

ABSTRACT

Title of Dissertation: MULTIMODAL ANALYSIS OF NEURAL
 SIGNALS RELATED TO SOURCE MEMORY
 ENCODING IN YOUNG CHILDREN

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The emergence of source memory is an important milestone during memory development. Decades of research has explored neural correlates of source memory using electroencephalography (EEG) and functional magnetic resonance imaging (fMRI). However, connections between findings from the two approaches, particularly within children, remain unclear. This dissertation identified fMRI-informed cortical sources of two EEG signals during memory encoding, the P2 and the late slow wave (LSW), that predicted subsequent source memory performance in a sample of children aged 4 to 8 years. Both P2 and LSW were source localized to cortical areas of the medial temporal lobe (MTL), reflecting MTL's crucial role in both early-stage information processing and late-stage integration of memory, which also validated LSW's suspected role in memory updating. The P2 effect was localized to all six tested subregions of cortical MTL in both left and right hemispheres, whereas the LSW effect was only

present in the parahippocampal cortex and entorhinal cortex. P2 was additionally localized to multiple areas in the frontoparietal network, a cortical network known as the “attention network”, highlighting interactions between memory encoding and other cognitive functions. These results reflect the importance of considering both spatial and temporal aspects of neural activity to decode memory mechanism, and demonstrated the potential of combining multimodal measures in children, paving the way for future developmental research.

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ENCODING IN YOUNG CHILDREN

by

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List of Abbreviations

ANTs	Advanced Normalization Tools
BET	Brain Extraction Tool
BH	Benjamini-Hochberg
BOLD	Blood-oxygen-level-dependent
CDR	Current Density Reconstruction
EC	Entorhinal Cortex
eLORETA	Exact Low-resolution Brain Electromagnetic Tomography
EEG	Electroencephalograph
ERP	Event-related Potentials
FDR	False Discovery Rate
fMRI	Functional Magnetic Resonance Imaging
FuG	Fusiform Gyrus
ICA	Independent Component Analysis
IFG	Inferior Frontal Gyrus
IOG	Inferior Occipital Gyrus
IPL	Inferior Parietal Lobule
ITG	Inferior Temporal Gyrus
LOoC	Lateral Occipital Cortex
LPC	Late Positive Component
LSW	Late Slow Wave
MFG	Middle Frontal Gyrus
MRI	Magnetic Resonance Imaging
MTG	Middle Temporal Gyrus
MTL	Medial Temporal Lobe
MVOcC	Medioventral Occipital Cortex
Nc	Negative component
OFG	Orbital Frontal Gyrus
OrG	Orbital Gyrus
PFC	Prefrontal Cortex
PhG	Parahippocampal Gyrus
PPHC	Posterior Parahippocampal Gyrus
ROI	Region-of-Interest
SFG	Superior Frontal Gyrus
SPL	Superior Parietal Lobule
TI	Temporal Agranular Insula

Chapter 1: Memory in Children

Episodic Memory

Episodic memory, the ability to recall personal experiences within a specific spatial and temporal context, is fundamental for navigating daily life and forms the basis of personal identity, enabling individuals to encode, store, and retrieve event information for future use (Tulving, 2002). The ability to form and recall episodic memories undergoes significant development during early childhood (Riggins, 2014), due to rapid changes in the brain and associated cognitive functions, such as attention, during this this period.

In contrast to recognition memory, which relies on familiarity, episodic memory requires recollection, or the ability to associate corresponding information or features with a particular memory item or event. There are two enduring models regarding the processes underlying episodic memory: the single-process account (e.g. Rovee-Collier, & Cuevas, 2009, Hayes et al., 1007), which suggests memory recognition and recollection differ in the strength of a memory signal, and the dual-process account (e.g. Brown & Aggleton, 2001; Mandler, 1980), which suggests memory recognition and recollection involve two distinct mechanisms. Although debates remain regarding which account provides a better account of memory, the present study adopts a dual-process perspective in that we discuss familiarity and recollection as two functionally distinct cognitive processes, given that memory familiarity and memory recollection show differing developmental trajectories and originate from overlapping yet distinct neural regions (see review by Bauer, 2004).

Although memory recognition capabilities via familiarity emerge as early as infancy (Rose et al., 2004), episodic memory via recollection shows a more protracted developmental trajectory throughout childhood (Ghetti & Bunge, 2012), with accelerated rates of change between five to seven years of age (Riggins, 2014). Thus, early childhood is an important time period to examine memory recollection mechanisms underlying the emergence of episodic memory.

However, assessing episodic memory and recollection processes in young children remains a unique challenge for a variety of reasons, including children's developing language and cognitive abilities (for a discussion see Rollins & Riggins, 2021). These factors necessitate adaptations in experimental methodologies to accurately gauge episodic memory capabilities in this age group. Traditional methods that rely on metacognitive judgments that are commonly used in assessments with adults, such as lexical tasks (e.g., K.J. Gilhooly & M.L. Gilhooly, 1979) and free recall measures (e.g., Underwood et al., 1978), are often unsuitable for young children due to their limited introspective and verbal reporting skills. Consequently, research strategies are tailored to circumvent these limitations by focusing on more simplified judgements. For instance, studies might probe memory for specific details of an event or object, which inherently requires recollection but is assessed via a straightforward response (e.g., Drummey & Newcombe, 2002; Ghetti et al., 2010). This approach allows for the assessment of episodic memory through direct engagement with memory content, providing insights into the child's ability to recall experiences with context.

Source Memory in Young Children

One way to assess episodic memory is to probe the **source** of the information (i.e., such as from whom or where the information was learned/acquired). The ability to remember the source of information in early childhood reflects episodic memory, as it probes children's ability to establish and recall connections between a memory item and its contextual aspects (Raj & Bell, 2010). Such detailed memories are vital in children as they learn to navigate and interpret their experiences – source memory is repeatedly practiced as children's social interactions and academic demands increases, motivating them to remember who told them certain pieces of information or who/where they were when they encountered an item previously. Image the scenario where a five-year-old child Alice receives a picture book from her friend Sally for her birthday. When Alice is being asked where she got her picture book, she needs to identify the source of the picture book, Sally, to answer this question.

Studies often assess source memory in young children by mimicking or simulating scenarios similar to real life experiences, such as learning new facts from others (e.g., Drummey & Newcombe, 2002; Riggins, 2014), or remembering the corresponding owner of a list of objects (e.g., Geng et al., 2019). For example, in the novel fact task (e.g. Drummey & Newcombe, 2002;), children are taught novel information from 1 of 2 sources (person 1 vs person 2) and subsequently asked to recall not only the information, but from whom they learned it. Other source memory studies teach children “favorite items” belonging to different cartoon characters, and children are later asked to recall the character associated with each item (e.g. Geng et al., 2018, 2019). Despite variations in the specific task, each is designed to test

children's ability to recall contextual information about the origin of a memory (Johnson et al., 1993) and requires them to directly engage in memory recollection and to retrieve contextual information of recognized memory items (Tulving, 1985; Spaniol et al., 2009, Ghetti et al., 2010).

Chapter 2: Examining Source Memory Encoding

As alluded to above, source memories first have to be made (or encoded), then stored, and retrieved at a later point in time. Researchers interested in dissecting the labyrinth of source memory can focus on any of these stages (i.e., encoding, storage or retrieval). This dissertation focuses on the encoding stage of source memory.

Encoding is interesting for several reasons. For example, memory encoding is the starting point. It involves the formation of new memories and thus provides the foundation for all subsequent stages. Second, memory encoding is deeply interweaved with other cognitive processes, such as attention, that are also developing in young children. Third, memory encoding is practically straightforward to isolate for examination in young children (Bauer et al., 2012).

Encoding of source memory involves taking in information from the environment through sensory and perception (Johnson et al., 1993), and then converting the contextual information into a form that can be stored as a feature associated with another memory representation, together leading to the creation of a new memory trace (Tulving & Watkins, 1975). Thus, attention is required for the formation of “detailed” memories: one needs to “attend” to the details in their environment, in order for it to be encoded.

Selective attention influences memory encoding as an information filter. In young children, memory-guided attention allows them to focus on information that is considered important to the memory event, to use cognitive resources more efficiently and to gain better learning outcomes (Amso et al., 2021). Previous studies examining interactions between attention and memory systems have shown that attention plays a

pivotal role in facilitating memory encoding in children (e.g., Decker et al., 2023). Specifically, in a study with seven- to ten-year old children, sustained attention causally determined which pieces of information were encoded into lasting memories. Moreover, children's attention lapsed twice as frequently as adults', making the relation between attention fluctuation and memory formation more closely tied together in children than adults. These attentional processes not only direct cognitive resources towards relevant stimuli (Amso & Kirkham, 2021) but also support the integration of sensory, spatial, or other contextual information with existing knowledge (Amso et al., 2021), a key aspect of source memory. To summarize, source memory encoding in young children is modulated by variations in attention, and thus differences in attention may contribute to age-related improvements in source memory performance during childhood (Amlen et al., 2018; Canada et al., 2022; Decker et al., 2023; Shing et al., 2010).

Chapter 3: Neural Correlates

Multiple methods have been used to examine the neural correlates of source memory, the most popular ones being Electroencephalography (EEG) and functional Magnetic Resonance Imaging (fMRI). Neuroimaging research in adults has suggested that memory encoding and retrieval rely on overlapping but separable brain regions (Spaniol et al., 2009). As stated earlier, work during development has largely focused on encoding, likely because it is easier from a practical standpoint (i.e., children are asked to form memories as opposed to retrieve them; Ghetti et al., 2010; Geng et al., 2018, 2019; Ofen et al., 2007). Examining the neural mechanisms underlying memory encoding helps us demystify the story underlying young children's protracted development of episodic memory.

EEG

EEG provides a non-invasive and relatively inexpensive method to study the electrical activity of the brain associated with memory encoding. The event-related potential (ERP) technique uses EEG voltages elicited during brain activity, time-locked with an event of interest (e.g., presence of a stimulus) and averaged across multiple trials within each subject (Luck, 2014), to examine neural differences between conditions of interest. ERPs have been used extensively to measure neural activity associated with different aspects of memory in infancy (reviewed by de Haan, 2002), childhood (reviewed by Barry-Anwar et al., 2020) and adulthood (Friedman & Johnson, 2000; Rugg & Curran, 2007). Previous research has identified multiple ERP components related to memory performance including the P3 or novelty P300

component (Polich, 2012), the late positive component (LPC; Friedman & Johnson, 2000) and/or the late slow wave component (LSW; e.g. DeBoer et al., 2005; de Haan, 2002; Nelson, 1994; Geng et al., 2018), and the negative component (Nc; Paller et al., 1987; DeBoer et al., 2005; Geng et al., 2018; Rollins & Riggins, 2021). However, only a subset of these components are observed in children, as ERP correlates tend to be less distinct and more diffuse in young children compared to adults (Cycowicz, 2000; DeBoer et al., 2005; Sprondel et al., 2011). Encoding-related ERP components present different timing and features in adults and in children; as children develop, there are changes in the timing, amplitude, and distribution of ERP components (for a discussion see Riggins et al., 2013).

To the best of our knowledge, only four studies have used ERPs to examine neural correlates of memory encoding differences related to subsequent source memory performance in children (Rollins & Riggins, 2013, 2018; Geng et al., 2018; Bettencourt et al., 2021). These studies examined the effect of ERPs during source memory encoding at different latency windows consistently identified the crucial role of late-stage activities, or the LSW component.

LSW is distinct positive-going component often recorded in frontal and prefrontal sites, occurring with a latency >400ms after stimulus onset in adults (e.g., Rollins & Riggins, 2013; for review see Friedman & Johnson, 2000) and >800 ms in children (Riggins et al., 2013). It does not have a distinct peak, and is more widely distributed across the scalp (reviewed by DeBoer et al., 2007; de Haan, 2007).

Previous research has shown that LSW predicts whether a subsequent correct

recognition judgment will be made, in both adults and children (Geng et al., 2018; Rollins & Riggins, 2013), suggesting its role in memory encoding.

LSW is particularly important in the context of source memory because it is thought to reflect memory updating especially for partially encoded stimuli (DeBoer et al., 2005; de Haan, 2002). Research in young children has shown that performance on a source memory task is positively related to differences in the LSW amplitude between source correct and source incorrect trials in the left hemisphere (Rollins & Riggins, 2018; Geng et al., 2018), but negatively related to the difference in the right hemisphere (Geng et al., 2018). The lateralization is possibly caused by the dipole nature of the neural sources that generated this ERP, since the underlying electrical activity holds opposite polarities at the two ends of the sources (Schimpf et al., 2002). On the contrary, other memory ERPs such as the Nc component (mid-latency negative component from 300ms -500ms) are only indicative of memory recognition performance, but not source memory encoding (Riggins et al., 2013; Geng et al., 2018). However, whether there are other components during encoding are indicative of source memory performance in young children remains an open question.

