Ageing and the Impact of Cognitive Demand on the Strength of Functional Connectivity Throughout the Brain

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Abstract

Functional connectivity refers to the way brain regions interact during various cognitive tasks. The current study examined how functional connectivity changes with increasing task difficulty and whether these effects are influenced by age. Two hypotheses were tested in the current study. The first hypothesis is that the strength of functional connectivity during increasing cognitive demand will differ with age in some brain regions. The second hypothesis is that the strength of functional connectivity will change due to cognitive demand, independent of age in other regions. Results showed that increasing cognitive demand was associated with increased connectivity in regions such as the middle temporal gyrus and the right planum temporale, while other regions showed decreased connectivity independent of age. These findings suggest that cognitive demand and age may have different effects on functional connections within the brain.

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Introduction

Cognitive health has been a longstanding area of interest in health science. Healthy cognitive processes allow individuals to make decisions, retain information and function in daily life (American Psychological Association, 2023). Severe cognitive deficits can cause problems such as learning difficulties, loss of memory, impaired vision, and even the inability to live independently (Dhakal & Bobrin, 2023). To be able to prolong cognitive health, it is essential to first understand the mechanisms involved in cognitive decline. These impairments can occur for various reasons, such as a head injury or disease progression (Haarbauer-Krupa, 2022; Dhakal & Bobrin, 2023). Age is also one of the main factors involved in this impairment (Murman, 2015). In 1997, around 17% of Canadians aged 65 or older had cognitive impairments, unrelated to dementia (Graham et al., 1997). This impairment, while more common at older ages, is not inevitable (Rowe & Kahn, 1987). As the population's lifespan continues to increase, the rate of cognitive impairment may also increase. Dementia is projected to rise by 187% from 2020 to 2050 in Canada alone (Goldman, 2022). Understanding the process of cognitive decline is the first step towards the prevention of deficits and innovation of treatments. One of the ways to investigate declining cognitive processes is through the analysis of functional connectivity.

Background

Functional connectivity refers to the way different regions of the brain interact during the performance of cognitive tasks or challenges, and it is linked to both structural and functional connections (Zhang et al., 2021). Structural connectivity refers to the brain's physical connections through white matter tracts linking different regions (Sporns et al., 2005). In contrast, functional connectivity describes the statistical relationship of neural activation between different brain regions, as derived from fMRI-based data (Rogers et al., 2007). If these connections are intrinsic then they are related to the brain's natural activity,

and are therefore considered spontaneous activity that would be present even at rest (Iraji et al., 2022). If the connections are extrinsic, they are related to the task a person is participating in, such as the delayed match to sample task (Mennes et al., 2012).

Functional connectivity has been used in various areas of neuroscience and psychology to investigate disorders such as Alzheimer's Disease (Berron et al., 2020). It has also been used to investigate brain organization and communication, showcasing networks such as the Default Mode Network (DMN) and the Frontoparietal Network (FPN) (Tripathi et al., 2025; Zhu et al., 2014). The DMN is implicated in passive rest (Azarias et al., 2025), while the FPN is associated with attention and control (Marek & Dosenbach, 2018). For instance, studies on working memory have shown increasing connectivity in the FPN and decreasing activation of the DMN in response to tasks of varying cognitive demand (Pongpipat et al., 2021). Additionally, functional connectivity has been used in studies looking at changes in resting versus task states and how the brain changes in response to various stimuli (Fox & Raichle, 2007). These connectivity patterns can be used in studies on ageing, such as the theory of dedifferentiation, along with identifying individual differences in behaviour and cognitive abilities (Zhao et al., 2023).

There are various types of functional connectivity, each reflecting patterns of communication between different regions of the brain, including resting state, task-based and task model-fit connectivity (Zhao et al., 2023). Studies using task-based functional connectivity involve participants completing a task corresponding to a cognitive process (Huang et al., 2024). Researchers would then measure the overall connectivity in the brain during the task of interest, including connections associated with the task, along with connections associated with intrinsic and background activation (Cole et al., 2014). Task-model fit refers to the connectivity explained by the task design, representing the neural activations that are attributed to the demands of the cognitive task (Zhao et al., 2023). Task

model-residual represents the remaining brain activity after removing the task design, which is generally interpreted as background noise (Tran et al., 2019). Lastly, resting state data represents the participant at rest, in their neutral state, without any stimuli or tasks (Smallwood et al., 2014).

Most studies on functional connectivity have examined participants at rest (Amador et al., 2025). For instance, Sanchez et al. (2023) investigated the clinical relevance of resting state FC data as a predictor of Alzheimer's disease. Similarly, Zhang et al. (2015) found increased FC at resting state in patients with Parkinson's disease, showcasing its importance for understanding neurological disorders. Outside of diagnostic use, resting state FC has also been used to follow functional brain maturation in developing children (Kardan et al., 2022). Zou & Bokde (2026) used neonatal resting state FC data to predict behavioural and temperament outcomes in infants, highlighting the link between early functional organization to later behavioural differences. While resting state FC provides insight into intrinsic brain organization, it may not fully represent neural interactions during cognitive tasks (Cole et al., 2021). Therefore, recent research has turned more towards task-based functional connectivity as a way to examine how brain networks interact in response to various behavioural or cognitive tasks (Mitchell et al., 2025).

