements are controversial (Weiss & Bikson, 2014). The point remains that the functional connectomes are less limited than their structural relatives.

The above three explanations are not mutually exclusive, and each may contribute to the relative supremacy of MEG connectomes to their DTI counterparts. A good example of a distributed, age-related, uncoupled networks would be those supporting language. Language function is supported by interactive, distributed networks (Fedorenko & Kanwisher, 2009; Fedorenko & Thompson-Schill, 2014). Functional activity in this network has shown to be decoupled from structure measured by DTI (Morgan et al., 2009). It is also more spatially distributed in children relative to adults (Friederici et al., 2011). This could be one constituent source of our network differences. Any SES impact on this system is likely to be less reflected in the direct structural connections in our age group, but quite possibly picked up by the MEG connectome, which is what we see.

5.5. Potential impact

Variance in SES has huge significance to our society, particularly for those who experience socio-economic hardship and adversity. In this thesis I outline how variability in SES is reflected in structural and electrophysiological networks, and how this may be involved in some cognitive activities. As mentioned above, a strength of this thesis is the focus on different contributors to SES. The results outline differential influence on task performance and neurophysiology. This underlines the importance of separating out SES for policymakers when attempting to address negative outcomes. For instance, attempting to improve household income may not have the expected impact if the issue in a community lies in bedrooms sharing due to available housing stock. Improving the quality of housing to provide more space to families and children could be a better use of limited resources. One benefit of this understanding may be in informing targeted interventions. For instance, perhaps working memory training could lift some of the burden experienced by low-SES children. However, I think this may be

a distraction from the issue at hand. These impacts are caused by material deprivation, stress placed on parents through work, and a society which discriminates on a cultural level. Any intervention that does not address these root causes is likely to act as a sticking plaster. Treating the symptoms, if you will. I spoke about how the UK is currently experiencing an increase in *both* relative and absolute poverty. Reversing that will do far more to benefit children and families than any piecemeal intervention. I therefore view the work presented here as documentation of the impact my SES factors has on children, rather than solely as a route to inform interventions.

5.6. Conclusions

I present a body of work which attempts to capture the complex set of associations between SES and a child's brain and cognition. I do so by traversing a granular analysis of large-scale networks, to a passive electrophysiological processing task, and finally into visual working memory. Subjective ratings of SES seem to act as a vein, running through all these levels, and is particularly predictive of functional data. Household factors also have an impact, possibly reflecting the impact of poor sleep. A factor representing income and parental education was less predictive and appeared to operate on a more structural level. Finally, in general, I show that functional measures are more sensitive to SES than their structural counterparts. These data support some existing models of the impact of SES, but also that there are many small effects that indicate a much broader relationship than these models imply

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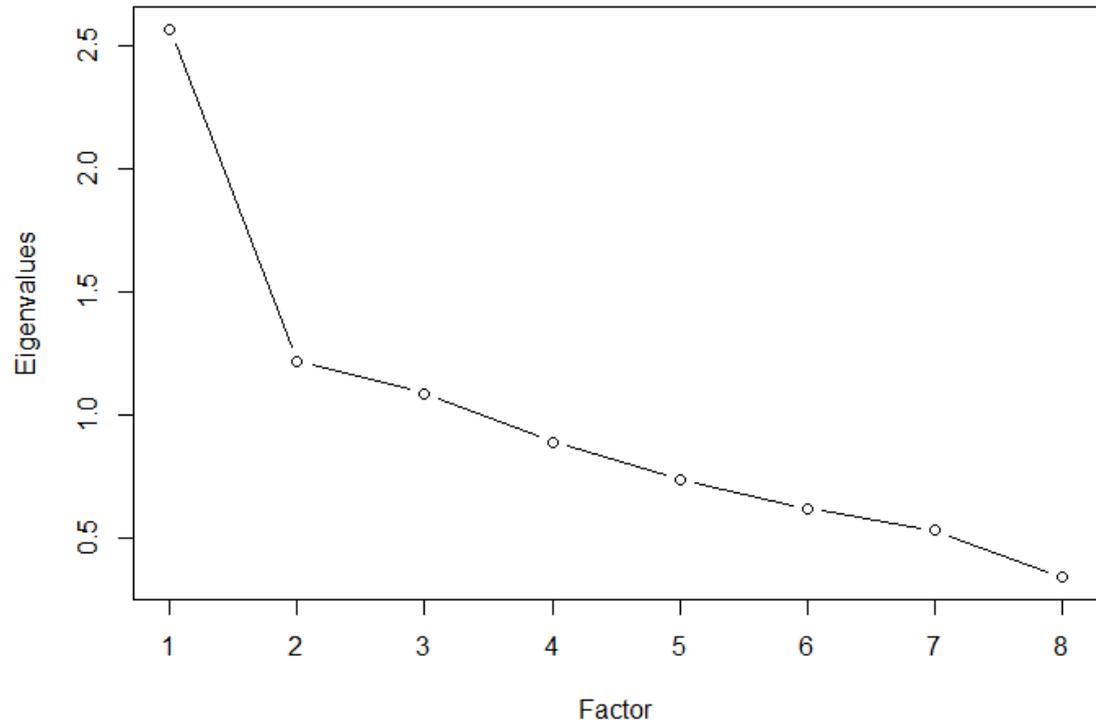
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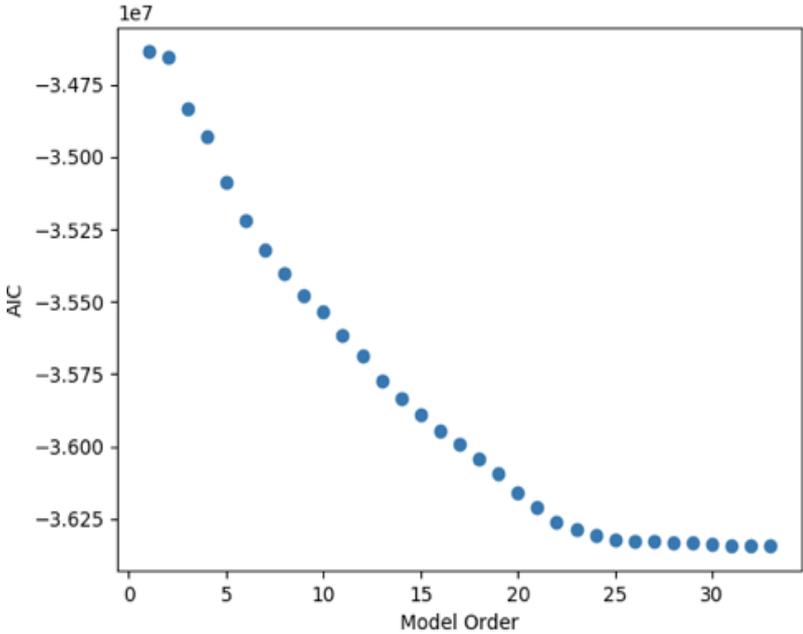
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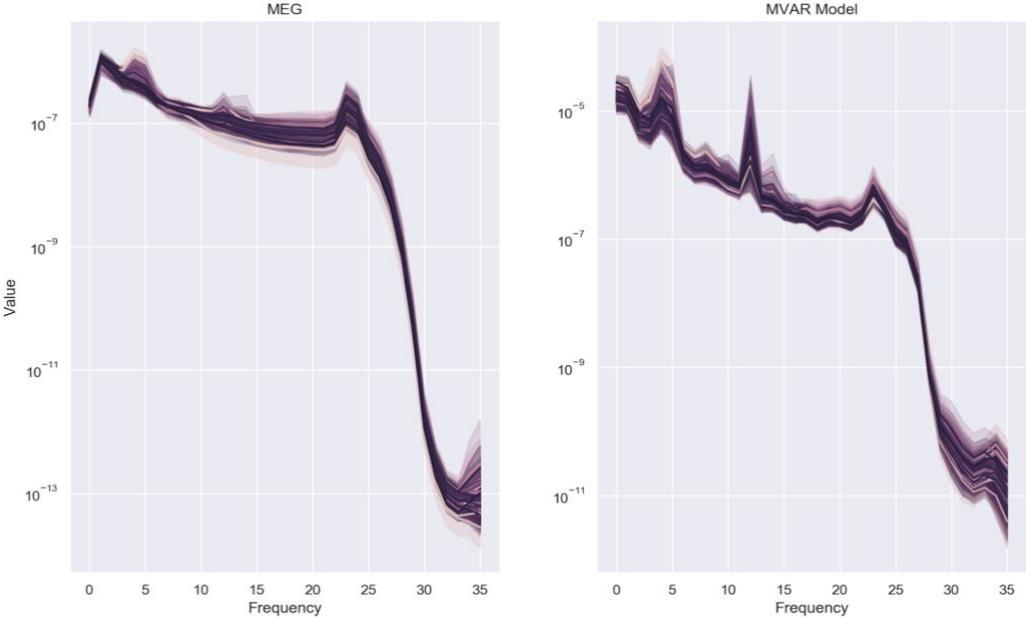
Supplementary Material