The latency and topography of this LSW effect evolve across early childhood (Geng et al., 2018; Rollins & Riggins, 2013). Preschool-aged children show subsequent source memory effects between 900–1500 ms, distributed broadly over the entire scalp (Riggins et al., 2009; Riggins et al., 2013). By middle childhood, children show a subsequent memory effect comparable to the effect shown in adolescents and young adults (Rollins & Riggins, 2018). Young children's different neural signatures associated with source memory compared to adults reflect ongoing

developmental changes in brain areas involved in memory processing. These changes indicate that young children experience not only a quantitative increase in memory ability, but also qualitative changes in the neural mechanisms employed for memory encoding.

fMRI

fMRI plays a crucial role in developmental memory research as it allows researchers to observe which different brain regions are involved in the processes of memory encoding. Previous research has identified important brain networks associated with episodic memory via fMRI, such as the hippocampus and the parahippocampal area in MTL (Spaniol et al., 2009, Qin et al., 2009, Geng et al., 2019), the frontal-parietal network involving prefrontal cortex (PFC) and parietal cortex (Ofen et al., 2007; DeMaster & Ghetti, 2013), and the prefrontal-temporal encoding circuit recruiting not only the MTL but also the surrounding middle temporal gyrus (MTG) and the inferior temporal gyrus (ITG; Kirchhoff et al., 2000).

In both adults and school-aged children (i.e., older than 8 years), the MTL region (including hippocampus, parahippocampal cortex, entorhinal cortex, perirhinal cortex, and agranular insular cortex) is actively involved in the formation of new episodic memories (Ghetti et al., 2010; Qin et al., 2009), and is often considered one of the most important brain regions for memory. Neuroimaging studies have shown multiple MTL subregions' involvement at memory encoding (Tulving et al., 1994; Rugg et al., 1998; Stark and Okado, 2003; Strange et al, 2002). For example, the hippocampal, the parahippocampal and the perirhinal regions all show greater activity at subsequently recalled than forgotten items (e.g. Davachi et al., 2003; Diana et al.,

2007; Strange et al, 2002); parahippocampal and anterior hippocampal regions show primacy effect to initial, subsequently remembered memory items during encoding, possibly reflecting enhanced attention orientation (Strange et al, 2002). MTL shows significant age-related decreases in activation (Menon et al., 2005) and age-related increases in selective activation for memories that contain contextual details (e.g., Ghetti et al., 2010). This crucial, selective role and the unique age-related changes in MTL make it particularly important when examining source memory encoding in young children.

The wide-spread cortical network outside of MTL is also important for memory encoding. This network includes multiple areas in PFC and parietal lobe, fusiform (FuG), ITG and MTG adjacent to the parahippocampal area, and nearby gyri in the lateral occipital cortex (LOoC) and the medioventral occipital cortex (MVOoC; e.g. Duarte et al., 2011; for review, see Spaniol et al., 2009). Most of these regions are considered a part of the frontoparietal network, an integral network to attention process that largely interacts with other cognitive processing network (Marek & Dosenbach, 2018). In general, the PFC is implicated in the organization and strategic encoding of memories, and contributes to different cognitive components of the encoding process (reviewed by Paller & Wagner, 2002). Research has shown that semantic and phonological processing activates different areas within the prefrontal cortex, highlighting its role in organizing and strategically encoding memories based on the content's nature. It is hypothesized that children's difficulties in source memory originate partially from the protracted development of PFC (Shing et al., 2010). Several other fronto-parietal regions, including bilateral FuG, bilateral

occipital gyri, right superior parietal lobule, and bilateral inferior frontal gyrus (IFG), are recruited in during memory formation (Geng et al., 2022). FuG, MTG and ITG have high functional connectivity to MTL and are considered as areas that support the processing of sensory information and facilitate the integration of memory information within broader memory network. For example, there has been evidence showing that FuG is involved in category-specific encoding of visual information (discussed in Mitchell & Johnson, 2009). Activities within the posterior medial cortex (i.e., precuneus/medial parietal cortex involving IPL and SPL) are found to modulate memory performance and emerges with age (Amlien et al., 2018). Posterior regions of the brain, including certain parts of the occipital cortex (Yonelinas et al., 2001), though less often associated with memory encoding¹, have also been suggested to engage in feature binding and representations of information (Dennis et al., 2007, 2008). The involvement of multiple cortical regions in memory encoding suggests a complex integration of sensory information, attention, cognitive strategies, and other cognitive processes in order to form coherent memory representations that involve different aspects of contextual information in episodic memory, underscoring the multi-faceted nature of memory formation.

Not only do MTL and other cortical regions show age-differences in activation, but so does connectivity between the two parts. It has been proposed that young children often struggle with source memory tasks due to the underdevelopment

¹ These areas are more commonly associated with memory retrieval rather than encoding (e.g. Wagner et al, 2005).

of the connectivity between MTL and other cortical regions (Menon et al., 2005; Shing et al. 2010), though the exact mechanism remains to be empirically tested. Multiple studies have found that the functional connectivity from MTL to frontal and parietal cortical regions is largely associated with episodic memory performance (Geng et al., 2019, 2022; Johnson et al., 2018), and matures along the developmental trajectory (Geng et al., 2019; Johnson et al., 2018). Interestingly, as children and adolescents age, MTL's response during memory encoding tasks decreases, while its connectivity with the left dorsolateral PFC increases. This suggests there may be a possible developmental shift in neural dynamics underlying memory encoding, where there is a transition from relying primarily on local MTL processing to more distributed processing involving enhanced coordination between the MTL and PFC (Menon et al., 2005). This developmental change reflects the maturation of neural mechanisms towards more effective memory processing, potentially by recruiting more PFC or other fronto-parietal regions along with MTL to facilitate strategic memory encoding.

It is noteworthy that few studies have used fMRI to investigate brain regions engaged during memory encoding in children younger than 8 years of age. This is problematic, as behavioral studies (reviewed above e.g., Riggins, 2014) have suggested early childhood (5-7 years) is a period of rapid improvement in this ability. Thus, it remains unclear whether younger children are utilizing these same brain regions. One study has explored brain activations during source memory encoding in children 4–8-year-old and has suggested that encoding contextual details activates several cortical regions alongside the hippocampus, including the inferior/superior

parietal lobule (IPL/SPL), ITG, the inferior occipital gyrus (IOG), IFG, the orbital frontal gyrus (OFG) and FuG (Geng et al., 2019), mostly consistent with findings in adults. Among these regions, IPL/SPL is considered to contribute to the visual processing of the stimuli, while IFG, IOG, ITG and FuG are related to the transformation from visual input to memory representations, as well as complex organization processes. Further investigation has found that functional connectivity between hippocampus and multiple fronto-parietal regions is also significantly related to subsequent source memory performance (Geng et al., 2022).

In conclusion, fMRI research has revealed crucial brain networks involved in source encoding, the MTL region and the frontoparietal network. Given the extensive development of both memory and the brain during early childhood, continued fMRI studies in young children are essential for understanding the developing brain in action.

Chapter 4: Multimodal Analysis of Neural Signals

Although both EEG and fMRI studies have indicated multiple neural regions/components associated with memory encoding, findings from these two methods remain largely separate in the field. This is unfortunate because although the measures are distinct, there are commonalities across findings suggesting that combining results could be complementary. For example, both measures have identified age-related changes in the neural signals associated with source memory encoding (Geng et al., 2018; Menon et al., 2005). Multimodal neuroimaging approach has been utilized in memory research in adults (Herzmann et al., 2012) and infants (Reynolds & Richards, 2005, 2019) for the synergy between EEG and fMRI. However, a review of those studies is beyond the scope of this dissertation.

EEG and fMRI have markedly different spatial and temporal resolutions and they probe neuronal activity through distinct biophysical processes. While surface EEG is commonly used to explore brain development in infants and young children and is often regarded as a direct measure of neuronal activity, a complete understanding of its underlying neurophysiological correlates has not been achieved. Despite its high temporal resolution, the main limitation of surface (i.e., scalp) EEG is its relatively poor spatial resolution, which makes it difficult to identify the precise neural sources underlying the measured activity, especially when it comes to the neurocognitive mechanism underlying source memory, which often engages activities happening deep in the brain (e.g., hippocampus). In contrast, fMRI measures a complex and poorly understood combination of hemodynamic and metabolic effects and has been commonly used to explore brain development in older children,

adolescents, and adults. Given that changes in the metabolic demands of neural activity have inherently slower dynamics and cannot capture the precise timing of the underlying mechanism, it is difficult to tease apart effects of encoding activity, attention and other intertwined cognitive mechanisms employed during a memory encoding through fMRI.

The integration of fMRI and EEG provides an opportunity to overcome the limitations of each technique and to provide a more comprehensive understanding of the neural correlates of source memory. Multimodal studies integrating both EEG and fMRI measures benefit from information with distinct spatial and temporal resolutions, and through different neurophysiological processes. Given that early childhood is a crucial time for memory research, uniting and discerning neural signals presented by EEG versus fMRI may be particularly important, especially since data collection is much easier for young children using the former. Comparing and combining findings from these two methods may shed new light on current literature of memory encoding, as it will help provide new constraints to the functionality and mechanisms behind the understudied ERPs of memory encoding, especially in terms of the LSW component.

EEG Source Localization

There is some question whether the sources of memory-related ERPs are in the same location as the hemodynamic blood-oxygen-level-dependent (BOLD) responses related to memory processing. A common multimodal approach among these studies is EEG source localization (Biessmann et al., 2011), a technique allowing us to identify the brain sources that are responsible for specific EEG

activity. While EEG measures the electrical activity of the brain, signals are often recorded on the scalp, collecting a mixed activity of many different brain regions and neural pathways (Luck, 2014). Source localization techniques aim to identify specific brain regions that are responsible for the signals, given EEG electrode locations relative to the brain, head model, and hypothesized constraints of brain sources (Michel & He, 2019). In general, EEG source localization requires the construction of a forward model to predict scalp electrical activity that would be measured based on hypothetical sources neural activity within the brain, and then an inverse model which solves the location and strength of neural activities given the measured EEG data (Mosher et al., 1999).

Multiple challenges arise when applying these techniques to children, including individual variability in head size and shape, the need for age-specific brain templates, and data quality (Conte & Richards, 2022). Young children have heads that are smaller and more variable in shape than adult heads, making it difficult to accurately model the electrical activity of the brain. Electrodes are located differently on each child's scalp, leading to spatial misalignment between EEG electrodes and MRI images. Children tend to have more difficulty than adults to stay still during the data recording, creating motion artifacts in the EEG and fMRI data. Recent advancements in this field have started to address some of these challenges regarding EEG source analysis in developmental populations (see review by Conte & Richards, 2022), including the development of age-specific head models (Richards et al., 2016), improved modeling of head geometry through hexahedral or tetrahedral meshes (Vorwerk et al., 2014), advanced inverse modeling algorithms (see review by Grech

et al., 2008) including exact low-resolution brain electromagnetic tomography (eLORETA; Pascual-Marqui et al., 2006) and Finite Element Method (FEM; Jatoi et al., 2013), and co-registration methods between EEG channel locations and MRI coordinate system (Richards et al., 2014).

Existing studies have demonstrated the feasibility of combining fMRI information with EEG source localization procedures to investigate certain cognitive processes including working memory and attention in adults (Jonmohamadi et al., 2020), children (Buzzell et al., 2017) and infants (Reynolds & Richards, 2019). Some of these studies have localized the anatomical locations of neural sources underlying certain ERP components engaged in memory processes, such as the Nc component (Reynolds & Richards, 2005; Reynolds et al., 2010), in a wide range frontal and prefrontal cortical areas. Yet, to our knowledge, few, if any, studies have looked at the neural correlates of source memory using source localization analysis (with the exceptions of Alhaj et al., 2006; Kim et al., 2009, and a clinical case study, all three looked at source memory retrieval in adults), especially within young children.

Additionally, no previous study has used cortical source analysis to quantify the sources of the LSW component in children. Research in adults has localized cortical sources of a frontal-central late positive ERP component (~1100ms) at the SPL/IPL, postcentral gyrus, precentral gyrus, MTL, and superior frontal gyrus (SPG), with largest clusters in the left parietal lobe and right temporal lobe (Kim et al., 2009). Research in infants has localized a positive late slow wave component (1000ms - 2000ms) sensitive to novelty at temporal cortical areas (Reynolds & Richards, 2005). Given developmental changes in the temporal and spatial features of

LSW (Geng et al., 2018; Rollins & Riggins, 2013), more research is needed to inspect whether the same cortical sources are the origins of LSW in young children.