Zhao et al. (2023) used a publicly available dataset to compare how different functional connectivity measures predict behavioural performance. They used the results from three cognitive tasks: the N-back, stop-signal and monetary incentive delay, comparing the task-based, task model-fit, task model-residual and resting state data (Zhao et al., 2023). Their findings demonstrated that task-based functional connectivity and task-model fit were better at predicting behavioural differences between participants than resting state and task-model residual, especially for the N-back and the monetary incentive delay task (Zhao et al., 2023). Similarly, Cole et al. (2021) highlighted the importance of using connectivity

measured during active cognition as a predictor of brain activity during various tasks. These studies effectively demonstrate the importance of using task-based fMRI data over resting-state data. These studies also emphasized the importance of ensuring the chosen task is related to the behaviour of interest.

Another use for functional connectivity can be to explore different cognitive processes, such as semantic processing, across various age groups. Garcia et al. (2022) looked at whether the connections between brain regions related to semantic processing weakened as adults aged by having 38 older adults complete a word association and rhyme task while undergoing an fMRI scan. Results demonstrated that the connections between the regions associated with semantic processing stayed strong across the age group (Garcia et al., 2022). Similarly, Rosenberg et al. (2016) examined how functional connectivity related to sustained attention, finding that patterns of connectivity across the brain could predict participants' attention performance during cognitive tasks. Thompson et al. (2017) examined the effects of working memory training and found that changes in functional connectivity were associated with cognitive adaptation and learning. These collective findings highlight functional connectivity as a tool for understanding the mechanisms of the brain in a variety of contexts.

In addition to examining functional connectivity on its own, researchers have also investigated the relationship between functional and structural connectivity (Litwinczuk et al., 2022). Some evidence suggests that functional networks with stronger underlying structural connectivity tend to be more reliable and reproducible (Kemmer et al., 2018) and that functional connectivity is partially shaped by underlying structure (Honey et al., 2009). Satake et al. (2024) compared structural and functional connectivity during active cognition, using the N-back task. The N-back is a common tool used to assess working memory and involves presenting participants with a series of stimuli in which they must determine

whether the current stimulus matches the one that was presented to them N steps back (Kirchner, 1958; Gilmour et al., 2019). The higher N is, the more difficult the task, as participants have to store more information in their short-term memory (Gilmour et al., 2019). To examine structural connectivity, Satake et al. (2024) used diffusion tensor imaging and assessed task accuracy on different levels of the N-back. They found a moderate correlation between structural connectivity and accuracy on the task in the 1-back condition, a strong correlation in the 2-back condition and no significant correlation in the 3-back condition. These results suggest that the relationship between structural connectivity and task performance may depend on task difficulty, with moderate difficulty (e.g., 2-back) providing the clearest link between brain structure and performance. For functional connectivity, Satake et al. (2024) found that the neural responses also varied depending on task difficulty. The 1-back showed no noticeable changes in neural connectivity compared to rest, suggesting minimal additional neural coordination was required. In contrast, the 2-back showed both increases and decreases in functional connectivity across various regions, while the 3-back showed further increases in connectivity primarily in areas related to memory, attention and cognitive control (Satake et al., 2024). These results suggest that as cognitive demand increases, the brain recruits and coordinates additional regions to support performance.

Together, the findings from Satake et al. (2024) highlight the differences between structural and functional connectivity in the context of working memory. Satake et al. (2024) reported that some of the regions, including the middle frontal gyrus, showed alignment between structural connectivity and task-related functional connectivity, suggesting those regions may be in sync with both physical and functional connections. However, this was not true for all regions; most areas that showed functional connectivity patterns did not line up with the areas that demonstrated structural connectivity (Satake et al., 2024). Consistent with this, previous research has indicated that resting-state functional connectivity is more tied to

structure, whereas task-based does not fully follow the structural wiring of the brain (Greicius et al., 2008). Likewise, Fjell et al. (2016) found that the default mode network was the only region to demonstrate a moderate link between structure and function. In the literature, structural connectivity is used more for identifying morphological and volumetric changes (Worbe, 2022) and white matter integrity (Bergamino et al., 2022). Overall, these findings suggest the importance of differentiating between structural and functional connectivity for a comprehensive understanding of cognitive processes like working memory.

Changes in the strength of brain connections have also been found in various disorders. Individuals with autism spectrum disorder have been shown to have decreased connectivity in the occipital cortex, which is theorized to contribute to the impairment of communication they experience (Jung et al., 2019). In Alzheimer's Disease, reduced connectivity has been observed between the medial and anterior temporal lobe systems, likely contributing to disease symptomatology (Berron et al., 2020). If the weakening of connections between brain regions may be contributing to a decline in cognitive abilities, it's imperative that more research is done in this area. Di and Biswal (2019) demonstrated task-modulated functional connectivity during tasks testing for language, working memory, social cognition and inhibition. By analyzing functional connectivity during various tasks, they were able to identify the brain regions implicated. For instance, they found increased connectivity in the cingulo-opercular, frontoparietal, and occipital modules when participants partook in a social cognition task. Additionally, most of the previous research has focused on disorders, with limited studies looking at the cognitive abilities in individuals with no diagnoses (Carballedo et al., 2011; Canu et al., 2022). Among those that do, the focus tends to be on working memory and emotional processing (Mishra et al., 2022; Hampson et al., 2006). It remains unclear whether these findings extend to other cognitive abilities such as the ability to manage increasing task demands. Specifically, the literature is missing an

investigation into how increasing task demand and age relate to the strength of functional connectivity between brain regions.