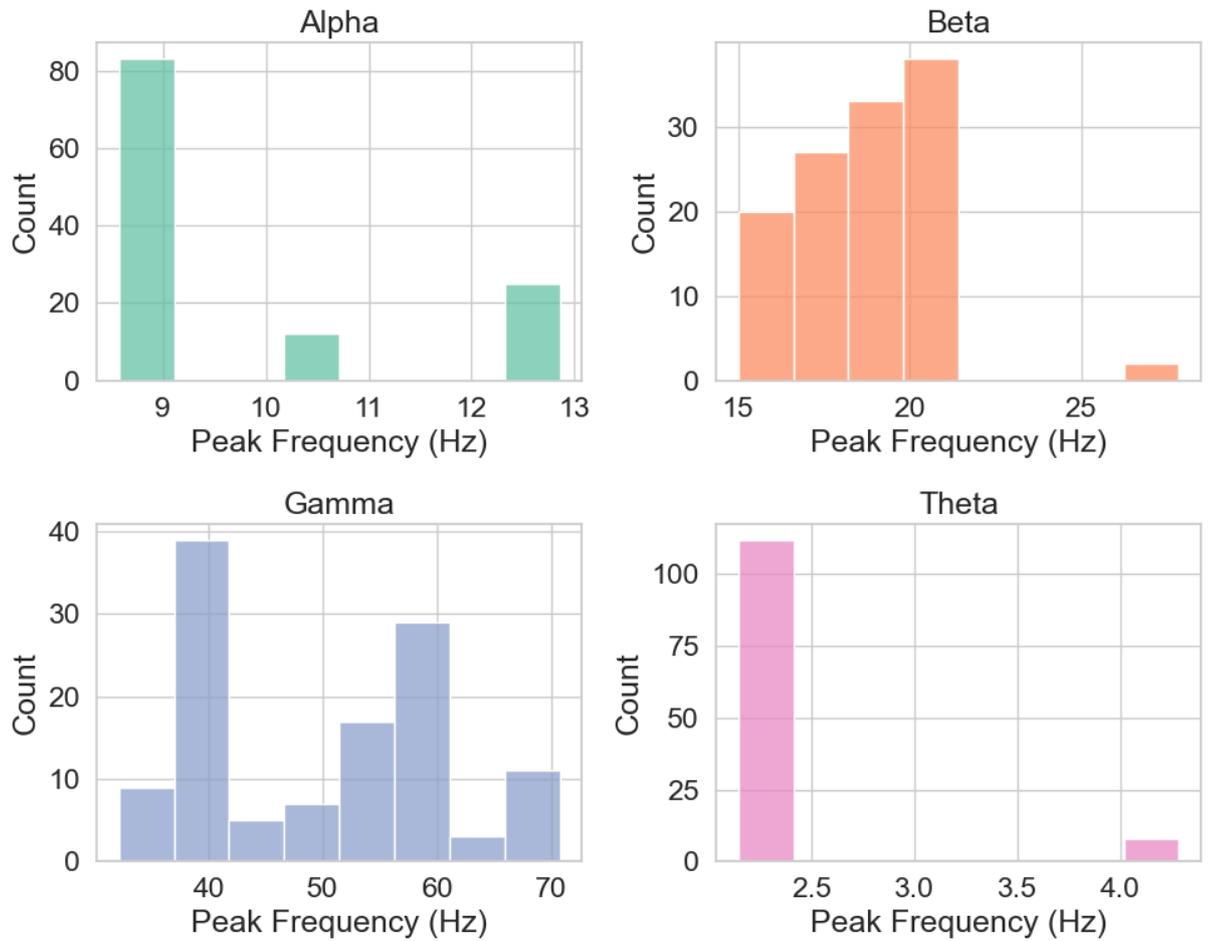
Supplementary Figure 1. Cattel's Scree plot of eigenvalues showing a three-factor solution as the most appropriate according to Kaiser's criterion.