Chapter 5: The Present Study

Understanding why source memory develops so rapidly in young children may provide insights into the fundamental workings of human episodic memory. Toward this end, the goal of this dissertation project was to identify the neural correlates of source memory encoding in young children through a multimodal approach, leveraging an existing EEG and fMRI dataset collected from a sample of children aged 4 to 8 years (Canada et al., 2020, 2022; Geng et al., 2018, 2019, 2021, 2022; Riggins et al., 2018). In this dataset, ERP and MRI measures were recorded from the same group of young children, when they performed a memory encoding paradigm on two different occasions using different sets of memory stimuli, approximately 1-week apart. Participants were instructed to remember the cartoon character associated with each item at encoding (task adapted from Ghetti et al., 2011), while being recording by EEG or fMRI, asynchronously. At the subsequent retrieval stage, participants made recognition (i.e., old/new), and source memory recollection judgments for each item (previously reported in Geng et al., 2018, 2019; Canada et al., 2022). The dataset also included structural MRI brain images from the same group of participants, benefiting the construction of individual head models.

To fulfill the project goal through MRI-informed EEG source localization, ERP results were re-visited from Geng et al., 2018. During this process a P2 component sensitive to source memory performance was identified. Given the temporal order of these two components, we discuss them in the order of P2 and LSW for organization and consistency purposes, though P2 was an exploratory component.

Both P2 and LSW ERPs during memory encoding were examined for how they relate to subsequent source memory performance.

Source localization techniques were applied to explore the cortical origins of ERPs, and to compare neural sources identified by the two modalities (EEG and fMRI) that were associated with successful source memory encoding. Cortical source differences were compared between trials with subsequent successful source memory retrieval versus unsuccessful source memory retrieval during P2 and LSW time window, in literature-inspired and fMRI-informed memory regions-of-interests (ROIs), to spotlight cortical regions that may serve as the neural origins of source-memory-related P2 and LSW ERP components. Given the nature of EEG signals and the deep anatomical locations of subcortical structures (Luck, 2014), source analyses were only performed on cortical areas of the brain, due to the lack of consensus whether EEG detection of subcortical activities is possible (e.g., Krishnaswamy et al., 2017). We concluded three sets of hypothesized brain regions from an overview of the memory-fMRI literature and from fMRI results directly obtained from this dataset. A list of all tested source areas can be found in Table 1. These regions were:

- a) All cortical subregions of MTL defined in the Brainnetome atlas (Fan et al., 2016).
- b) Cortical ROIs identified in previous fMRI metaanalyses. These included regions most likely to be activated during episodic memory encoding in adults (Spaniol et al., 2009) and the fMRI analysis of this dataset from children (Geng et al., 2019, 2022), which were constructed using the Brainnetome atlas (Fan et al., 2016).

c) fMRI-constrained ROIs extracted from the fMRI results in the current dataset. Unlike the previous ROI set, these fMRI ROIs were obtained from the same group of children who performed the EEG session, during the same task paradigm. Brain regions that showed greater activation in source correct versus incorrect conditions were extracted (see *Chapter 6: Method*), and were used to constrain EEG source analysis in this dissertation.

It was hypothesized that differences in the surface-level neural activities (i.e., EEG signals collected from the scalp) related to source memory encoding would be (at least partially) anatomically projected to regions showing task-relevant metabolic changes in the brain. Specifically, during P2 and LSW windows, greater source scores (as indexed by current density reconstruction or CDR scores from the inverse solution to the source model; see *Chapter 6: Method*) in encoding trials with subsequently correct source judgment, compared to encoding trials with subsequently incorrect source judgment, would be present within all three sets of cortical regions explored. However, which exact regions would show these effects were exploratory.

Table 1

All Brainnetome-based regions of interest for the analysis of CDR data.

<i>ROI</i>	<i>Brainnetome Label</i>	<i>Area</i>
Aim 1: Medial Temporal Lobe		
rostral PhG	109,110	rostral parahippocampal gyrus (L,R)
caudal PhG	111,112	caudal parahippocampal gyrus (L,R)
lateral PPHC	113,114	lateral posterior parahippocampal gyrus (L,R)
EC	115,116	entorhinal cortex (L,R)
TI	117,118	temporal agranular insular cortex (L,R)
medial PPHC	119,120	medial posterior parahippocampal gyrus (L,R)
Aim 2: Comprehensive Memory ROIs		
SFG	1-14	superior frontal gyrus (L,R)
MFG	15-28	middle frontal gyrus (L,R)
IFG	29-40	inferior frontal gyrus (L,R)
OrG	41-52	orbital gyrus (L,R)
MTG	81-88	middle temporal gyrus (L,R)
ITG	89-102	inferior temporal gyrus (L,R)
FuG	103-108	fusiform gyrus (L,R)
PhG	109-120	parahippocampal region (L,R)
SPL	125-134	superior parietal lobule (L,R)
IPL	135-136	inferior parietal lobule (L,R)
MVOcC	189-198	medioventral occipital cortex (L,R)

LOoC	199-210	lateral occipital cortex (L,R)
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Aim 3: fMRI-constrained ROIs

left IPL/SPL	/	left inferior/superior parietal lobule
IOG	/	inferior occipital gyrus
left ITG	/	inferior temporal gyrus
left IFG	/	inferior frontal gyrus
FuG	/	fusiform gyrus
OFG	/	orbital frontal gyrus

Chapter 6: Method

Participants

Participants included typically-developing 4- to 8-year-old children. Data for this dissertation were derived from the first wave of a published research study examining the development of the brain in relation to memory (n=200; Canada et al., 2020, 2022; Geng et al., 2018, 2019, 2021, 2022; Riggins et al., 2018). Prior to data collection, all methods were approved by the Institutional Review Board at the University of Maryland. Children were screened via caregiver report to ensure they were not born premature (via gestational age), had normal or corrected-to-normal vision, and had no diagnoses for any neurological conditions, developmental delays, or disabilities. Informed consent was obtained from parents, written assent was obtained for children aged 7 years or older than, and verbal assent was obtained for children younger than 7 years. The majority of the children included were Caucasian (57%), from middle- to high-income households (median income greater than \$105,000 per year). A total of 95 4- to 8-year-old children (40 reported females, 55 reported males, mean age 6.46 years) provided usable ERP data for source localization analysis (83 were not administered the task, 22 were excluded due to lack of usable ERP data or lack of trials in either memory condition). Ninety-two out of 95 participants simultaneously provided usable structural MRI data. A total of 44 children provided usable fMRI data (27 reported females, 17 reported males, mean age 7.12 years (129 were not administered the task, 27 were excluded due to lack of

useable MRI data or not enough trials in either memory condition). Forty-one children provided usable task performance data in both EEG and fMRI sessions for cross-session behavioral analysis.

Table 2

Number of participants included in each analysis type.

<i>Analysis Type</i>	<i>Sample size</i>
ERP	95
ERP Source Localization	92
fMRI Mask (previously published)	44
Between-session Behavioral	41

Materials and Procedures

Children visited the laboratory twice, approximately 7 days apart. During the first visit, they completed an MRI scan including a structural MRI scan and two runs of task-based fMRI sequence during the encoding phase of the source memory task. During the second visit, they completed the same source memory encoding task with a different set of stimuli, while EEG activity was recorded. There were four exceptions where the participant performed the MRI session before their EEG session.

Source Memory Task (see Geng et al., 2018, 2019, 2022). The source memory paradigm was adapted from Ghetti et al. (2011). In short, participants underwent a brief training session to ensure that they understood the task requirements. During the training, the experimenter introduced the child to the encoding and retrieval phases of the task. In the encoding phase, the experimenter showed a picture of a character on the screen and verbally labeled the character's name. Then, one item was presented next to the character, and the experimenter verbally labeled the item. The child was instructed to remember both the item and the character “source” of the item, as the items were framed as the characters’ “favorite thing that belong to them” (see *Appendix A* for detailed task prompt). This process was repeated for each of the three characters, resulting in six paired items. Following the encoding phase, the child was presented with each of the six old items and three new items and asked to identify whether they were old or new (item memory), and for old items, with which character the item had been presented (source memory). During the training retrieval phase, the experimenter corrected inaccurate responses. After training, the child practiced both the encoding and retrieval phases. During the encoding practice, each character was paired with five different items sequentially, and children were instructed to observe and remember which items went with which characters (trials were blocked by character such that they saw the five items for character one, then the five items for character two, and then the five items for character three). During retrieval practice, inaccurate responses were not corrected, and children were required to achieve an accuracy score of 80% or higher on both item and source memory judgments for the 15 old items and five new items. If the

accuracy requirement was not met, the experimenter explained the task rules again, and the child completed another practice session with different stimuli. Following successful completion of the practice, participants completed three blocks of 40 trials



Figure 1. Task paradigm of the source memory task (Geng et al., 2018, 2019, 2022). During the encoding phase, each item is associated with one of three cartoon characters that are familiar to young children (Winnie the Pooh, Batman, and Minnie Mouse in version 1, Little Mermaid, Mickey Mouse, SpongeBob in version 2). fMRI or ERP data were collected during encoding. Approximately 15 minutes after the encoding phase of the task, participants were asked to perform the retrieval phase outside the fMRI/ERP recording environments. In each trial, participants were first asked to identify if they had seen the presented stimulus during the encoding phase, and if they answered “yes”, they were asked to identify to which of the characters did the stimulus belong.

of source memory encoding, while being recorded by fMRI (first visit) or EEG (second visit). The retrieval phase began approximately 15 minutes after the encoding phase for both fMRI and EEG. Children were instructed to respond "yes" if the item presented was one they had seen during encoding and "no" if the item was new. For

items children identified as “old,” children were then asked to indicate to which of the three characters the item belonged. Items remained on the screen until children identified them as old or new. For old items, the three characters remained on the screen until children indicated to which character the item “belonged.” All answers were given verbally, and responses were recorded by the experimenter.

EEG Recording and Preprocessing. A BioSemi Active 2 EEG recording system was used to measure data continuously from 64 Ag/AgCl EEG electrodes and two vertical and two horizontal electrooculogram channels at a sampling rate of 512 Hz. Data were preprocessed using procedures described in the previous publication (Geng et al., 2018). In summary, bad channels were interpolated and ocular artifacts were corrected using BESA. A maximum of 8 bad channels were allowed for inclusion in the dataset. Data was filtered, denoised, and re-referenced in EEGLab (Delorme & Makeig, 2004). EEG data were filtered with a low pass of 0.1 Hz and a high pass of 30 Hz. Ocular artifacts were removed through Independent Component Analysis (ICA). Data were initially segmented into epochs starting 100 ms before and ending 1500 ms after stimulus onset. Segments were rejected if any artifact was detected or if the maximum amplitude $> 200 \mu\text{V}$ or if the minimum amplitude $< -200 \mu\text{V}$. Data was referenced to Pz during recording and referenced to average offline.

MRI Data Acquisition and Preprocessing. Participants underwent scanning in a Siemens 3.0-T scanner (MAGNETOM Trio Tim System, Siemens Medical Solutions, Erlangen, Germany) using a 32-channel coil. A T1-weighted magnetization prepared rapid gradient echo sequence was completed with a duration of 4 minutes and 26 seconds (TR 1.9s, TE 2.32ms, slice thickness 0.9mm with no gap, voxel size

0.9mm $\times$ 0.9mm $\times$ 0.9mm, voxel matrix 256 $\times$ 256mm, flip angle 9°, field of view 230 $\times$ 230mm), during which the participants watched a movie of their choice. Task fMRI data were collected while participants completed the encoding part of the source memory task using a T2*-weighted gradient echo-planar imaging sequence. During task fMRI scans, participant head motion was monitored in real-time. If a participant exhibited excessive head motion (> 3mm in any direction) during the first half of any run, the scan was restarted, and the participant was reminded to stay as still as possible. Group level fMRI results have been previously analyzed and described in a previous publication from our lab (Geng et al., 2019). In summary, task fMRI data were preprocessed through slice timing correction, motion correction, normalization smoothing, coregistration and brain extraction using the Advanced Normalization Tools (ANTs; Avants et al., 2011), AFNI (Cox, 1996), Freesurfer 5.1 (Fischl, 2012), FSL (Smith et al., 2004), SPM8 (Wellcome Trust Centre for Neuroimaging, UCL, London, UK), and customized scripts.

Behavioral Analysis

Source memory performances from EEG and fMRI sessions were summarized using R and compared to previous reports using this dataset (Geng et al., 2018, 2019). R. We additionally examined differences in participants' performance between fMRI and EEG recording task sessions (n=41), using paired t-tests and mixed-effect linear models. Performance differences between first and second task sessions are reported and discussed in Appendix B.