Cognitive Demand

Cognitive demand provides the theoretical basis for the current study and refers to the mental effort involved in performing a task (Ranchet et al., 2017). In contrast, task demand refers to the requirements imposed by the task itself, such as its complexity or the amount of information being presented (Hancock & Meshkati, 1988). As task demands increase, the cognitive demand placed on the individual may also increase, particularly as the amount of information presented increases. Individuals often differ in their response to these increasing cognitive demands, resulting in differences in task performance (Deck et al., 2021). Increasing cognitive demand, such as varying memory loads, has also been associated with changes in patterns of brain activation, suggesting that neural networks adapt in response to greater task requirements (Braver et al., 1997). These changes in brain activation differ across age groups, suggesting that ageing may influence how the brain responds to different levels of cognitive demand. For instance, older adults have shown a lower ability to handle cognitive load and stress compared to younger adults (Crosswell et al., 2021). Additionally, older adults demonstrate a decrease in executive control as a whole, including aspects such as task management (Craik & Bialystok., 2006). These age-related changes become more pronounced as cognitive demand gets higher and more difficult (Earles et al., 2004). Increased cognitive demand may place additional strain on the neural systems involved in cognitive control and task maintenance (Maki-Marttunen et al., 2019). However, the extent to which functional connectivity is implicated in this decline in cognitive performance remains unclear. Additionally, the impact of increasing levels of cognitive load on functional connectivity across individuals, regardless of age, is not yet fully understood, underscoring the importance of further research in this area.

It is evident that not all older adults experience a decline in their cognitive abilities to the same extent (Glisky, 2007). There is a difference in the onset of this decline and how quickly it progresses (Karr et al., 2019). The concept of cognitive reserve may be one of the factors behind why some individuals decline earlier and more prominently than others (Stern, 2002). Cognitive reserve refers to the accumulation of neural resources that lessen the impact of age-related cognitive decline (Steffener & Stern, 2012). There are various factors that promote cognitive reserve, such as education, occupation and lifestyle (Cabeza et al., 2018). The protective effects of cognitive reserve may be particularly important in tasks with high cognitive demand. When participants face increasing cognitive demands, cognitive reserve may help mitigate declines in cognitive performance despite age-related neural changes (Stern, 2009). Cognitive reserve may also impact the strength of functional connectivity between brain regions (Weiler et al., 2018). Therefore, for a full understanding of the mechanisms behind cognitive decline, it's important to understand how individuals respond to varying levels of cognitive demand.

Analysis Methods

There are many ways of assessing functional connectivity, such as through seed-based analysis, correlation analysis and independent component analysis (Steffener et al., 2012; Seewoo et al., 2021). One of the most common analysis approaches is through psycho-physiological interactions (PPI) (O'Reilly et al., 2012). PPI analysis is a measure of functional connectivity that examines changes in connectivity between various areas of the brain relative to a seed region and depending on context, such as a task condition (Friston et al., 1997). There are various types of PPI, such as standard PPI, connectivity PPI and generalized PPI, which all take different approaches to modelling interactions during specific cognitive tasks (McLaren et al., 2013).

sPPI

Friston et al. (1997) developed the standard psycho-physiological interactions (sPPI) approach. When assessing functional connectivity, researchers select a specific area of the brain, known as the seed region, that is believed to play a role in the task of interest. The sPPI approach then models how connectivity changes between the seed region and other areas of the brain during one psychological state (Friston et al., 1997). In sPPI, the psychological state refers to a contrast between two conditions, typically a task condition and a rest condition (O'Reilly et al., 2012). For instance, the analysis may compare connectivity during condition A, which would be a task, relative to baseline. Therefore, the sPPI model identifies the areas of the brain that are increasing or decreasing in connectivity with the seed region as a function of the psychological condition (Friston et al., 1997). The main limitation of the sPPI approach is the limited number of conditions it can assess, making it less suitable for a research design with more than one condition (Huang et al., 2024). It also can't assess causality or make any implications of the seed region being the driver of the connection (O'Reilly et al., 2012).

Functional connectivity analyses could be conducted by comparing a single seed region against the rest of the brain or by testing connectivity between all possible brain regions (Hahn et al., 2018). However, whole-brain analyses generate a large number of results, making it more difficult for the results to be interpreted (Bullmore & Sporns, 2009). Therefore, sPPI is conducted using the regions of interest (ROI) approach, which focuses analyses on specific brain regions (O'Reilly et al., 2012).