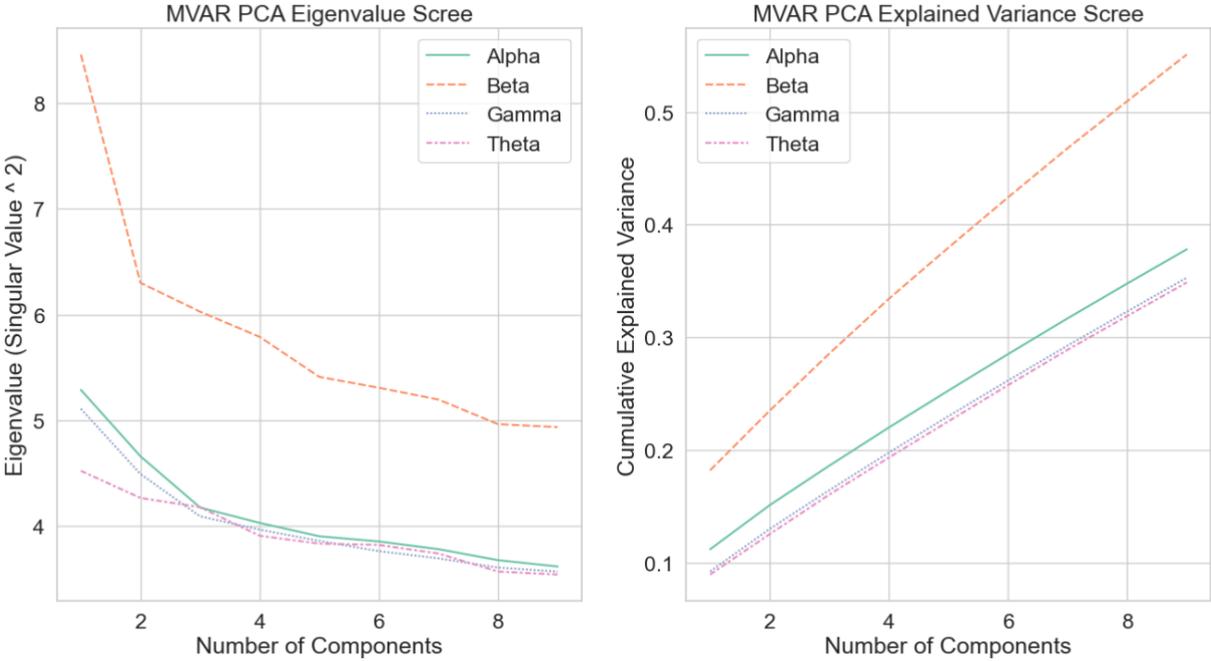
Supplementary Figure 2. MVAR Model order comparison using Akaike information criterion (AIC). Dots represent models, AIC is shown on the Y axis and Model Order is shown on the X axis. This is an average across participants



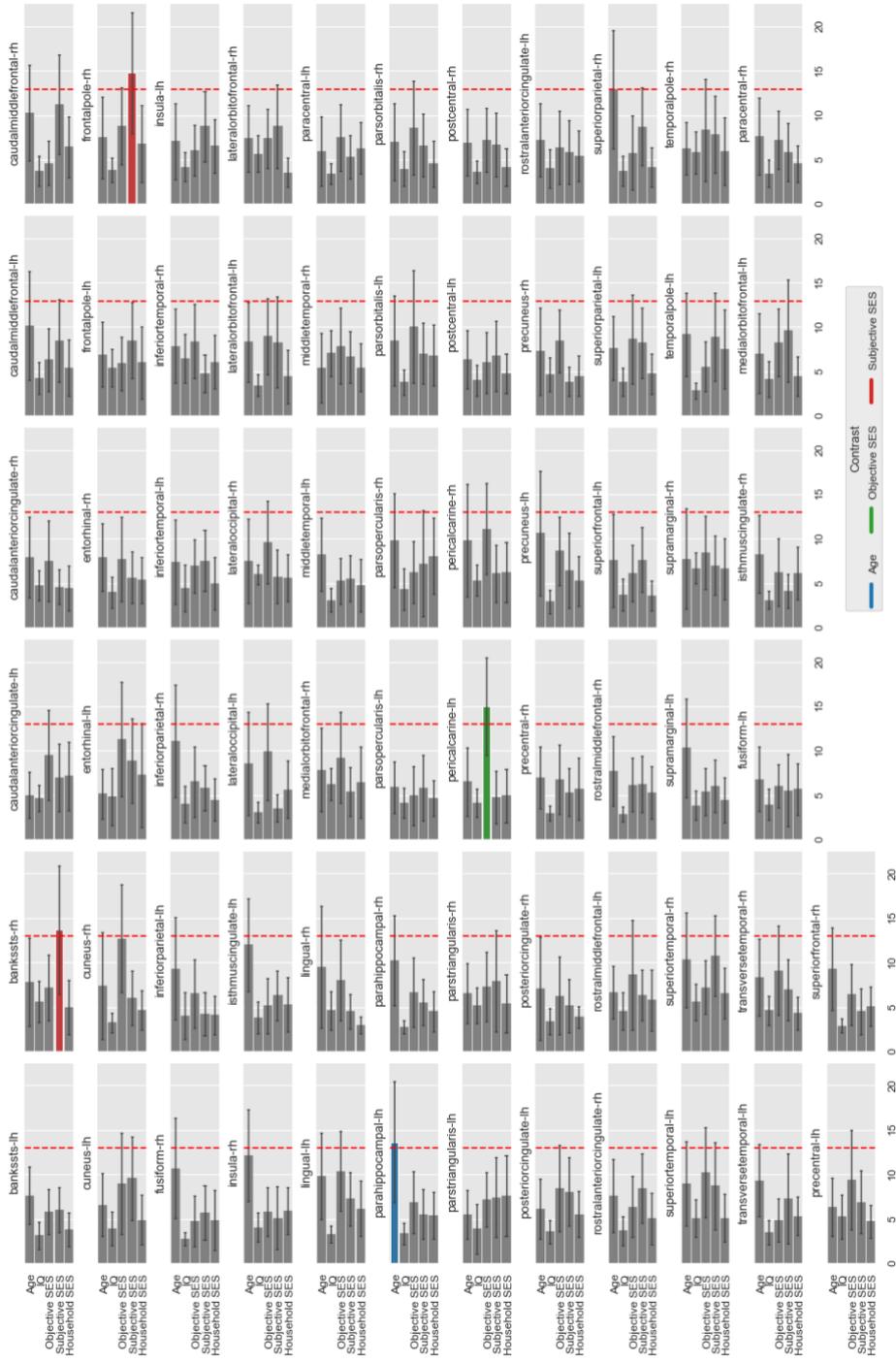
Supplementary Figure 3. Comparison of Power Spectrum Density between MEG data and MVAR Models. Y axis represents the density value and is on a log scale. The X axis represents frequency bin. Mean time courses of 68 Parcels are represented by lines, with SD shaded across participants in a lighter shaded area.