ERP Analysis

P2 and LSW components were separately quantified for each participant. A 50ms-long early frontal positivity was extracted, centered around the median peak amplitude during typical P2 time range (between 120-250 ms), for each participant across trials to correct for fluctuation and asynchrony across participants. A 50ms-long late frontal positivity was extracted and centered around highest average amplitude across participants (1200 ms) during LSW time range (1100-1500ms; Geng et al., 2018; Bettencourt et al., 2021). These short epochs were to spotlight strongest ERP activity during task trials. The resulting P2 and LSW components were re-baseline corrected to the last negative component ahead (P2: 130 -140 ms; LSW: 610 - 620 ms) for source localization analysis, respectively, to ensure accurate CDR solutions during source analysis (Pascual-Marqui et al., 2011). Repeated-measures ANOVAs were conducted on mean amplitudes for epochs associated with the P2 and LSW components using a 2 Condition (subsequent source correct, subsequent source incorrect) $\times$ 3 Coronal Plane (frontal, central, posterior) $\times$ 3 Sagittal Plane (left, middle, right) design. Condition, Coronal Plane, and Sagittal Plane were included as within-subject factors. Only main effects and interactions involving Condition are reported. Interaction effects were further examined using post hoc analysis of estimated marginal means, pairwise tested and corrected through the Tukey method (Tukey, 1991). Age-related effects on ERP amplitudes were examined using mixed-effect linear models. Results from these analyses are reported in Appendix C. Conditional differences in P2 and LSW were also examined across all 64 EEG channels using paired t-test to pinpoint scalp regions showing largest amplitude

differences between conditions. Multiple comparison correction was conducted using Benjamini-Hochberg (BH) procedure to adjust for false discovery rate (FDR).

EEG Source Localization Analysis

Head model construction. Individual structural T1-weighted images were used to generate head models for each participant. Age-specific MRI templates were applied during brain extraction (Richards et al., 2016) to maximum volumes of extracted cortical tissues. Brain segmentation was completed using FSL (Smith et al., 2004) and Freesurfer (Dale et al., 1999). Each head model consisted of nine segmented head compartments of different types of media with corresponding estimated electric conductivities to create realistic head models: grey matter, white matter, cerebrospinal fluid, skull, muscle, dura, eyeballs, nasal cavity, and scalp (see Reynolds & Richards, 2009). Anatomical regions of eyeballs and nasal cavities (i.e., fiducials) were manually identified for each participant in MRICron (Rorden & Brett, 2000). Grey matter, white matter, and CSF were extracted using FSL's Brain Extraction Tool (BET). Scalp, skull, muscle and dura volumes were created using ANTs' ImageMath function, FSL's fslmaths function, and customized scripts.

Fiducial landmark marking. Three-dimensional coordinates of nine anatomical fiducial landmarks were manually marked on each participant's structural MRI scans using MRICron (Rorden & Brett, 2000), including the anterior commissure, the posterior commissure, the nasion, the inion, the left mastoid, the right mastoid, the left pre-auricular, the right pre-auricular, and the vertex. The first two anatomical landmarks are used to set up MRI coordination system, while the rest are for commonly used for the 10-10 system electrode placement (Richards et al.,

2015). The physical location of these anatomical landmarks on individual structural MRI scans were used to spatially re-align EEG electrode placement and MRI data within each participant. These procedures were to improve result accuracy and to account for individual variability in electrode placement as well as head shapes.

Source reconstruction. The source localization algorithm (adapted from Conte & Richards, 2022) was applied to individual head spaces from brain-extracted structural images. Source reconstruction procedures was performed using customized scripted adapted from Fieldtrip functions (Oostenveld et al., 2011). The source model was constructed as 3mm grids of grey matter and eyes within each participant's MRI, representing possible electric sources of observed ERPs (measured by current density). The segmented head model was constructed as a tetrahedral mesh of the head using the finite element method (FEM; Awada et al., 1997; for a discussion of geometry choices during mesh construction see Conte & Richards, 2002). Each tetrahedron was assigned to one of the nine head media described above. The lead field matrix (i.e., the forward model) integrated the source model, the head model, and re-aligned EEG electrode locations to simulate the process of electrical current within cortices flowing through layers of the head, projecting electrical activities onto the scalp that were subsequently captured by EEG electrodes (Hallez et al., 2007). The inverse model utilized the eLORETA method (Pascual-Marqui et al., 2011), producing a dipole moment vector at each 3mm source grid. A CDR score was estimated for each source grid from the magnitudes of the dipole moment vectors, separately for P2 and LSW activity and for each condition. CDR scores represent average source strength during entire epoch of ERP. eLORETA method is designed

to minimize total estimated squared current density, thereby offering a solution for the inverse model without requiring a priori information about the number of sources, allowing us to compute one average CDR score for each anatomical source ROI.

Anatomical source ROIs were constructed in individual head spaces using the Brainnetome atlas (Fan et al., 2016) and published fMRI results from this dataset (Geng et al., 2019). The Brainnetome Atlas offers greater detail (210 regions of cortical parcellation) of the brain compared to other commonly used brain atlases (e.g., the Desikan-Killiany atlas has 84 regions, the Yeo 2011 atlas has 17 regions). In addition to finer parcellation, it also bases the parcellation on both anatomical features and connectonal architecture of the brain, allowing for more accurate parcellation across diverse brain shapes. Though the atlas is not created from children's brain images, brain atlases created from adult brains are commonly used in developmental research, due to the lack of age-specific atlases (Altman & Bernal, 2011). Note that there are a few age-specific pediatric atlases out there, such as the UNC Human Brain Atlas (NeuroImage Research and Analysis Laboratories, 2010), but they are not appropriate ages for this study.

Average CDR scores for each ROI source area were compared between subsequent source memory correct versus source memory incorrect trials using paired t-tests. Age-related effects were examined using mixed-effect linear models and findings are reported in Appendix C. Multiple comparison correction was conducted using BH method to adjust for FDR. Left and right hemispheres were tested and corrected separately if the ROI is bilateral.

We focused on the three sets of source ROIs described above: 1) cortical MTL, 2) comprehensive memory ROIs, and 3) fMRI-constrained ROIs (details below). All ROIs are listed in Table1 along with the corresponding atlas labels from if they were derived from the Brainnetome atlases.

MTL ROIs. CDR scores within the cortical areas of all Brainnetome MTL subregions were tested bilaterally. Tested areas include various parts of the parahippocampal gyrus (PhG), the entorhinal cortex (EC), and the temporal agranular insula (TI). As mentioned above, subcortical regions were not tested due to limitations of the source localization method.

Comprehensive Memory ROIs. In addition to the MTL region, we constructed a list of 12 ROIs from previous fMRI research, including five ROIs established from an existing meta-analysis paper of source memory encoding in adults (Spaniol et al., 2009) and seven ROIs results showing significant subsequent source memory effects in this task (Geng et al., 2019, 2022). The five source areas from Spaniol et al., 2009 were the middle frontal gyrus (MFG), SFG, MTG, the parahippocampal region, and the MVOcC. The seven ROIs from Geng et al., were SPL, IPL, ITG, IFG, FuG, LOoC and orbital gyrus (OrG). We regrouped Brainnetome areas into these ROIs volumes. CDR values at each source dipole within a given ROI volume were summed across the entire volume and then divided by the total volume of that ROI. Note the parahippocampal volume is made of all MTL cortical subregions tested in Aim 1, representing the broad parahippocampal region.

In order to explore other possible cortical regions that contributed to source memory performance, we subsequently conducted a whole-brain ROI search across

40 areas (20 areas in each hemisphere). BH method was used to corrected for FDR separately for each hemisphere.

fMRI-constrained ROIs. A task-specific group mask was achieved from the whole-brain analysis of 44 participants' fMRI data and was described in a previous paper (Geng et al., 2019). In short, BOLD signal was compared between subsequent source correct and subsequent source incorrect trials. Mean framewise displacement, age, performance, and age performance interaction were included as covariates. Significant ROI clusters have a minimum of 12 voxel size after correction for multiple comparison. This analysis identified six cortical regions through whole-brain analysis that showed subsequent source memory effect. These regions are left-hemisphere IPL/SPL, IOG, left-hemisphere ITG, left-hemisphere IFG, FuG and OFG. These a priori identified cortical regions informed source model construction for ERP source localization.

In this project, the MNI-space group mask described above was re-processed to coordinate with EEG source analysis pipeline. The group mask was upsampled from 3mm to 1mm resolution and realigned to brain-extracted individual structural MRI scans using AFNI's 3dAllineate function. This transformation yielded one fMRI ROI mask for each participant, in their individual head space. All individual ROI masks were visually inspected and then used hypothesized EEG source regions.

Chapter 7: Results

Source Memory Performance

Behavioral analysis of task performance across both EEG and fMRI recording sessions, as reported by prior publications (Geng et al., 2018, 2019), indicated a mean source memory accuracy of 0.53 ($SD = 0.13$) in the MRI session, and a mean source memory accuracy of 0.49 ($SD = 0.11$) in the ERP session. Among children who performed both recording sessions and provided usable data, the majority (37 out of 41) completed the MRI session before the EEG session. Average number of days between the two sessions were 12.3 ($SD = 12.63$, $Mdn = 7$). Mean performances of this subset of children were consistent with previous reports of this dataset (Geng et al., 2018, 2019), with a mean source memory accuracy of 0.58 ($SD = 0.15$) in the MRI session, and a mean source memory accuracy of 0.49 ($SD = 0.13$) in the ERP session.

ERP Results

P2. Analysis of the P2 component showed a significant interaction between Condition and Sagittal plane, $F(2, 188) = 5.93$, $p = 0.003$, as well as a three-way interaction between Condition X Coronal plane X Sagittal plane, $F(4, 376) = 3.87$, $p = 0.043$. To further explore these interactions, post hoc pairwise testing was conducted in each Coronal plane X Sagittal plane clusters. In frontal ($t(396) = 2.99$, $p = 0.003$) and central ($t(396) = 2.39$, $p = 0.017$) clusters, P2 showed a significant subsequent source memory effect (greater amplitude to subsequent source correct

versus source incorrect trials) in left, but not middle and right channels. In the

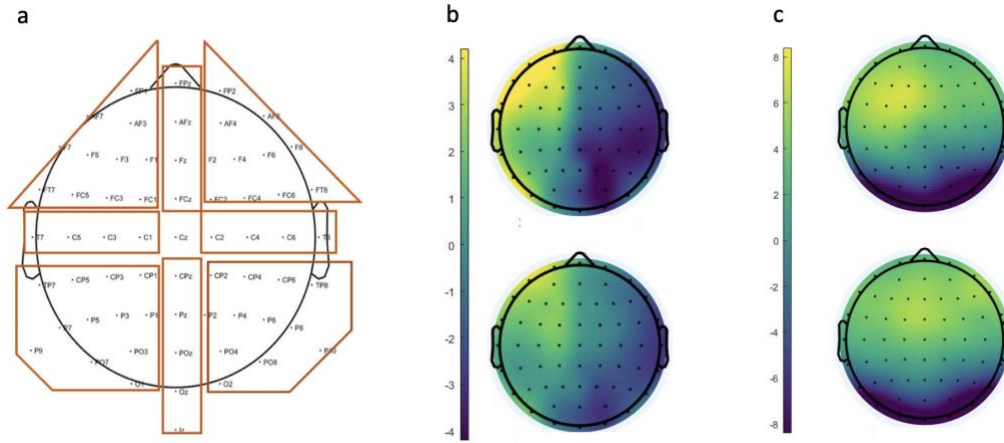


Figure 2. ERP signals between memory conditions. a) EEG channel locations and Coronal (frontal, central, posterior) X Sagittal (left, middle, right) channel clustering. b) Average P2 amplitude in subsequent source memory correct (top) and incorrect trials (bottom), averaged across 150 ms around P2 peak amplitude. c) Average LSW amplitude in subsequent source memory correct (top) and incorrect trials (bottom), averaged across from 1125-1275ms after trial onset.

central cluster, P2 amplitude showed the opposite effect (i.e. significant decrease in source correct condition, compared to source incorrect condition) in middle ($t(396) = -2.88, p = 0.004$) and right ($t(396) = -2.15, p = 0.03$) channel clusters. In the posterior area, P2 amplitude also showed the opposite source memory effect in right channel clusters, $t(396) = -2.28, p = 0.023$).