cPPI

Fornito et al. (2012) developed what is known as the correlational psycho-physiological interaction (cPPI) approach to functional connectivity. The cPPI approach differs from the sPPI approach by testing the differences between two or more

psychological contrasts (Huang et al., 2025). Similarly to sPPI, researchers select an area of the brain, the seed region, which is believed to be playing a large role in the task being studied. While the sPPI focuses on the interpretation of a single psychological variable (e.g., task versus baseline), cPPI focuses on the relationship between the seed region and the difference between contrasts of a psychological state (Fornito et al., 2012). For instance, the interaction between the seed region and the contrast of task A versus task B. It's able to identify whether the changes in brain connectivity are from the contrast between two conditions instead of always occurring during the task itself (Fornito et al., 2012). CPPI differs from the other PPI approaches as it's primarily intended for understanding how the brain changes between conditions, like correlated activity rather than causal interactions (O'Reilly et al., 2012). The cPPI approach is limited to one contrast at a time, so it cannot be used in studies with multiple contrasts (Huang et al., 2024).

gPPI

The gPPI approach is considered the most advanced and useful approach to functional connectivity as it addresses some of the limitations of the other methods (McLaren et al., 2012). The gPPI tests how connectivity changes for multiple psychological conditions by modelling various task conditions simultaneously in relation to a selected seed region. Masharipov et al. (2024) compared sPPI, gPPI and cPPI on two block design tasks and two event-related tasks, along with resting-state data. Both sPPI and gPPI gave similar results in the block and event-related designs, while cPPI couldn't pick up task-modulated connectivity changes. Additionally, McLaren et al. (2012) compared sPPI and gPPI using a simulated data set and real data. The simulated data was created with three conditions, a seed region time course and predicted psychological responses of the participants. They found that gPPI performed better than sPPI for the simulated data, providing more accurate results and serving as a better fit (McLaren et al., 2012). The same was true for the real data, where gPPI

was also able to identify new brain regions of interest that sPPI had missed. The gPPI approach also allowed researchers to explore connectivity both within and across conditions (McLaren et al., 2012). Furthermore, McLaren et al. (2012) found that gPPI was more sensitive to true positive results, while sPPI may have a higher risk of producing false negatives. The only potential limitation is that the accuracy of the gPPI approach depends on correctly specifying the psychological components of the model as misspecification may lead to inaccurate estimates of functional connectivity (McLaren et al., 2012; O'Reilly et al., 2012). However, the gPPI approach is generally considered one of the most comprehensive methods available for analyzing task-based functional connectivity.

Preprocessing

Before the fMRI data can be analyzed, it is necessary to preprocess the raw images to ensure they are clean and standardized. Preprocessing aligns and corrects images for head motion, differences in head size and shape, and for various physiological, thermal and other sources of noise (Whitfield-Gabrieli & Nieto-Castanon, 2012). To begin with, researchers generally realign the images and conduct slice-timing correction (Di & Biswal, 2023). Realignment is necessary as fMRIs work by taking a series of images over time, therefore if a participant's head moved even slightly, such as a tilt, the series of images will not end up lined up properly (Ardekani et al., 2001). If left uncorrected, any comparisons or conclusions made may not be accurate (Di & Biswal, 2023). Additionally, slice-timing correction ensures the images are aligned in time (Di & Biswal, 2018). The brain images are sliced at slightly different time points therefore this step is important for correcting the time differences between the first and last slices in the group (Calhoun et al., 2000).

The subsequent steps in preprocessing include artifact removal and noise correction. One of the key measurements used is framewise displacement, which represents the movements of participants over time that may negatively impact an image (Power et al.,

2011). Large and rapid movements by participants may induce image artifacts that distort estimates of functional connectivity (Power et al., 2012). Small movements of the head are generally corrected using motion correction procedures, whereas the larger movements require additional processing (Godenschwegger et al., 2017). Framewise displacement is a commonly used method to detect participant motion and control time points affected by movement (Power et al., 2014). Addressing these issues is important as movement-related artifacts may appear as spuriously strong correlations between brain regions (Power et al., 2012). To reduce these effects, a process known as scrubbing is often applied, which consists of the removal of timepoints with motion above a specific threshold, ensuring the participant's movements have less of an impact on the results (Di & Biswal, 2018).

The final two steps in preprocessing are spatial normalization and spatial smoothing. Spatial normalization is the process of reshaping the images to a common brain template, such as the Montreal Neurological Institute brain MRI template (Rorden et al., 2012). Brains can differ in size and shape so to make comparisons between participants, the images are adjusted to match a standardized reference (Schmidt et al., 2013). Spatial smoothing is the process of smoothing the data so that noise and other variabilities have less of an impact on the results (Candemir, 2023). The smoothing process spreads out the signal by averaging out the values of each voxel with the ones around it (Alakorkko et al., 2017). Conducting these preprocessing steps is crucial for ensuring the data is interpretable and the results are accurate.

In addition to the standard preprocessing procedures outlined above, further steps may be implemented to account for noise sources that can affect functional connectivity estimates. One commonly considered source of variance is the global signal, which represents the average activity signal across all of the brain at a specific time period (Li et al., 2019).

Global Signal

Activity in the brain is represented by signals across a timeseries, therefore the global signal is the mean signal across all brain voxels at each time point in the series (Li et al., 2019). The global signal includes physiological noise and whether it should be removed from functional connectivity data is highly debated (Hahamy et al., 2014). To remove the global signal, the global signal regression (GSR) is applied during the preprocessing of the fMRI data. Removal of the global signal has been shown to reduce artifactual connectivity, including heart rate and breathing fluctuations (Xifra-Porxas et al., 2025; Fox et al., 1998). However, the global signal may have some relevance, especially in clinical settings (Hahamy et al., 2014; Gotts et al., 2013). Hahamy et al. (2014) demonstrated that patterns of global signal functional connectivity differentiate individuals with schizophrenia from healthy controls, indicating that the global signal may be relevant for understanding clinical conditions. The CONN functional connectivity toolbox used in the current study removes the impact of the global signal through the preprocessing steps. Rather than applying the global signal regression, CONN removes global artifacts and the impact of white matter and cerebrospinal fluid (Whitfield-Gabrieli & Nieto-Castanon, 2012).