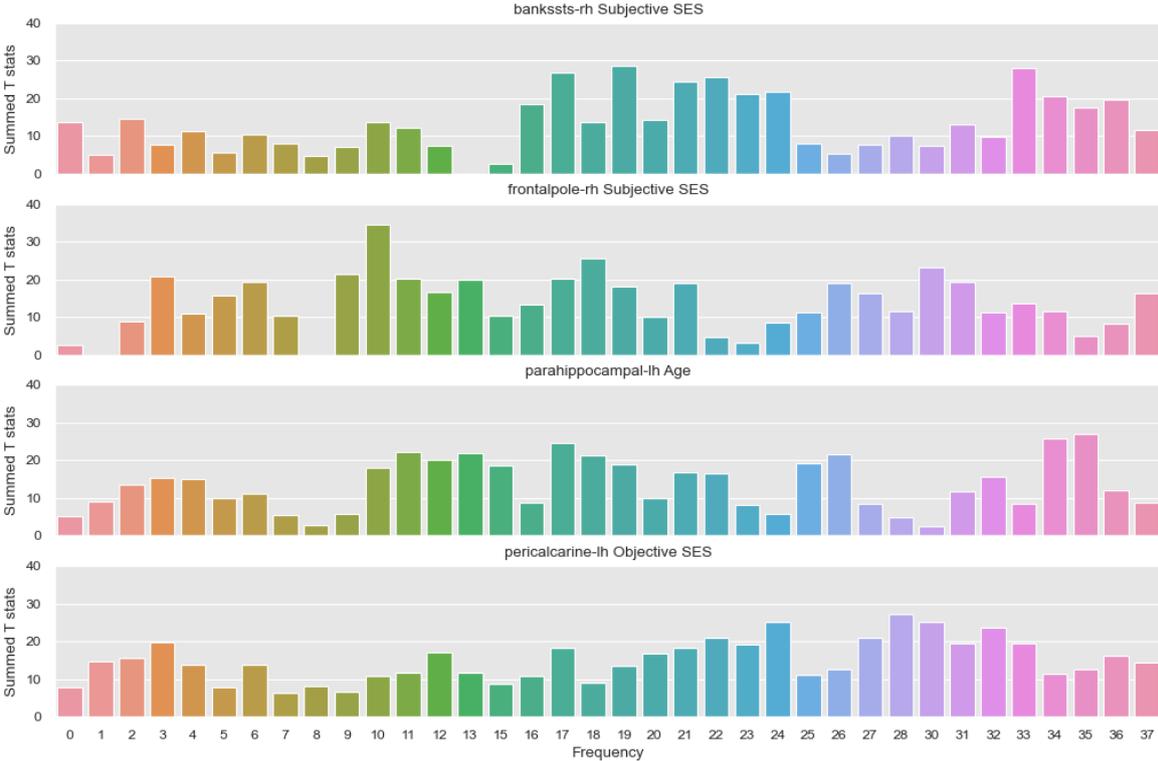
Supplementary Figure 4. Peak frequency distributions across participants for each frequency band: Theta (1-7Hz), Alpha (7-13Hz), Beta (13-30Hz) and Gamma (30-75Hz). The peak frequency was determined by the frequency within the band's range with highest mean Partial Directed Coherence value across all parcel-parcel connections.



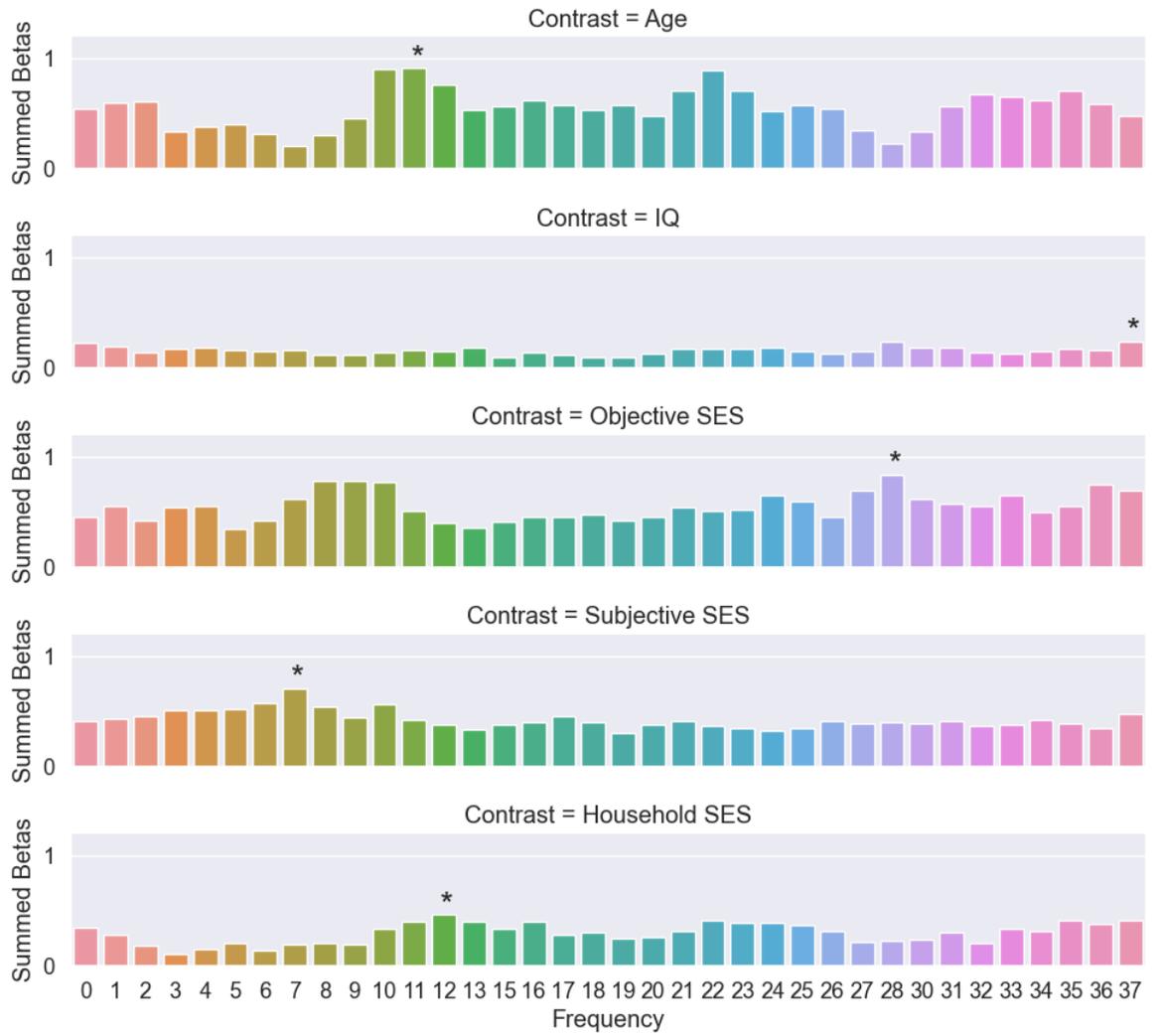
Supplementary Figure 5. Eigenvalue and Explained Variance scree plots for the MVAR PCA model. Eigenvalues were calculated as the square of the singular values and the explained variance was these value for each component divided by the degrees of freedom in the model and cumulated.