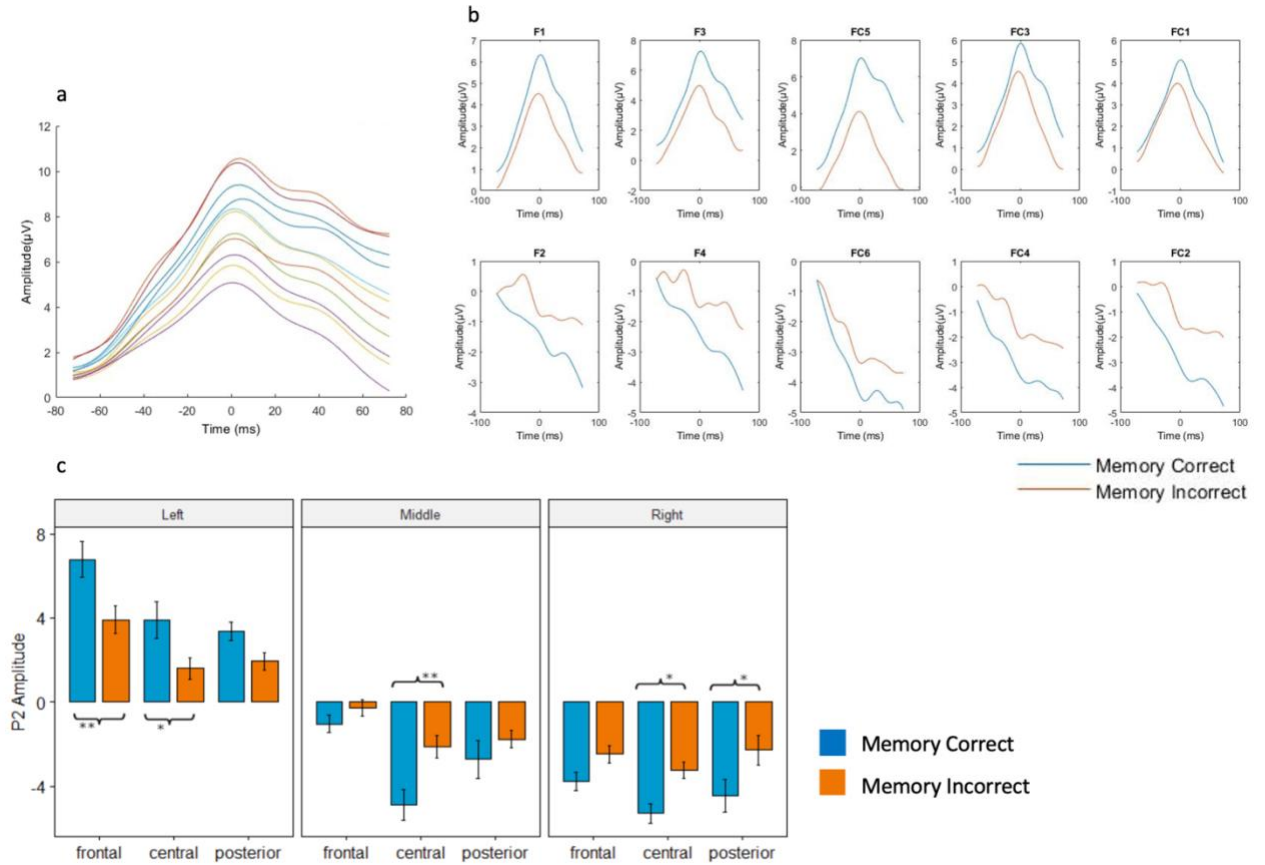


Figure 3. P2 component. a) P2 activity during source correct trials across all left frontal channels, centered around individual P2 peak. b) Conditional differences in frontal P2 by channel, contrasting left hemisphere (top) v.s. right hemisphere (bottom) channels. c) P2 activity by Coronal x Sagittal clustering.

Analyses in individual channels showed significant conditional differences in P2 amplitude at multiple channels following FDR correction for multiple comparisons. As illustrated in Figure 3c, greater P2 amplitudes were observed over left frontal and left central electrode locations in source correct conditions compared to source incorrect conditions, including channel FP1, $t(94) = 2.10$, $p = 0.042$; AF7, $t(94) = 2.43$, $p = 0.042$; F5, $t(94) = 2.52$, $p = 0.042$; F7, $t(94) = 3.33$, $p = 0.021$; FT7, $t(94) = 3.40$, $p = 0.020$; FC5, $t(94) = 2.71$, $p = 0.038$; C5, $t(94) = 2.25$, $p = 0.042$; T7,

$t(94) = 3.26, p = 0.041$; TP7, $t(94) = 2.84, p = 0.041$; CP5, $t(94) = 2.05, p = 0.044$; P5, $t(94) = 1.54, p = 0.042$; P7, $t(94) = 2.57, p = 0.019$; P9, $t(94) = 2.77, p = 0.019$; and PO7, $t(94) = 1.69, p = 0.043$. Comparatively, the opposite effect was observed in right frontal and right central channels, including F2, $t(94) = -1.09, p = 0.026$; F4, $t(94) = -1.24, p = 0.021$; FC4, $t(94) = -1.64, p = 0.002$; FC2, $t(94) = -1.76, p = 0.003$; FCz, $t(94) = -1.53, p = 0.002$; Cz, $t(94) = -2.42, p = 0.006$; C2, $t(94) = -2.54, p < 0.001$; C4, $t(94) = -2.15, p = 0.003$; C6, $t(94) = -1.47, p = 0.020$; CP6, $t(94) = -1.99, p = 0.020$; CP4, $t(94) = -2.34, p = 0.020$; CP2, $t(94) = -2.94, p = 0.009$; and P2, $t(94) = -2.88, p = 0.014$.

LSW. As illustrated in Figure 4c, Analysis of the LSW component also indicated a significant interaction between Condition and Sagittal plane, $F(2, 188) = 4.02, p = 0.020$. Post hoc pairwise testing of this interaction showed that left (but not middle and right) LSW was significantly greater for subsequent correct source memory, compared incorrect source memory, $t(217) = 2.30, p = 0.023$.

There were conditional differences at individual channel locations in amplitude over several frontal and central electrode locations across the scalp, including F5, FC5, FC3, C3, C5, CP3, Pz, P2. However, these findings did not survive FDR corrections.

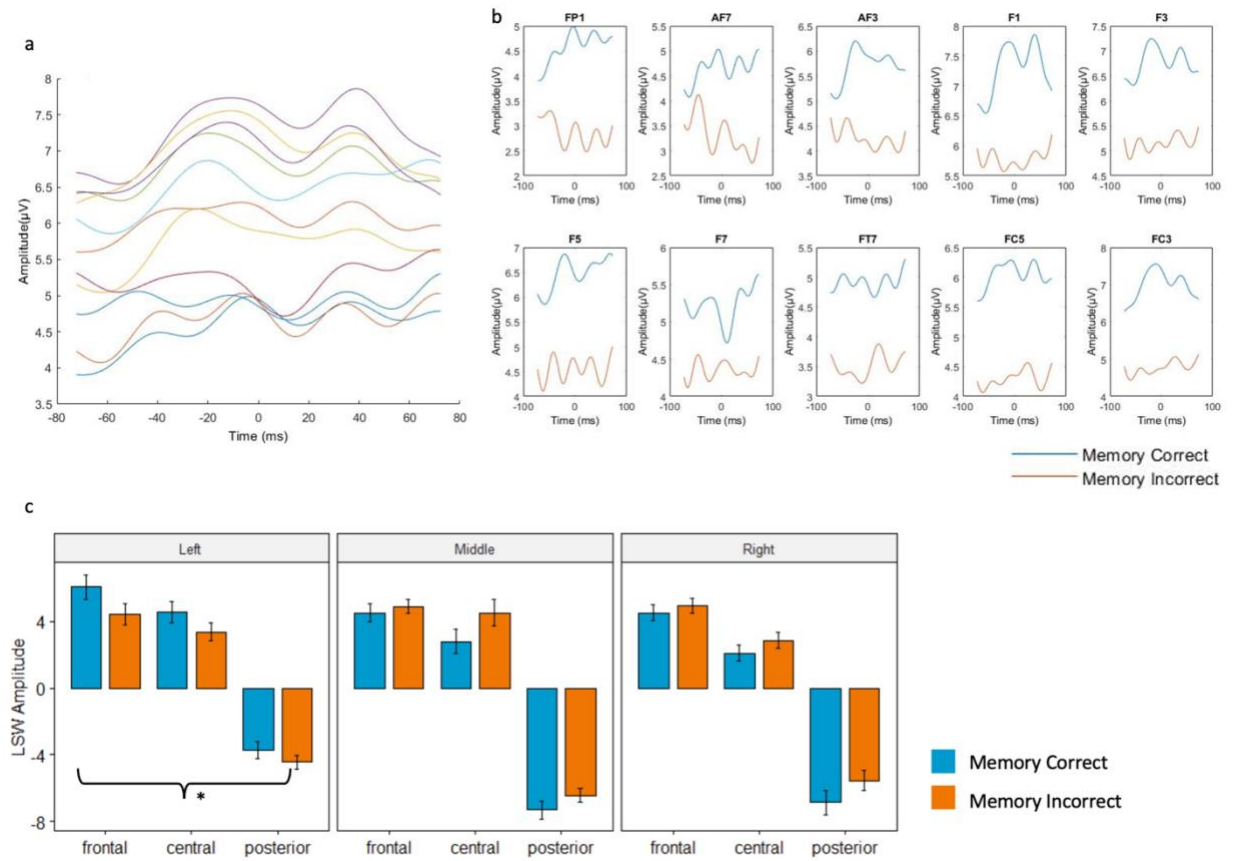


Figure 4. LSW component. a) LSW activity during source correct trials across all left frontal channels, centered around 1200ms after trial onset. b) Left frontal LSW activity by channel and condition. c) LSW activity by Coronal x Sagittal clustering.

Source Localization Results

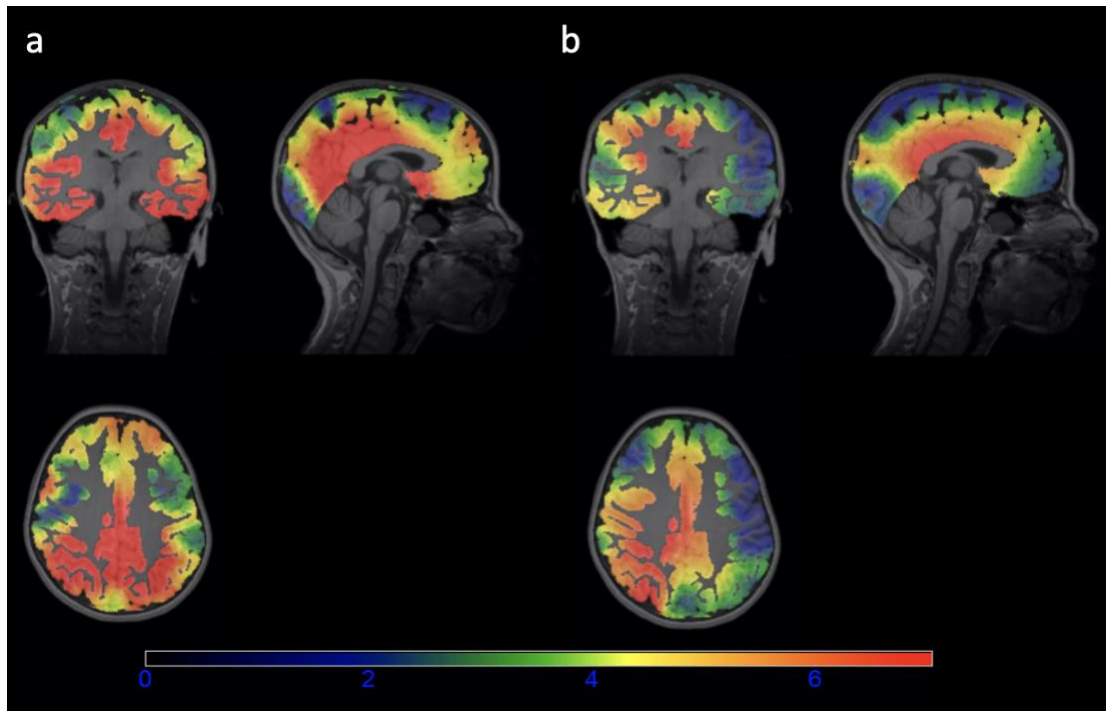


Figure 5. An illustration of the source localization outcome in individual head space. Panels show the average CDR scores during LSW at each source grid of the participant's head model, for a) the source memory correct and b) source memory incorrect conditions, respectively. Regions exhibiting strong conditional differences in their CDR scores (hot colors) include several frontal and parietal regions as well as MTL and its surroundings, consistent with quantitative results discussed below.

We estimated a CDR score for each source grid in individual participants' head models based on epoched P2 and LSW activity, for source correct and source incorrect memory conditions separately. These CDR scores were then averaged across all source grids in each hypothesized ROI and compared between the two conditions (Figure 5).