To summarize, the current study uses functional connectivity measures derived from fMRI data to examine age-related differences in brain function during a task with varying cognitive demand. Although both age and cognitive demand have been shown to influence brain activity, less is known about how these factors interact to shape the functional connections within the brain (Cheryl et al., 2006). The current study addresses this gap by examining functional connectivity across varying levels of task difficulty and the role that ageing plays.

Hypothesis

The current study tests two hypotheses (see Figure 1). The first one is that the strength of functional connectivity during increasing cognitive demand will differ with age in some brain regions. The second one is that the strength of functional connectivity will change due to cognitive demand, independent of age in other regions.

Research Question

Are increasing levels of cognitive demand related to the strength of functional connectivity between brain regions, and how is this relationship influenced by age?

Objectives

To use fMRI to investigate the relationship between increasing cognitive demands and the strength of functional connectivity and how that effect is moderated by age.

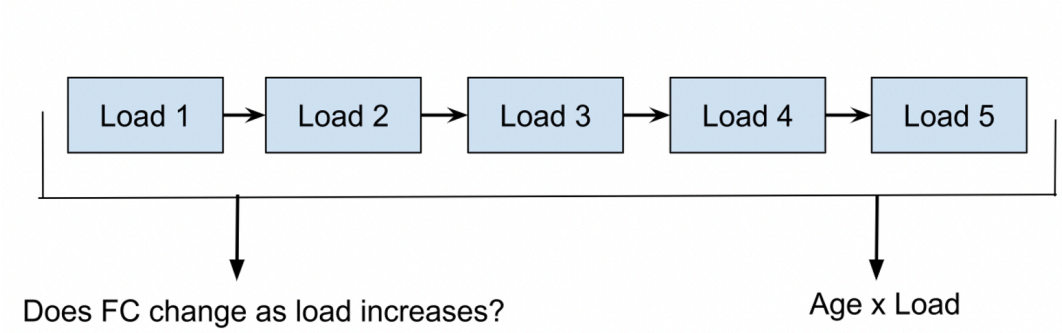


Figure 1

Diagram representing the current analysis.

Note. Load = The number of letters shown in the task. The load is individualized to each participant's performance during a pre-assessment of the delayed match-to-sample task.

Hypothesis 1 = Age x Load interaction

Hypothesis 2 = Does FC change as load increases, independent of age?

Methods

Study Participants

The data to be used in the current study has already been collected, with participants completing a verbal delayed match-to-sample task. Participants were recruited from the University of Ottawa and its surrounding area. Younger adults were recruited via posters on billboards throughout the university and on social media sites (i.e., student researchers' Facebook pages, our lab website). Older adults were recruited via flyers posted in community centers, exercise classes, grocery stores and retirement communities, advertisements placed in local newspapers, supermarkets, list-servs, word of mouth, through social media and adult organizations, such as Canadian association of retired people (CARP).

Inclusion criteria required participants to be 18 - 30 or above 60 years old, right-handed, normal or corrected to normal vision, and speak English as a first language. In addition, eligible participants must have been in good self-reported health, had no past incidence of a severe head injury, and had not been severely ill or hospitalized within the past six months. Participants were excluded if any neurological disorders were likely to affect cognitive function, the use of any psychoactive drugs, and significant cardiovascular disease or atherosclerosis. The study received ethical approval from the Research Ethics Board (REB) of the University of Ottawa, and all participants were informed on the nature of the study and signed informed consent forms.

Behavioural Task

The delayed match-to-sample task used visually presented letter stimuli (Rypma et al., 1999; Sternberg, 1966) with relatively minor adaptations from previous use (Hillary et al., 2003; Steffener et al., 2009; Stern et al., 2008). This experiment was trial-based, where each trial consisted of three parts (see Figure 2). A trial began with the presentation of letters in a 3x3 grid on the screen for 2.5 seconds. The participant had to study and remember the letters.

After the letters were removed from the screen, a green crosshair appeared for 3.5 seconds. During this time, the participants had to remember the letters they studied. Finally, a probe letter appeared for 2.5 seconds in the center of the screen. During this time window, participants were to determine whether or not they recognized the probe letter as one they studied for this trial. Responses were recorded via a keyboard press. Upon a response, the probe letter was removed from the screen.