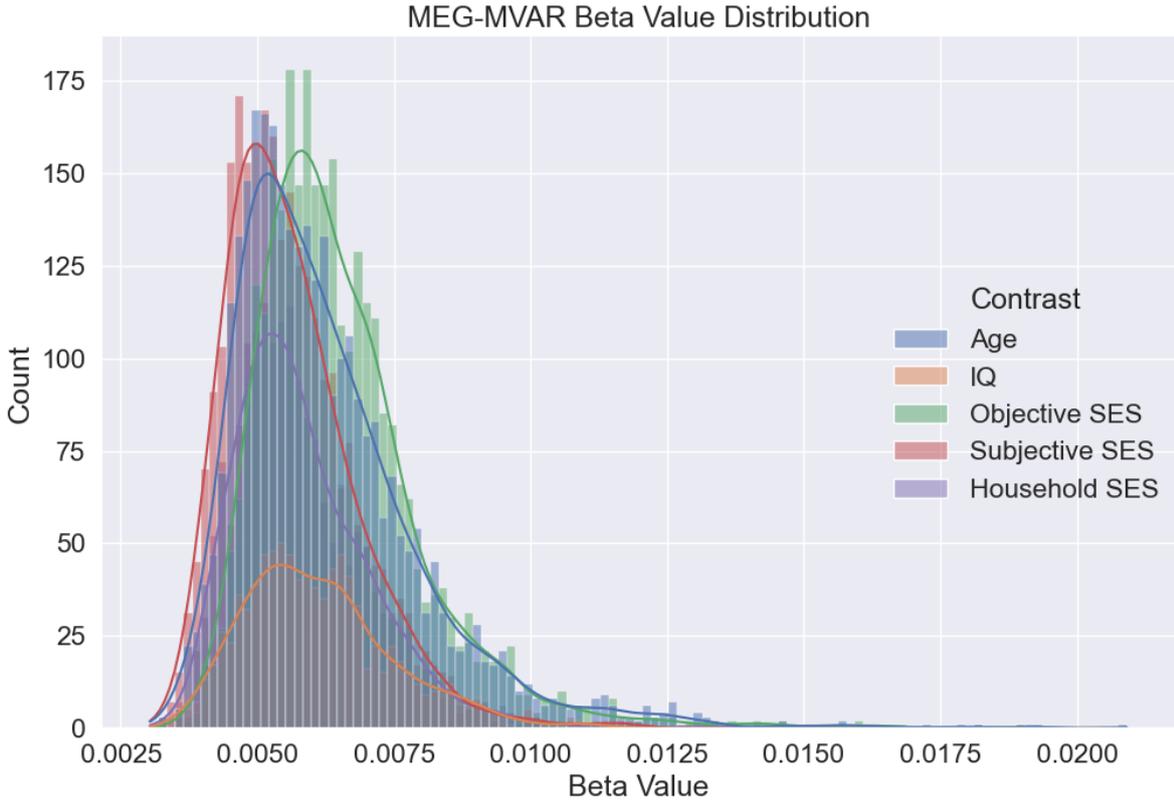
Supplementary Figure 6. Bar plot showing summed T statistic for each parcel and contrast averaged over frequency. Highlighted bars represent the parcel-contrast combinations that passed the 10% threshold. The highlighted bars show a clear distinction in t values from most of the other contrasts in their parcel



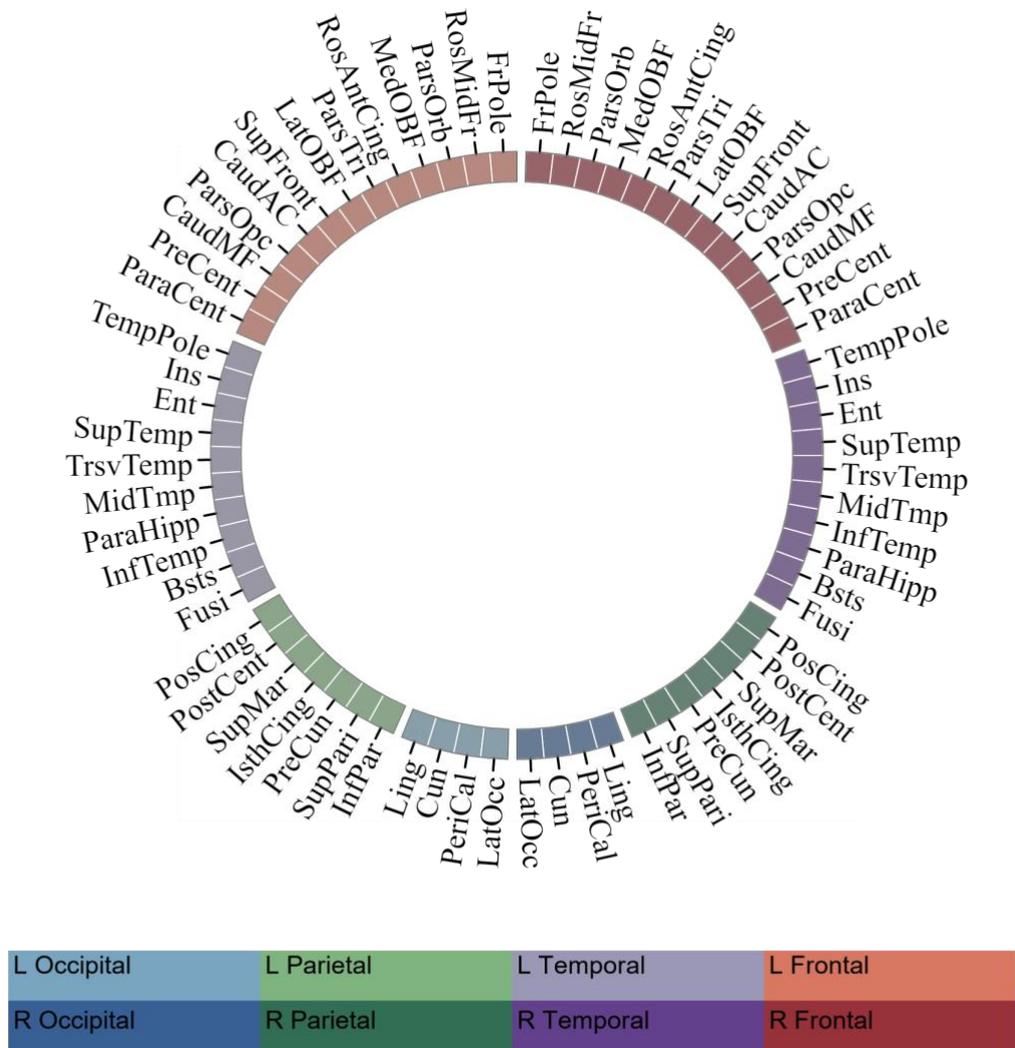
Supplementary Figure 7. Frequency distribution for parcel-contrast combinations above 10% threshold by t-statistic in the MVAR GLM model.