MTL. As illustrated in Figure 6c, within the MTL region, multiple subregions showed significant CDR differences during peak P2 activity between source correct and source incorrect conditions. All left hemisphere subregions showed greater CDR

scores in source correct condition than incorrect condition, and survived FDR corrections (left and right hemisphere were corrected separately). The areas include rostral PhG (left: $t(91) = 0.48, p = 0.031$; right: $t(91) = 0.27, p = 0.060$), caudal PhG (left: $t(91) = 0.49, p = 0.034$; right: $t(91) = 0.29, p = 0.060$), lateral PPHC (left: $t(91) = 0.53, p = 0.036$; right: $t(91) = 0.30, p = 0.060$), medial PPHC (left: $t(91) = 0.57, p = 0.031$; right: $t(91) = 0.34, p = 0.060$), EC (left: $t(91) = 0.50, p = 0.031$; right: $t(91) = 0.29, p = 0.060$), and TI (left: $t(91) = 0.60, p = 0.034$; right: $t(91) = 0.46, p = 0.060$). Right hemisphere subregions showed marginal results. No areas showed greater activity in subsequent source memory incorrect condition compared to source memory correct condition. These results indicate stronger P2-related cortical activity during memory encoding in subsequent successful retrieval of source memory.

As illustrated in Figure 6e, LSW sources also showed conditional differences within multiple areas within MTL, including left, but not right, rostral PhG, $t(91) = 0.54, p = 0.039$; caudal PhG, $t(91) = 0.44, p = 0.053$; medial PPHC, $t(91) = 0.58, p = 0.039$; and EC, $t(91) = 0.60, p = 0.039$. No areas showed greater activity in subsequent source memory incorrect condition compared to source memory correct condition.

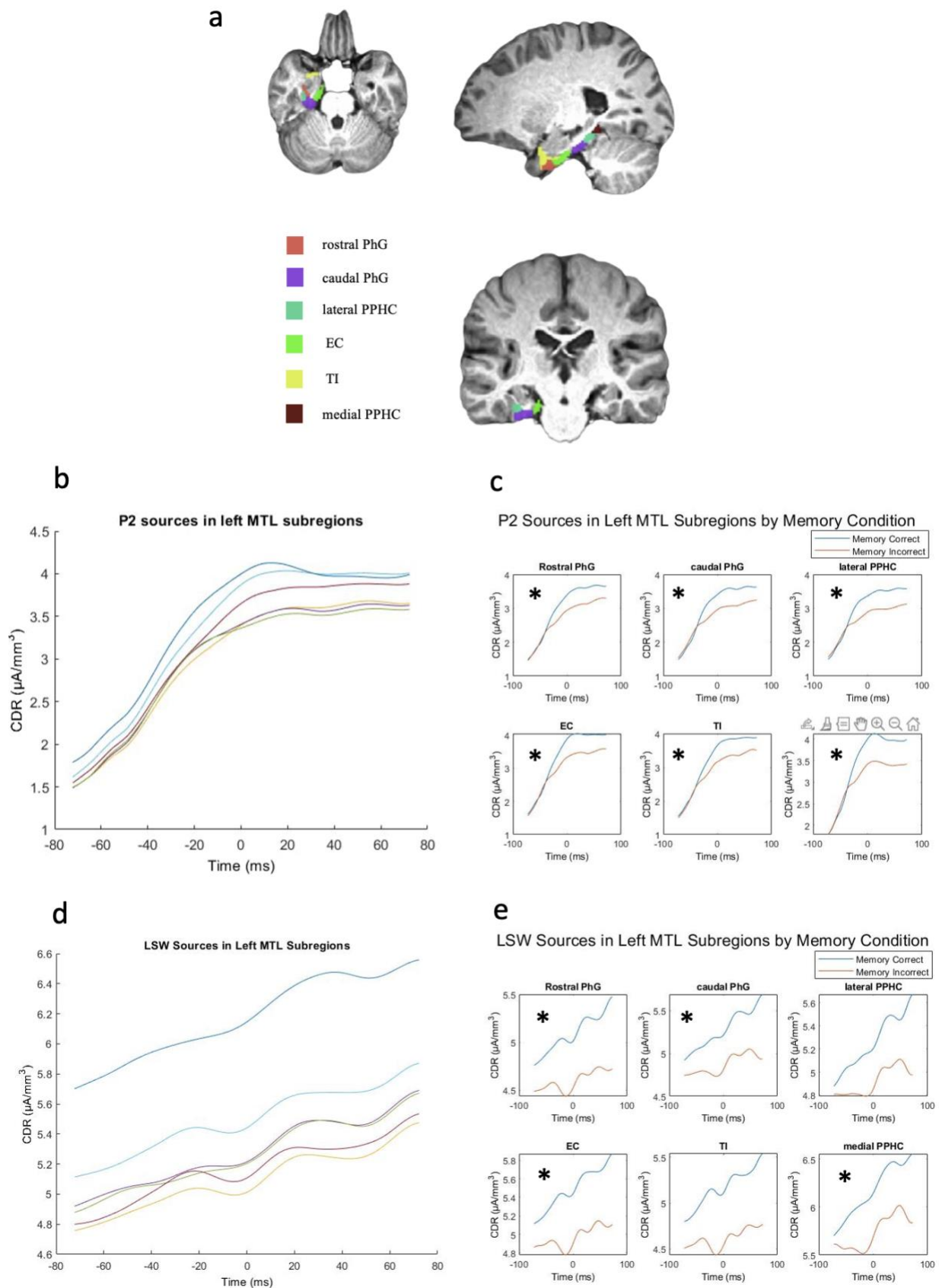


Figure 6. a) Subregions in left MTL. b) P2 sources across all left MTL subregions. Cortical CDR scores steadily increased until hitting peak P2 activity. c) P2 source activity by memory conditions in each left-hemisphere subregion of MTL. d) LSW sources across all left MTL subregions. Cortical CDR scores steadily increased overtime. e) LSW source activity by memory conditions in each left-hemisphere subregion of MTL. (* $p < 0.05$)

Comprehensive Memory ROIs. As illustrated in Figure 7b and 7c, within multiple ROIs showed significant CDR differences during peak P2 activity between source correct and source incorrect conditions. These areas are left SFG, $t(91) = 0.44$, $p = .030$; right SFG, $t(91) = 0.23$, $p = 0.021$; right OrG, $t(91) = 0.40$, $p = 0.041$; right SPL, $t(91) = 0.28$, $p = 0.008$; right IPL, $t(91) = 0.17$, $p = 0.008$; and right LOoC, $t(91) = 0.26$, $p = 0.041$. Left MFG, OrG, FuG, PhG, SPL, IPL and bilateral MVOoC showed marginal results ($p < 0.06$). All significant results showed greater CDR scores in source correct condition versus source incorrect condition. As illustrated in Figure 7d and 7e, LSW sources also showed conditional differences within left OrG and left PhG, but the result did not survive FDR corrections. No areas showed greater activity in subsequent source memory incorrect condition compared to source memory correct condition.

Whole-brain exploratory analysis (for lists of results from all tested regions, see Appendix D) identified several previously unidentified brain regions showing significant CDR differences between the source memory conditions for the P2 component, including bilateral paracentral lobule (left: $t(91) = 0.57$, $p = 0.016$; right: $t(91) = 0.53$, $p = 0.007$), bilateral precuneus (left: $t(91) = 0.42$, $p = 0.044$; right: $t(91) = 0.42$, $p = 0.017$), right postcentral gyrus ($t(91) = 0.10$, $p = 0.029$), bilateral cingulate gyrus (left: $t(91) = 0.57$, $p = 0.016$; right: $t(91) = 0.51$, $p = 0.007$), and right posterior

superior temporal sulcus ($t(91) = 0.178, p = 0.043$). No previously unidentified regions showed significant CDR differences between the source memory conditions for the LSW component.

fMRI-constrained ROIs. As illustrated in Figure 8b, within task ROIs from fMRI data, two regions showed significant CDR differences during peak P2 activity between source correct and source incorrect conditions. These two ROIs are OFG, $t(91) = 0.36, p = 0.024$, and left IPL/SPL, $t(91) = 0.27, p = 0.024$. As illustrated in Figure 8c, LSW-related CDR scores were also significantly greater in OFG in source correct condition compared to source incorrect condition, but the result did not survive FDR correction. No areas showed greater activity in subsequent source memory incorrect condition compared to source memory correct condition.

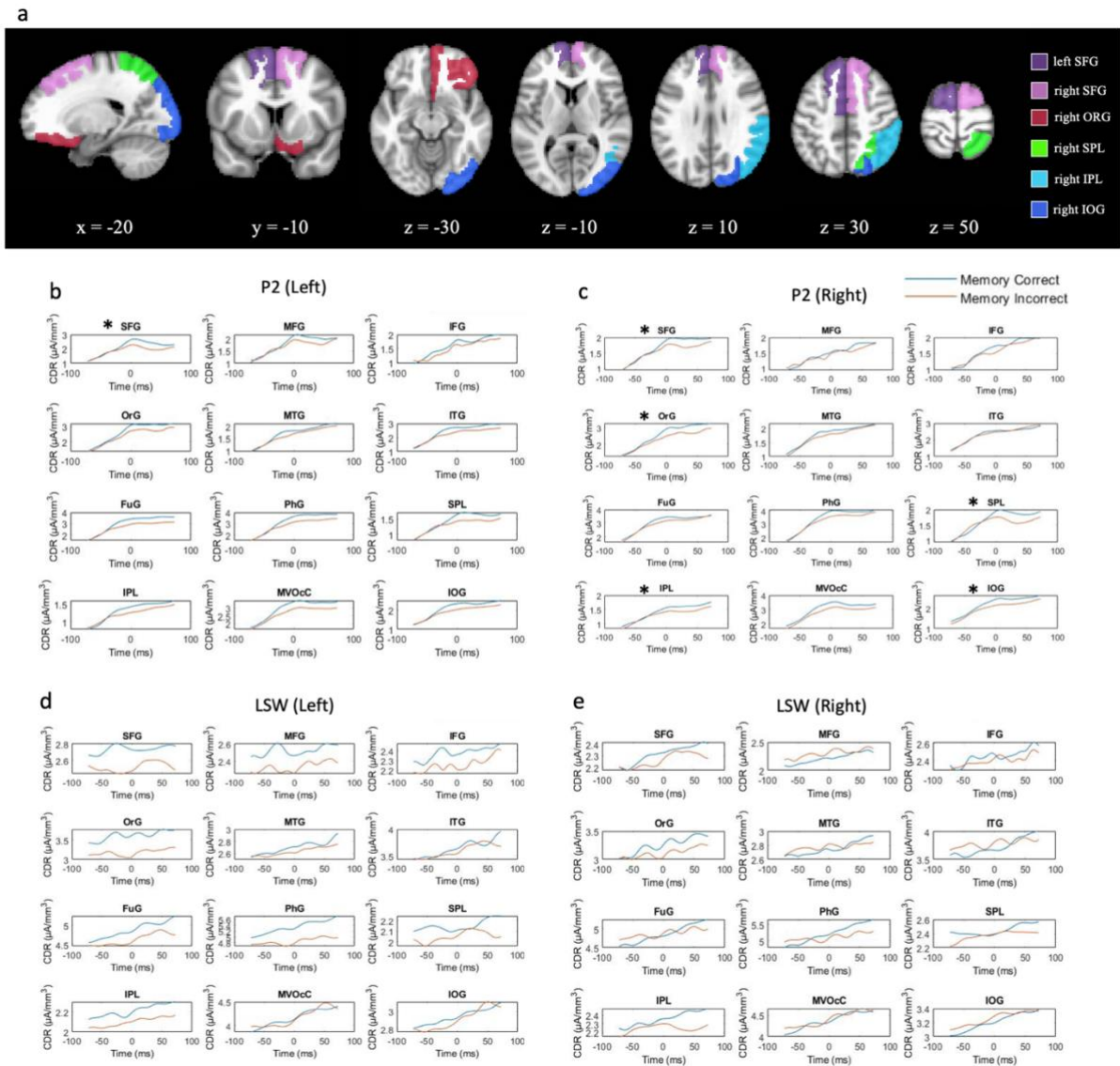


Figure 6. a) ROIs showing significant P2 effect in talairach coordinates. b) P2 source activity in each left hemisphere memory ROI by source memory condition. c) P2 source activity in each right hemisphere memory ROI by source memory condition. d) LSW source activity in each left hemisphere memory condition. e) LSW source activity in each right hemisphere memory ROI by source memory condition. (* $p < 0.05$)