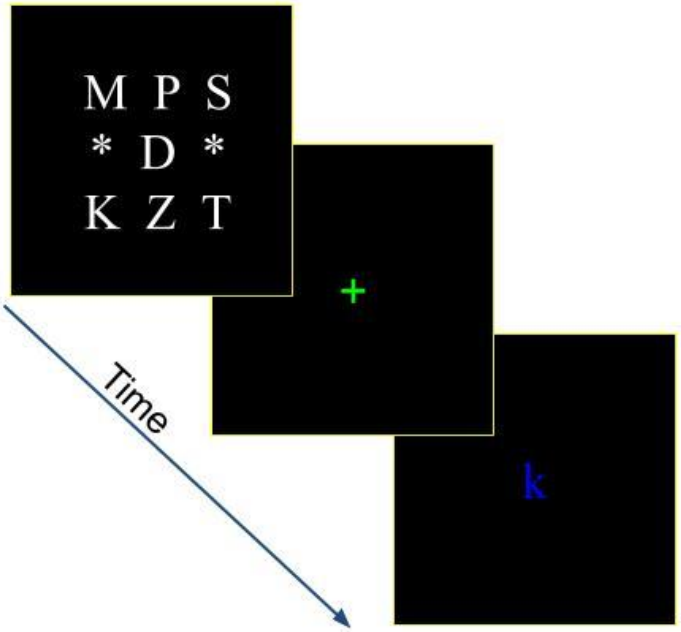


Figure 2

Presentation of Verbal Stimuli

Note. A single trial of the simultaneous presentation of verbal stimuli in the delayed match-to-sample experiment. The three panels represent the three phases of the experiment. The stimulus encoding phase presented one to nine letters in white font color; the rehearsal phase presented only a crosshair. The recognition phase presented a single probe letter in blue font color.

The cognitive demand for this task was manipulated based on the number of letters shown at each trial, with nine levels of demand possible. When the load level for a trial was

less than nine, asterisks filled the grid's remaining locations. The screen position of stimulus letters was the same for all trials of a particular load level. For example, in Figure 3, a trial with seven letters is presented. The stimulus letters will always be in these positions for all trials with seven letters. The experiment only used consonant letters (except for the double syllable letter "W") to minimize word-forming in the studied letters. No letters in one trial could contain any of the letters used in the previous trial. Letters were not in alphabetical order; study letters were in uppercase, and probe letters were in lowercase. Using a lowercase probe ensured that letters were not matched based on visual features. The task was implemented and administered using PsychoPy2 (Peirce et al., 2019). All software to deliver this task is publicly available at: https://github.com/NCMlab/CognitiveTasks.

During the delayed match-to-sample task, both behavioural and fMRI data were collected. Although behavioural measures were acquired as part of the broader dataset, the current study focused on the fMRI data relevant to the research question. The behavioural data was not included in the current analysis.

Cognitive Capacity

Cognitive capacity is the level of task demand at which a participant consistently performs at 80% accuracy as assessed using an adaptive difficulty version of the task (Leek, 2001), see Figure 3. The adaptive difficulty used a three-up, one-down staircase design. The procedure started with the lowest level of task demand, one letter, and initially increased by one letter of difficulty for each correct response. After making the first incorrect response, task demands decreased by one letter. Then, task demands increased by one letter only after three correct responses. Each point where the direction of difficulty changed was considered a reversal. Cognitive capacity was the average cognitive demand across all reversal points. This three-up/one-down staircase procedure provided approximately 80% accuracy. As this measure is an average value, it is not limited to integer values of load. This procedure was

limited to 7 minutes or 20 reversals (Karmali et al., 2016). The number of letters shown to participants in each trial was individualized based on their cognitive capacity. This approach allowed cognitive demand to be adjusted to individual differences in ability, helping to ensure that participants were challenged at comparable levels.

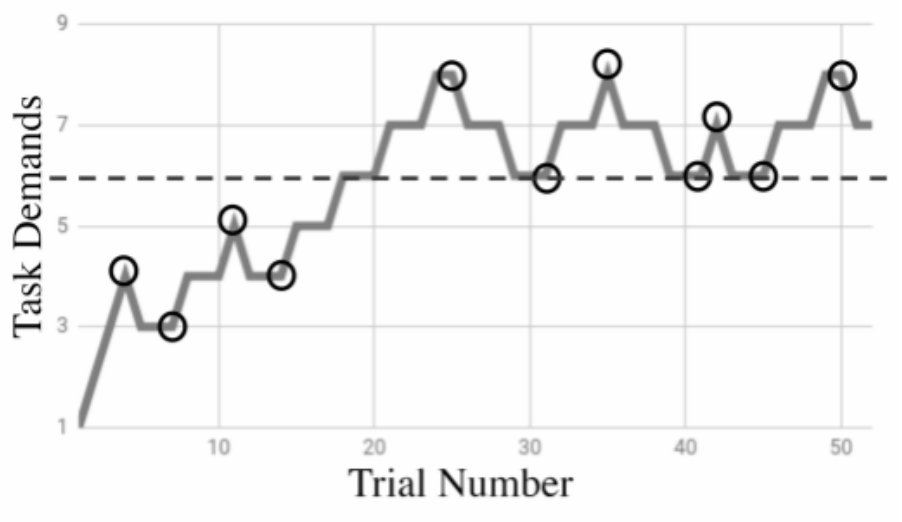


Figure 3

An Individual's Changes in Cognitive Demand

Note. A plot of one individual's changing task demand. The number of letters presented (task demands) changed as the participant responded correctly and incorrectly. After the initial increase in task demands, task demands increased after three responses in a row, task demands increased. After one error, task demands decreased. Changes in direction are reversals, as seen circled above. Someone's cognitive capacity is the average of all task demands at reversal values (circled trials); this is the dashed line for this example.