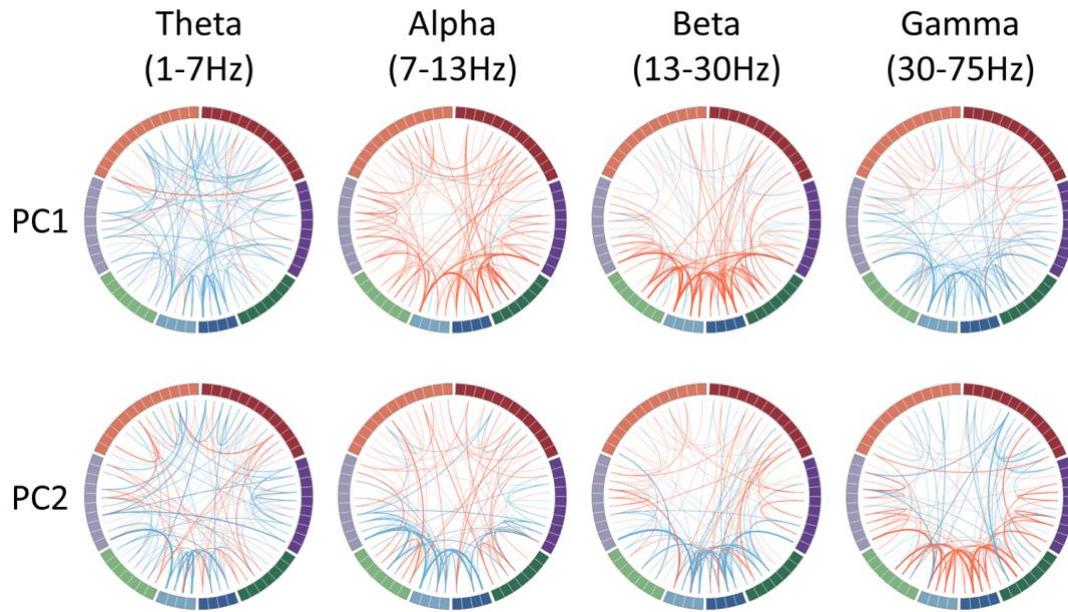
Supplementary Figure 8. Frequency distribution for each contrast in the MEG-MVAR GLM. Stars denote the peak frequency chosen for illustration and analysis.



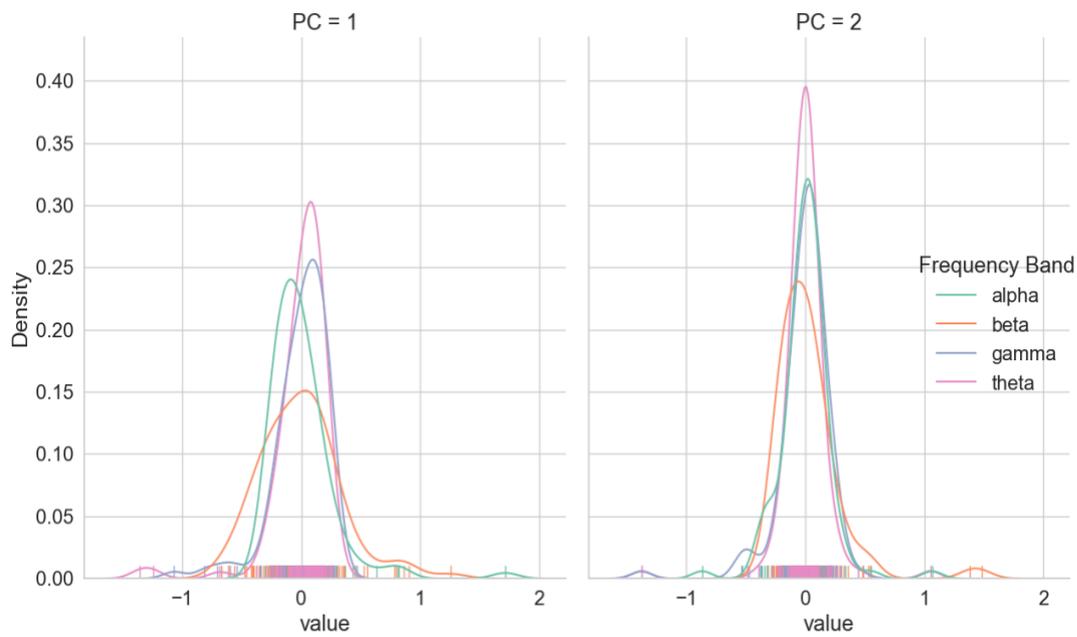
Supplementary Figure 9. Distributions of the significant beta values for each contrast in the MEG-MVAR GLM. Histogram with bins of .0002 and kernel density estimation lines.



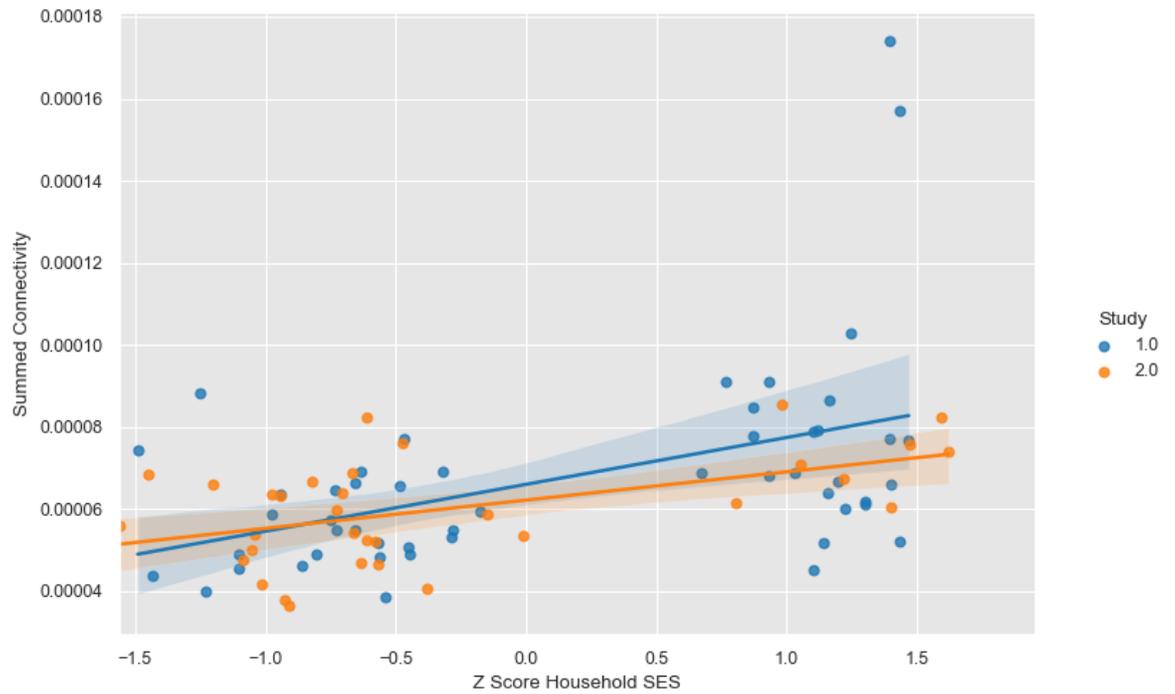
Supplementary Figure 10. Labels and colour key for the circos plots. The labels are all shortened versions of the aparc parcellation.