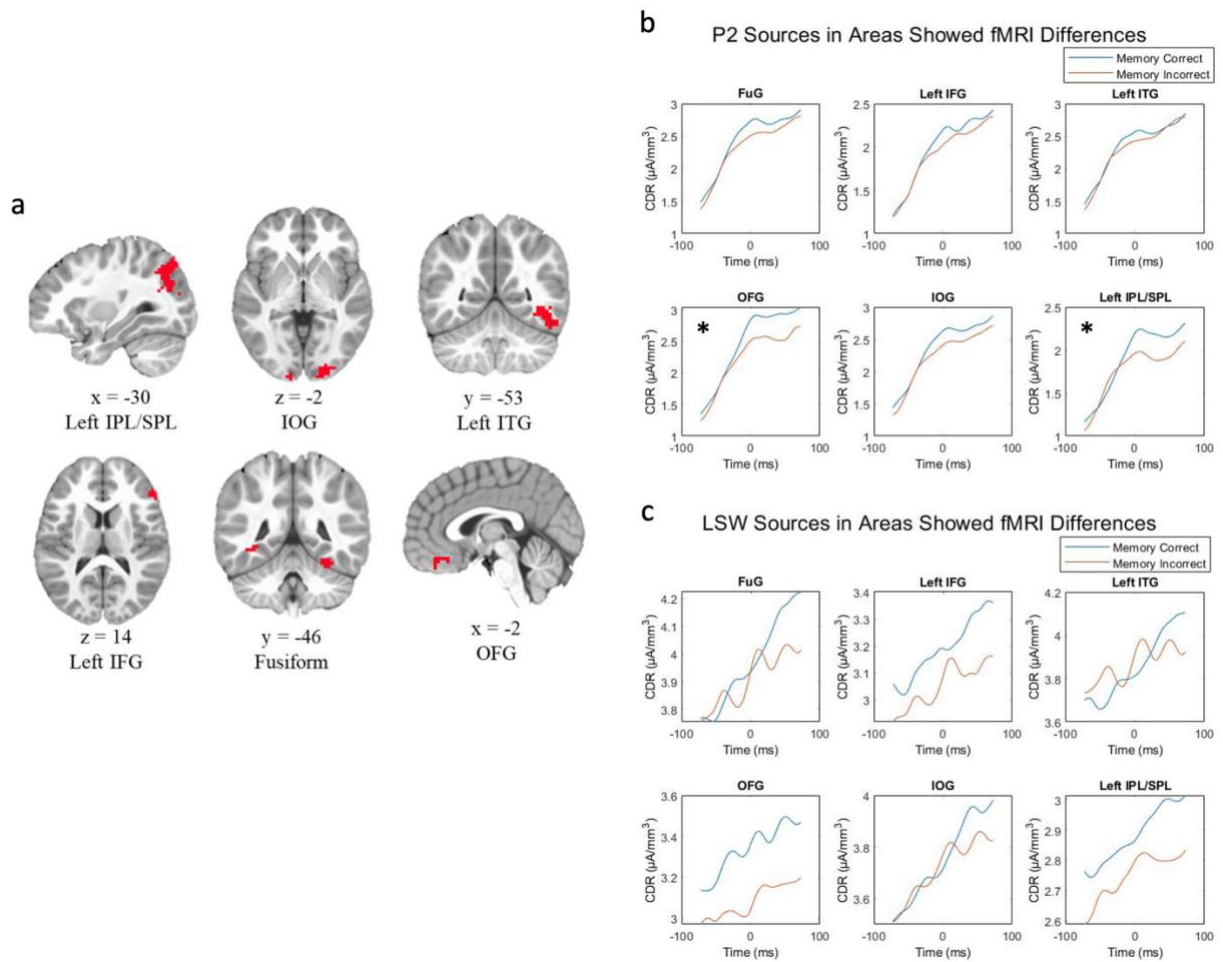


Figure 8. fMRI-constrained source localization. a) Adapted from Geng et al., 2019. Cortical regions showing greater fMRI activation in source memory correct versus incorrect condition. b) P2 source activity in each fMRI-identified ROI by source memory condition. c) LSW source activity in each fMRI-identified ROI by source memory condition.

Chapter 8: Discussion

The emergence of source memory in early childhood accompanies dynamic, mutual influences on and from brain maturation and other cognitive changes (Amlen et al., 2018; Canada et al., 2022; Decker et al., 2023; Geng et al., 2021; Shing et al., 2010; Yang et al., 2017). Neural signals associated with source memory encoding from EEG and fMRI studies reveal important underlying mechanisms of how the brain associates and represents context with memory items (e.g., Geng et al., 2018, 2019; Ghetti et al., 2010; Riggins et al., 2009; Riggins et al., 2013). However, signals between these different neurophysiological methods are not unified. Examining source memory encoding in young children through multimodal analysis allows us to assess how these memories take shape with complementary temporal and spatial information from each of the modalities. Understanding the neural mechanisms of source memory encoding in young children from this integrated perspective has implications for developmental research on episodic memory.

ERPs at Encoding Predicted Subsequent Source Memory Performance

P2. During encoding, stimulus-induced P2² was predictive of subsequent source memory performance. The P2 component showed subsequent source memory effect in frontal v.s. posterior, and left v.s. right channel clusters, and in individual

² The P2 component is a positive voltage deflection occurring approximately 150-250 milliseconds after stimulus onset in bilateral frontal recording sites (e.g. Potts, 2004; Smith, 1993; Spitzer et al., 2008). P2 is associated with allocation of attentional resources and early processing of information in infants (discussed by de Haan, 2002) and adults (e.g. Cooper et al, 2006; Freunberger et al., 2007; Potts, 2004; Smith, 1993; Wolach & Pratt, 2001), as well as contextual processing in adults (Cao et al, 2023).

frontal and frontocentral channels. Although the role of the P2 component in memory has not been previously established, existing research in adults suggests a role in early memory processing during the integration of information. For example, P2 amplitudes have been shown to vary with repetition of memory stimuli and are sensitive to item familiarity (Rugg & Curran, 2007). Specifically, P2 shows increased amplitude in response to the first memorized item during a memory encoding task compared to the rest of the items (Wolach & Pratt, 2001), and decreased amplitude to immediately repeated memory stimuli (Smith, 1993), suggesting that P2 amplitude reflects the “amount” of early processing to memory items.

Given the unique role of P2 in attention and contextual information processing, it may be crucial for encoding new information into memory. Results of the present study showed greater P2 amplitudes in left frontal regions for trials in which source information was subsequently correct, potentially reflecting the engagement of a lateralized frontoparietal network associated with attentional processes, crucial for the encoding of source information (Geng et al., 2022).

LSW. During encoding, LSW was predictive of subsequent source memory performance. The LSW component showed greater amplitude in left v.s. right channel clusters. This finding is consistent with the previous analysis examining LSW in this dataset (Geng et al., 2018). However, LSW component did not show differences at individual channels after corrections for multiple comparisons. This lack of significance is likely attributed to its broad topographical distribution (Riggins et al., 2009; Riggins et al., 2013), as well as variability across individuals at different ages (Geng et al., 2018; Rollins & Riggins, 2013). Previous studies suggested that LSW

may reflect the updating of memory for a partially encoded stimulus (Reynolds & Richards, 2005; Riggins et al., 2013), and thus there could also be variability in this component due to its association with later stages of memory processing, which might be more susceptible to individual differences in memory strategies.

In conclusion, P2 and LSW were sensitive to source memory encoding. The timing differences in these components reveal information about encoding processes. The effects at the earlier P2 and later LSW suggest processes related to evaluating or integrating the source of memory are distributed across a wide time range. Their respective timing is consistent with previous work on the role of attention and its early impact on memory encoding, and the role of LSW in updating and integrating memory with details.

Cortical Sources of P2 and LSW

Although P2 and LSW both exhibited subsequent source memory effects in young children, their neural origins and exact functionalities are not fully understood. We utilized EEG source localization to project scalp ERP potentials into individual cortical spaces, in order to examine the underlying anatomical sources of these two components.

MTL. Source analysis revealed that P2- and LSW- associated cortical activity showed significant effects in multiple areas of MTL. Specifically, the P2 effect was found in all six tested subregions of cortical MTL in both left and right hemispheres, while the LSW effect was only present in PhG and EC. The MTL is a key region for information integration, memory association, and updating. Importantly, the PhG is known for its role in processing environmental contexts, and the EC is the principal

site of cortical input into the hippocampus (Suzuki et al., 1994), heavily involved in relaying contextual information to hippocampus. Given MTL's unique role in information integration, the P2 result adds new evidence to previous research suggesting P2's role in the processing and integration of contextual information (Cao et al., 2023), and underscores the finding that children start to process contextual details associated with a memory item as early as 200-250ms. The LSW result in PhG and EC supports previous work suggesting the LSW reflects activity during memory association and information updating (Nelson, 1994; Reynolds & Richards, 2005; Riggins et al., 2013), especially given the late latency it has during memory encoding. Given previously reported age-related changes in the timing and amplitude of LSW (Geng et al., 2018; Rollins & Riggins, 2013), its localized neural sources in the MTL region converge with neuroimaging findings showing decreased activation in the MTL during memory encoding as children age (Ghetti et al., 2010; Menon et al., 2005; Ofen et al., 2007). Both P2 and LSW results show that scalp EEG signals capture activities in the cortical MTL area regardless of some of its deep anatomical locations in the brain (e.g., PhG) and suggest the important role of MTL in both early and late stages of encoding process.

Comprehensive Memory ROIs. Source localization results outside of MTL additionally revealed a complex and extensive network of cortical regions implicated in the process of source memory encoding. Significant subsequent source memory effects were observed in several cortical regions during peak P2 activity, involving frontoparietal areas critical for a range of cognitive functions such as attention, working memory, and sensory integration -- processes critical for the encoding of

episodic memories (Spaniol et al., 2009; Ofen et al., 2007). Among these significant regions were the SFG, SPL, and IPL, all of which are integral to the frontoparietal network, a crucial network in cognitive control, attention and information processing (Marek & Dosenbach, 2018). P2 was additionally source localized to OrG, which aligns with a previous study of attention in adults (Potts, 2004). OrG is extensively interconnected with the frontoparietal network as well as the hippocampus (Wikenheiser & Schoenbaum, 2016), and is considered to encode complex relationships between cues, actions, outcomes and other features of the environment in parallel with the hippocampus. Thus, the P2 activity suggests a blend of activations in a wide-spread memory network that is recruited early on during the encoding, performing a list of cognitive tasks including attention orientation, sensory and contextual information processing, as well as information integration and updating.

fMRI-constrained ROIs. fMRI-constrained multimodal analysis provides a more nuanced understanding of the neural underpinnings of memory encoding, demonstrating a significant overlap between localized ERP sources and fMRI ROIs. Specifically, source memory effect was identified during P2 in two out of six fMRI ROIs that showed conditional differences in BOLD activation (i.e. the OFG and the left IPL/SPL ROIs). Although LSW presented similar trends in both of these areas (Figure 8c), the results did not survive multiple comparison corrections. The multimodal results further indicate that EEG and fMRI results, while being different modalities of neurophysiological measures, are pointing at the same or shared source memory encoding mechanism. The differences in the localized sources between early stage P2 and the late stage LSW provide additional temporal information to the

potentially roles of fMRI-identified areas. The P2 component, occurring early in the processing timeline, suggests that these specific fMRI-identified areas are engaged during the initial stages of encoding, implicating their role in the attentional and perceptual aspects of memory formation.

Limitations

The spatial accuracy of scalp-level EEG activity and its source localization results are still a matter of debate. A large portion of memory-related neural activity happens in the subcortical regions, especially within the hippocampus (e.g. Geng et al., 2019; Ghetti et al., 2010; Ofen et al., 2007). However, there is a general agreement that scalp EEG has very limited access to subcortical activity. The present analysis excluded subcortical regions from the source analysis due to this concern, though some debates that such detection can be made possible using high-density EEG system (Seeber et al., 2019).

The LSW component, unlike the P2 component, exhibits a plateau-like slow increase after reaching local maximum, pointing to underlying oscillatory activities that tend to be anatomically widespread and reflect neural activity in a broadly distributed network. The lack of a “peak” in the LSW component makes it challenging to identify the appropriate time window to conduct source localization, especially across participants at different ages who may exhibit different latency of LSW (Geng et al., 2018; Rollins & Riggins, 2013). Adding on to the challenge is individual differences in sustained attention (Decker et al., 2023) and memory strategies (Sprondel et al., 2011) during late-stage memory encoding. Given these challenges, it is possible that LSW is contributed by other cortical regions in addition

to MTL, and those results are not meeting significance threshold due to high signal-to-noise ratio.

Another limitation in current EEG source localization techniques is the absence of robust validation methods to examine the “confidence” of identified sources; in other words, there are no statistical measures to examine the estimation errors in its results (Michel et al., 2004). This gap in methodology restricts the ability to assess the reliability of the localized neural activity associated with any particular ERP component. It is necessary to interpret source localization results alongside reasonable, a priori identified cortical ROIs.