Structural MRI

A T1-weighted multi-echo magnetization prepared rapid acquisition gradient echo (MEMPRAGE) image was acquired sagittally (TR = 2530ms; TE 1/2/3/4 = 1.69/3.55/5.41/7.27ms; flip angle = 7°; 1mm isotropic resolution; 192 slices; 256mm field of view, ipat (acceleration) = 2, with 32 ref lines and a non-selective inversion time of 1150 ms

and 650 Hz/Px BW). Duration: 6:03 minutes (van der Kouwe et al., 2008).

Functional MRI

The following acquisition parameters were used for all task-based data collection. A multi-band accelerated EPI sequence (Moeller et al., 2010) using an acceleration factor of 6, TR = 1110ms, TE = 16.6ms, 52-degree flip angle, phase partial Fourier 6/8, 56 slices collected in an alternating increasing slice order, 2.5x2.5mm in-plane resolution, slice thickness = 2.75mm, field of view: 220x200mm.

Analysis Plan

The current study conducted the analysis using gPPI, as it has been shown to be the best fit and produces the most accurate results (McLaren et al., 2012). The analysis has been done using the software CONN Functional Connectivity Toolbox (Whitfield-Gabrieli & Nieto-Castanon, 2012). There were two levels of processing in the toolbox: the first-level and second-level analysis. The first-level analysis builds the general linear model for each subject, calculating functional connectivity for each one (Whitfield-Gabrieli & Nieto-Castanon, 2012). The second-level analysis looks at the functional connectivity differences across subjects, comparing the varying levels of task demand and the two age groups (Jahn, 2025).

Statistical significance was assessed using a threshold of $\alpha < 0.05$, corrected for multiple comparisons using the false discovery rate (FDR). FDR correction was applied to the results to control for type 1 errors associated with multiple comparisons (Noble, 2010).

Preprocessing

The following text was provided by the CONN Functional Connectivity Toolbox, as all analyses were done through the toolbox.

Functional and anatomical data were preprocessed using a modular preprocessing pipeline (Nieto-Castanon, 2020) including realignment with correction of susceptibility distortion interactions, slice timing correction, outlier detection, direct segmentation and MNI-space normalization, and smoothing. Functional data were realigned using SPM realign & unwarp procedure (Andersson et al., 2001; Whitfield-Gabrieli & Nieto-Castanon., 2012) where all scans were coregistered to a reference image (first scan of the first session) using a least squares approach and a 6 parameter (rigid body) transformation (Friston et al., 1995), and resampled using b-spline interpolation to correct for motion and magnetic susceptibility interactions. Temporal misalignment between different slices of the functional data (acquired in interleaved bottom-up order) was corrected following SPM slice-timing correction (STC) procedure (Henson et al., 1999; Sladky et al., 2011) using sinc temporal interpolation to resample each slice BOLD timeseries to a common mid-acquisition time. Potential outlier scans were identified using ART (Whitfield-Gabrieli et al., 2011) as acquisitions with framewise displacement above 0.9 mm or global BOLD signal changes above 5 standard deviations, (Power et al., 2014; Nieto-Castanon., n.d) and a reference BOLD image was computed for each subject by averaging all scans excluding outliers. Functional and anatomical data were normalized into standard MNI space, segmented into grey matter, white matter, and CSF tissue classes, and resampled to 2 mm isotropic voxels following a direct normalization procedure (Nieto-Castanon., n.d; Calhoun et al., 2017) using SPM unified segmentation and normalization algorithm (Ashburner & Friston., 2005; Ashburner, 2007) with the default IXI-549 tissue probability map template. Last, functional data were smoothed using spatial convolution with a Gaussian kernel of 8 mm full width half maximum (FWHM).

Denoising

In addition, functional data were denoised using a standard denoising pipeline (Nieto-Castanon, 2020) including the regression of potential confounding effects characterized by white matter timeseries (5 Component Correction (CompCor) noise components), CSF timeseries (5 CompCor noise components), motion parameters and their first order derivatives (12 factors) (Friston et al., 1996) outlier scans (below 79 factors) (Power et al., 2014), session and task effects and their first order derivatives (10 factors), and linear trends (2 factors) within each functional run, followed by bandpass frequency filtering of the BOLD timeseries (Hallquist et al., 2013) between 0.008 Hz and 0.09 Hz. CompCor (Behzadi et al., 2007; Chai et al., 2012) noise components within white matter and CSF were estimated by computing the average BOLD signal as well as the largest principal components orthogonal to the BOLD average, motion parameters, and outlier scans within each subject's eroded segmentation masks.

First-level analysis gPPI_01: Psychophysiological interaction analyses were used to study the changes in functional connectivity across four conditions (as load increased from 1 to 5). Seed regions included 169 ROIs. Separately for each pair of seed and target areas, a generalized psychophysiological interaction model (gPPI) (Friston et al., 1997; Mclaren et al., 2012) was defined with seed BOLD signals as physiological factors, boxcar signals characterizing each individual task condition convolved with an SPM canonical hemodynamic response function as psychological factors, and the product of the two as psychophysiological interaction terms. Functional connectivity changes across conditions were characterized by the Fisher-transformed semipartial correlation coefficient of the psychophysiological interaction terms in each model.