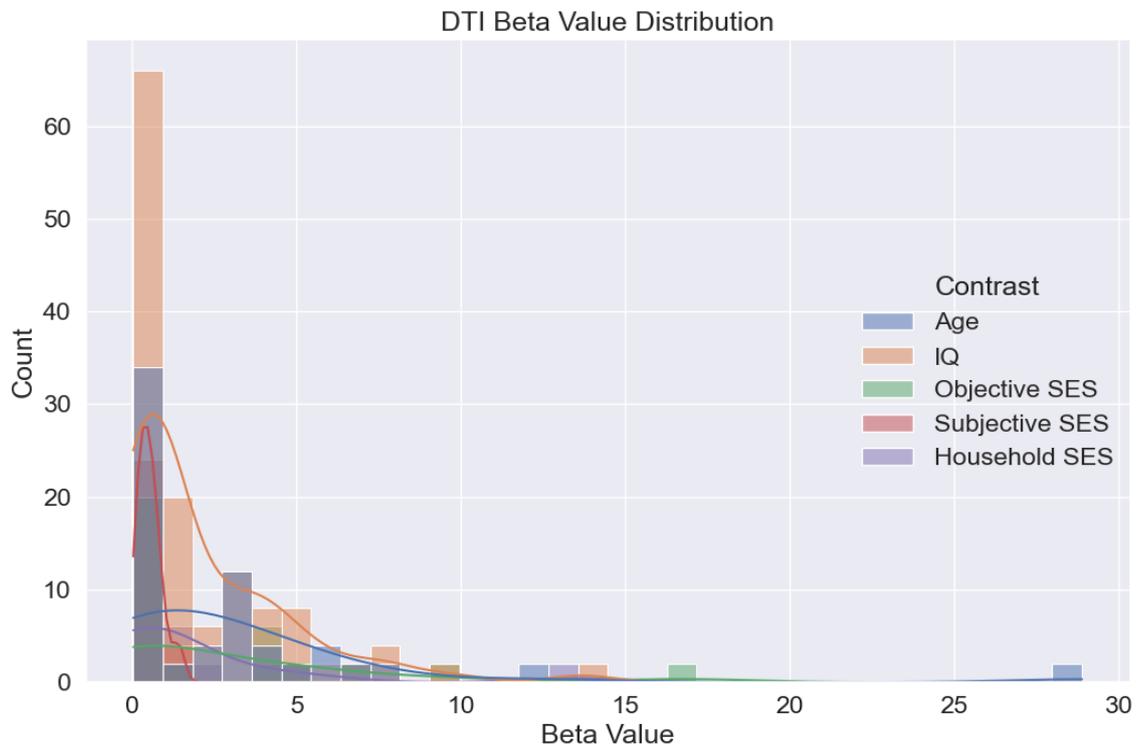
Supplementary Figure 11. Summary of all eight Principal Component networks from the MVAR-PCA approach. Columns represent the four frequency bands the separate PCA analysis were carried out on, rows the two principal components for these analysis.



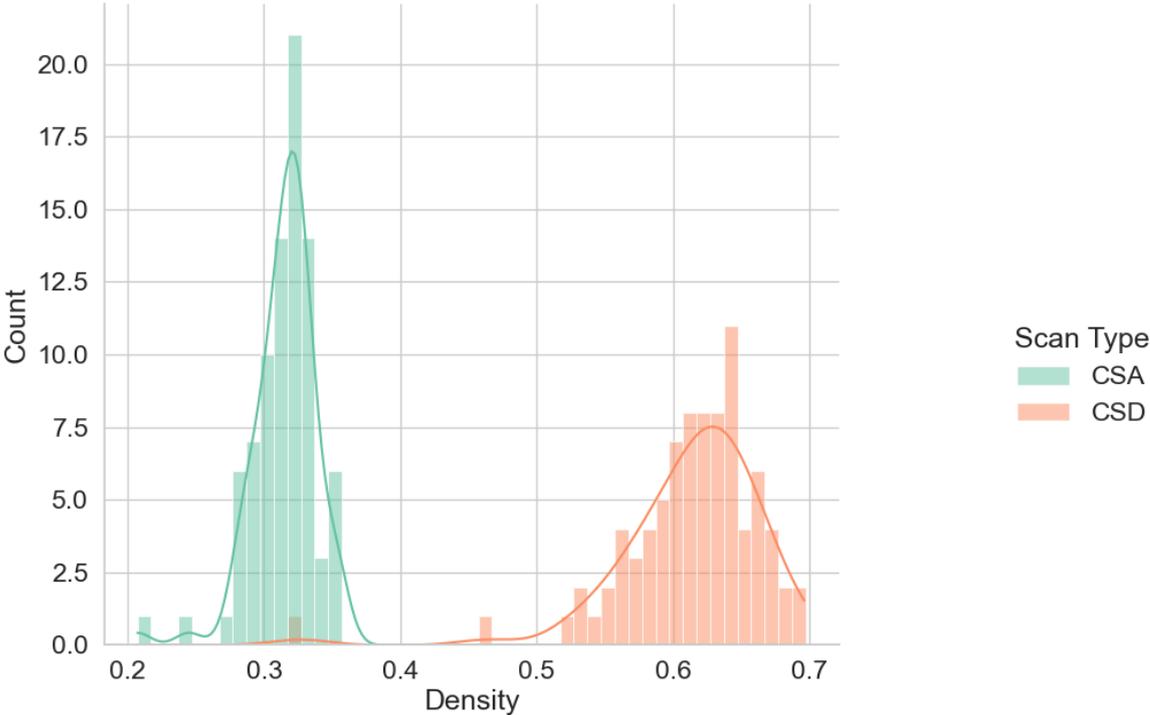
Supplementary Figure 12. Distribution of participant component scores for each frequency band and principal component. Density is calculated using kernel density estimation (KDE).