Finally, assessing source memory in young children itself is challenging in the task design, given their limited language and conceptualization abilities. Our experimental paradigm utilizes a popular source memory task that requires children to imagine that each memory item “belongs to” one of three cartoon characters (see *Chapter 6: Method* and *Appendix 1* for task prompt), but there could have been individual differences in children’s memory strategies during the task. However, these differences would likely not confound our results given their largely overlapping memory processes and underlying neural mechanisms. Future studies could benefit from asking for self-reported memory strategies to further validate the access to source memory during the task.

Implications for Multimodal Analysis in Children and Future Directions

Early childhood is a period requiring precision in both anatomical and temporal dimensions when identifying the changing neural signals associated with evolving memory (e.g., Geng et al., 2021). ERP and fMRI approaches have precision

in different domains, complementing each other in the information they provide. For example, activations in the frontoparietal regions (Geng et al., 2021; reviewed by Spaniol et al, 2009) have been hypothesized to modulate memory encoding via attentional/cognitive control processes, but the timing of such interaction is difficult to assess through fMRI alone. EEG source localization bridges between the two modalities, allowing us to link the timing of P2 component to its cortical sources in the frontoparietal regions, cross-validating results from each modality and creating a “chain of evidence” for the neural origin, timing, and effect of the underlying neural signal.

Future research may benefit from further integrating the two modalities to explore the intricate relations between different developmental stages of memory encoding and evolving neural dynamics during encoding processes. Longitudinal multimodal analysis is needed to shed a light on dynamic age-related changes among P2/LSW activities, their neural sources, and the matching fMRI activations during memory development. Changes in the temporal and spatial features of P2 and LSW components will help us better understand the developing mechanisms of episodic memory encoding.

As described above, slow wave activities are generally harder to localize and may benefit from analysis in the time-frequency domain. Recent research is beginning to support source localization of EEG activity in specific frequency bands through estimated functional connectivity. Source localization of functional EEG connectivity represents a relatively novel direction (Xie, Toll & Nelson, 2022), which has only recently become feasible due to advancements in computational power and

modeling methods. This approach might also offer new insights into the underlying neural origins of LSW that support source memory.

Conclusion

In conclusion, this dissertation contributes to our understanding of the neural foundations of memory in developing brain, by examining overlapping neural sources between EEG- and fMRI- identified cortical areas associated with source memory encoding, cross-validating results from memory literature using each of these modalities alone. This work stands to have substantial impact as it showed that findings from ERP and fMRI reflect overlapping or similar brain activity and that results from one measure could be better interpreted given information from the other measure. We hope that this project will begin to bring the literatures on EEG and fMRI during memory development together and allow for a more comprehensive characterization of memory-related neural signatures. Our multimodal analysis of neural signals involved during source memory encoding in young children, leveraging both ERP and fMRI data, highlights the dynamic and multifaceted nature of memory encoding processes in the brain, and calls for considerations in both spatial and temporal aspects of brain activity to fully understand memory-related neural signals.

Appendix A. Task Script

Experimenter: Today we're going to play a fun game! The game has 2 parts. The first part is the learning part of the game and the second part is the matching part of the game. Today you're going to play the learning part of the game inside the scanner, and you will play the matching part outside the scanner. Ready to learn how to play the game?

Practice

Experimenter: First, in the learning part of the game, you will get to meet three characters and you will get to learn about their favorite things that belong to them.

Experimenter: First you will meet Minnie Mouse. Do you know who Minnie Mouse is?

Experimenter: Next you will meet Winnie the Pooh. Do you know who Winnie the Pooh is?

Experimenter: Last, you will meet Batman. Do you know who Batman is?

Experimenter: Let's practice meeting the characters and learning their favorite thing that belong to them. Make sure you pay attention to which things belong to which character! This is important because Minnie Mouse, Winnie the Pooh, and Batman need your help remembering which things are theirs! If you can help them remember which things are their own things, they will each get a special present. Do you want Minnie, Winnie the Pooh and Batman to get a present?

(Display character 1 and present associated memory items.)

Experimenter: This is Minnie, and here are some of her favorite things!

(Display character 2 and present associated memory items.)

Experimenter: This is Winnie the Pooh, and here are some of his favorite things!

(Display character 3 and present associated memory items.)

Experimenter: This is Batman, and here are some of his favorite things!

Experimenter: Now you're going to play the matching part of the game! You're going to see some more pictures. Some of them you saw earlier, and some of them are new. I'm going to ask you if you saw the picture in the first part of our game today. If you say yes because you have seen the picture before, I want you to tell me whose favorite thing it was. You have to tell me if it was Minnie's, Pooh's, or Batman's. Are you ready?

(For each picture, ask if they have seen the picture before, or if the picture is new.)

Experimenter: Was this one of the characters' favorite things?

(If New: Go to next picture; if Old: Ask which character the thing belongs to.)

Experimenter: Whose favorite thing was this?

Task

Experimenter: Great job!

Experimenter: Now we're going to play the game for real! You're going to play the learning part of the game first, then we'll take a short break, and then we'll play the matching part of the game! Let's start the learning part of the game. Don't forget to pay attention to which favorite things belong to which characters!

(Perform Encoding Paradigm)

Experimenter: Great job! Now we're going to take a short break and then play the matching part of the game.

(5 min break)

Experimenter: Now we're going to play the matching part of the game! Let's go!

(Perform Retrieval Paradigm)

Experimenter: Now we're going to play the matching part of the game. If you are not sure, it's okay to make your best guess. Don't let the game trick you! Here we go!

Appendix B. Between-session Behavioral Analysis

We compared source memory performance between the first session and the second session to examine possible repetition effect on task performance. Paired t-test showed a significant decrease in *source memory accuracy* (i.e., correct source memory retrieval out of correctly recognized items), from the first session to the second session, $t(40) = -2.44, p = 0.010$. The decrease was driven by an increase in the number of correctly recognized items (i.e., correctly recognizing whether an item was “old” or “new”), $t(40) = 3.04, p = 0.004$. There were no significant between-session differences in *total source memory percentage* (i.e., percentage of correct source memory retrieval out of all trials).

To investigate whether children had consistent source memory performance between the two sessions, in spite of an improvement in recognition memory, we conducted a multiple regression using second-session total source memory percentage as the dependent variable, and first-session total source memory percentage as the predictor, controlling for age. First-session total source memory percentage strongly predicted second-session total source memory percentage, $\beta(38) = 0.62, p < 0.001$. This result suggests that differences in source memory performance were relatively stable between two recording sessions, despite the increase in recognition memory.

Appendix C. Age-related Analysis

In the ERP analysis, we additionally examined age-related effects on P2 and LSW amplitudes. Mixed-effect linear models were used to model P2 and LSW amplitudes as a function of age, controlling for Condition, Coronal Plane, Sagittal Plane, and their interactions, with a random intercept for subjects to account for within-subject variability. No main effects of age were identified in either P2 or LSW. We then modeled P2 and LSW amplitudes as a function of the interaction among Age, Condition, Coronal Plane, and Sagittal Plane, with a random intercept for subjects. No interaction with age was identified in P2 amplitudes. There were marginally significant interactions between Age X Sagittal Plane ($t(1674) = 1.785$, $p=0.075$), as well as Age X Sagittal Plane X Condition ($t(1674) = -1.646$, $p=0.100$) in LSW. To further explore these interactions, we used a median split and categorized age into two age groups (following approach in Geng et al., 2018). Post hoc pairwise comparison examined all Age Group X Sagittal Plane pairs for conditional differences in LSW amplitudes, corrected through the Tukey method. In the younger group, LSW amplitude showed significant conditional differences in left ($t(1581) = 3.754$, $p < 0.001$) and middle ($t(1581) = -3.240$, $p = 0.001$) channel clusters. In the older group, LSW amplitude showed significant conditional differences in right channel clusters ($t(1581) = -2.756$, $p = 0.006$). These LSW results are consistent with previously reported age effects on LSW in Geng et al., 2018.

In the source analysis, we also examined age-related effects for P2 and LSW CDR source scores separately. A mixed-effect linear model was applied to each source ROI, modeling the CDR score of the ROI as a function of age, controlling for

source memory condition. An alternative model was also tested, including an interaction term between Age and Condition. Both models included a random intercept for subjects. Multiple comparison corrections were conducted using BH procedure to correct for FDR. No age-related effects were identified for both P2 and LSW after correction in either model.

Appendix D. Whole-brain Exploratory Analysis

Table D1.

Conditional CDR Differences for the P2 component across all brain regions.

Brain region	<i>t</i> (left)	<i>p</i> (left)	adjusted <i>p</i> (left)	<i>t</i> (right)	<i>p</i> (right)	adjusted <i>p</i> (right)
<i>superior frontal gyrus</i>	0.44	0.00	0.02	0.23	0.01	0.02
<i>middle frontal gyrus</i>	0.23	0.02	0.06	0.08	0.13	0.15
<i>inferior frontal gyrus</i>	0.10	0.21	0.21	0.10	0.16	0.17
<i>orbital gyrus</i>	0.38	0.03	0.06	0.40	0.02	0.04
<i>precentral gyrus</i>	0.15	0.04	0.06	0.08	0.05	0.07
<i>paracentral gyrus</i>	0.57	0.00	0.02	0.53	0.00	0.01
<i>superior temporal gyrus</i>	0.13	0.13	0.15	0.15	0.05	0.07
<i>middle temporal gyrus</i>	0.08	0.17	0.18	0.08	0.14	0.16
<i>inferior temporal gyrus</i>	0.26	0.08	0.10	0.01	0.49	0.49
<i>fusiform gyrus</i>	0.46	0.04	0.06	0.18	0.12	0.15
<i>parahippocampal gyrus</i>	0.52	0.01	0.05	0.32	0.03	0.06
<i>posterior superior temporal sulcus</i>	0.13	0.14	0.16	0.18	0.02	0.04
<i>superior parietal lobule</i>	0.23	0.02	0.06	0.28	0.00	0.01
<i>inferior parietal lobule</i>	0.16	0.03	0.06	0.17	0.00	0.01
<i>precuneus</i>	0.42	0.01	0.04	0.42	0.00	0.02
<i>postcentral gyrus</i>	0.12	0.08	0.10	0.10	0.01	0.03
<i>insular gyrus</i>	0.24	0.08	0.10	0.20	0.05	0.07
<i>cingulate gyrus</i>	0.57	0.00	0.02	0.51	0.00	0.01
<i>medioventral occipital cortex</i>	0.41	0.03	0.06	0.32	0.03	0.06
<i>lateral occipital cortex</i>	0.24	0.05	0.08	0.26	0.01	0.04

Table D2.

Conditional CDR Differences for the LSW component across all brain regions.

Brain region	<i>t</i> (left)	<i>p</i> (left)	adjusted <i>p</i> (left)	<i>t</i> (right)	<i>p</i> (right)	adjusted <i>p</i> (right)
<i>superior frontal gyrus</i>	0.17	0.13	0.26	0.03	0.38	0.69
<i>middle frontal gyrus</i>	0.16	0.08	0.26	-0.08	0.71	0.71
<i>inferior frontal gyrus</i>	0.14	0.12	0.26	0.03	0.44	0.69
<i>orbital gyrus</i>	0.45	0.01	0.08	0.19	0.10	0.67
<i>precentral gyrus</i>	0.08	0.21	0.37	-0.04	0.66	0.69
<i>paracentral gyrus</i>	0.06	0.39	0.49	-0.04	0.58	0.69
<i>superior temporal gyrus</i>	0.20	0.04	0.17	0.01	0.47	0.69
<i>middle temporal gyrus</i>	0.08	0.25	0.38	-0.02	0.56	0.69
<i>inferior temporal gyrus</i>	0.03	0.43	0.51	-0.06	0.63	0.69
<i>fusiform gyrus</i>	0.25	0.12	0.26	0.03	0.46	0.69
<i>parahippocampal gyrus</i>	0.54	0.02	0.13	0.20	0.22	0.69
<i>posterior superior temporal sulcus</i>	-0.03	0.57	0.57	0.05	0.36	0.69
<i>superior parietal lobule</i>	0.04	0.38	0.49	0.05	0.34	0.69
<i>inferior parietal lobule</i>	0.12	0.13	0.26	0.15	0.09	0.67
<i>precuneus</i>	0.05	0.38	0.49	-0.02	0.55	0.69
<i>postcentral gyrus</i>	0.07	0.22	0.37	0.01	0.44	0.69
<i>insular gyrus</i>	0.42	0.00	0.07	0.12	0.19	0.69
<i>cingulate gyrus</i>	0.30	0.04	0.17	0.23	0.07	0.67
<i>medioventral occipital cortex</i>	0.01	0.48	0.51	-0.03	0.55	0.69
<i>lateral occipital cortex</i>	0.01	0.48	0.51	-0.04	0.61	0.69

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