Supplementary Figure 13. Scatterplot with regression lines. Showing study run bifurcation of DTI Household SES related connections. The colors relate to the first and second runs of data collection. This illustrates these effects are unlikely to be driven by study run differences.



Supplementary Figure 14. Distributions of the significant beta values for each contrast in the DTI GLM. Histogram with bins of 1 and kernel density estimation lines.



Supplementary Figure 15. Distributions of participant's scan densities for different DTI methods. Histogram with bin widths of 0.01 and a kernel density estimation plot overlaid. Density of 1 is all possibly connections exist between all parcels, 0 is no connections.

Contrast	<u>Unique Variance</u>		<u>Shared Variance</u>
	MEG-MVAR	MRI-DTI	
Age	57.88%	1.58%	18.71%
IQ	49.59%	0.87%	20.90%
Objective SES	35.01%	6.09%	18.00%
Subjective SES	44.17%	2.71%	28.17%
Household SES	48.37%	0.32%	13.62%
Mean	47.01%	2.31%	19.88%

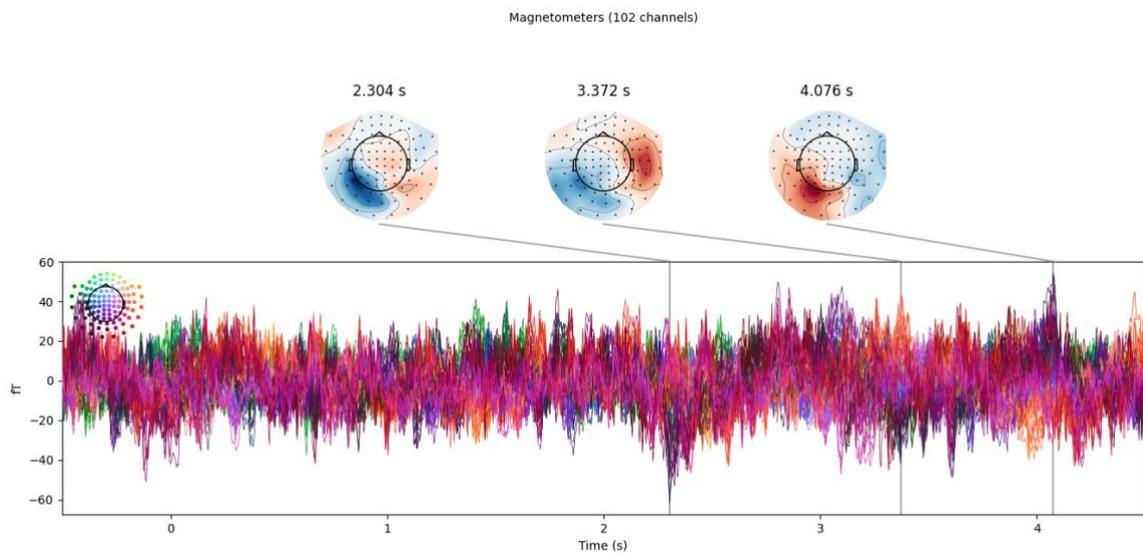
Supplementary Table 1. Unique vs shared variance comparison for density matched MEG-MVAR and MRI-DTI connectomes. Values are calculated from contrasts of R^2 values from OLS models. Unique variance is the residual R^2 when R^2 value from other predictors are subtracted from the multiple regression model. Shared variance is the R^2 not accounted for by unique variance in the multiple regression model.

Contrast	<u>Unique Variance</u>		<u>Shared Variance</u>
	MEG-MVAR	MRI-DTI	
Age	52.46%	0.85%	23.23%
IQ	38.73%	1.90%	28.57%
Objective SES	33.66%	0.26%	18.28%
Subjective SES	41.20%	1.65%	29.60%
Household SES	44.57%	0.75%	16.42%
Mean	42.12%	1.08%	23.22%

Supplementary Table 2. Unique vs shared variance comparison for CSA MEG-MVAR and MRI-DTI connectomes. Values are calculated from contrasts of R^2 values from OLS models. Unique variance is the residual R^2 when R^2 value from other predictors are subtracted from the multiple regression model. Shared variance is the R^2 not accounted for by unique variance in the multiple regression model.



Supplementary Figure 16. Illustration of the gradiometer cluster in the difference between informative and uninformative evoked responses. Shows the noise and inconsistent topography in this sensor type.



Supplementary Figure 17. Averaged difference time course over trial for all magnetometers. The difference is the subtraction of uninformative and informative cues – weighted average to re-balance inequality between conditions.

Screen	Text	Additional
Screen 1	<p>Welcome to the snake game.</p> <p>You will see some snakes on the screen, they will be facing different ways.</p> <p>The snakes aren't very good at remembering things, so you must help them.</p> <p>Try and remember where they face, then you will have to move them when they re-appear.</p> <p>(Press any button to continue.)</p>	
Screen 2	<p>Let's practice.</p> <p>Remember the way this snake is facing!</p> <p>When you are ready press a button to continue.</p>	A single snake is displayed in the center of the screen at 100 degrees.
Screen 3	<p>Can you remember which way the snake faced just now?</p> <p>Press the red and green keys in you right hand to turn the snake.</p> <p>Press the yellow key in your left hand to respond.</p>	The same snake is displayed at a random orientation, participant's move this snake with two buttons.
Screen 4	<p>Well done - you helped the snake to remember!</p> <p>Now we are going to practice with two snakes, try and remember which way both of them are going.</p> <p>But, you will only be asked to help one of them</p> <p>Press the key once you have looked at BOTH snakes.</p>	Now two snakes are presented at 10 and 145 degrees on the left and right.
Screen 5	<p>Which way was this snake facing?</p>	The left snake is shown and participants can move the snake to respond.
Screen 6	<p>Well Done!</p> <p>Now we are going to try a few more practices.</p> <p>This time you have to do it as fast as you can.</p> <p>But make sure to try and be accurate!</p> <p>You get a score after each one, try and make it as close to 100 as possible.</p> <p>(Press any button to continue.)</p>	After this the practice trials begin and feedback on that block is given
Screen 6	<p>OK, that is the practice over -- you did really well!</p> <p>Now it is time for the main part of the task.</p> <p>Remember to try and be as accurate as possible, but don't take too long.</p> <p>You will have ""+ str(int(n_trials/TRIAL_BREAKS)) +"" breaks in the task.</p> <p>(Press any button to continue.)</p>	This screen is shown after the practice block, and reminds the participants of the task goals.

Supplementary Table 3. Table with text and description of the VWM task instructions and tutorials.