Group-level analyses were performed using a General Linear Model (GLM) (Nieto-Castanon, 2020). For each individual connection a separate GLM was estimated, with

first-level connectivity measures at this connection as dependent variables (one independent sample per subject and one measurement per task or experimental condition, if applicable), and groups or other subject-level identifiers as independent variables. Connection-level hypotheses were evaluated using multivariate parametric statistics with random-effects across subjects and sample covariance estimation across multiple measurements. Inferences were performed at the level of individual clusters (groups of similar connections). Cluster-level inferences were based on parametric statistics within- and between- each pair of networks (Functional Network Connectivity) (Jafri et al., 2008), with networks identified using a complete-linkage hierarchical clustering procedure (Sorensen, 1948) based on ROI-to-ROI anatomical proximity and functional similarity metrics (Nieto-Castanon, 2020). Results were thresholded using a combination of a $p < 0.05$ connection-level threshold and a familywise corrected p-FDR < 0.05 cluster-level threshold (Benjamini & Hochberg, 1995).

Results

The present study included 79 participants, 47 female and 32 male. There were 39 participants in the older adult group, with a range of 61 to 89 and an average age of 73.76 years. There were 40 participants in the younger adult group, with a range of 19 to 30 and an average age of 23.41 years. There were 23 females and 17 males in the younger adult group and 24 females and 15 males in the older adult group.

Task-dependent functional connectivity was analyzed using the generalized psychophysiological interaction (gPPI) analysis. Brain regions were defined using the Harvard-Oxford cortical and subcortical structural atlases within the CONN Functional Connectivity Toolbox (Smith et al., 2004). Significant connectivity clusters were identified across frontal, temporal, occipital and parietal regions in the brain. These connectivity patterns varied with age group and task difficulty, with different effects observed for each hypothesis.

Although behavioural data was collected during the scanning session, it was not included in the current analysis. Descriptively, verbal cognitive capacity did not significantly differ between age groups (t(77)=0.56, p=0.57, mean (std) younger group=7.21 (0.96) and older group=(7.09) (1.03). Accuracy on the cognitive task performed during the fMRI was approximately 80% in both groups (younger adults: M = .84; older adults: M = .82). Table 1 includes age-group comparisons on other cognitive assessments to provide further context on the participants in the current study.

Table 1

Additional Behavioural Results

Task Name	Younger			Older				
	mean	std	N	mean	std	N	t-value	Effect size, d’
MoCA	27.9	1.76	39	27.3	1.73	38	1.33	0.30
Spatial delayed match to sample, capacity	6.95	3.98	40	4.12	1.63	35	3.93*	0.91
Digital span forwards, capacity	6.87	1.09	40	6.72	0.88	39	0.70	0.16
Digital span backwards, capacity	4.71	1.00	40	4.42	0.81	39	1.43	0.32
2-back, accuracy	0.83	0.12	40	0.76	0.17	38	1.49	0.34
Selective Reminding Immediate Recall (max=72)	58.9	8.55	40	49.5	11.0	37	4.22*	0.96
Select Reminding Delayed Recall (max=12)	10.2	1.57	40	7.4	3.07	37	5.13*	1.17

*p<0.001

Hypothesis 1

A group comparison between older and younger adults revealed significant differences in connectivity strength across various regions within the brain (see Table 2). The significant connectivity cluster identified in the current study consisted of 15 connections, $f(3,77)=8.00$, pFDR=.024. The left middle temporal gyrus emerged as an area of particular interest, with connections to a variety of other regions, such as the planum polare, the Heschl's gyrus, and the planum temporale (see Figure 4). These connections were observed across both hemispheres and they involve both temporal and auditory regions of the brain. The most notable connection was between the right planum polare and the left middle temporal gyrus $t(79) = 4.34$, $p< .05$, with older adults exhibiting greater functional connectivity than younger adults in this area (see Figure 5). The planum polare represents the anterior part of the superior temporal gyrus (Shapleske et al., 1999). The connection between the planum polare and the middle temporal gyrus was the only individual connection that remained significant following FDR correction.

Younger adults demonstrated greater functional connectivity than older adults for connections between the supramarginal gyrus and the inferior frontal gyrus, $t(79) = -2.80$, $p< .05$ (uncorrected), although these results did not individually survive FDR correction. Overall, the results were organized by brain network, with older adults showing greater connectivity in temporal/auditory regions, including the Heschl's gyrus and the middle temporal gyrus. Younger adults showed stronger connectivity in frontal-parietal regions, including the supramarginal gyrus and the superior frontal gyrus.

Table 2

Functional Connectivity in Younger versus Older Adults

Originating Region	Second Region	p value, unc	p value, FDR	T Values (df=79)
Planum Polare Right	Middle Temporal Gyrus, temporooccipital part Left	0.000041	0.006959	4.34
Planum Polare Left	Middle Temporal Gyrus, temporooccipital part Left	0.000334	0.050588	3.75
Middle Temporal Gyrus, temporooccipital part Left	Planum Polare Left	0.006973	0.234281	2.77
Supramarginal Gyrus, anterior division Left	Inferior Frontal Gyrus, pars triangularis Right	0.006404	0.246825	-2.80
Supramarginal Gyrus, anterior division Right	Inferior Frontal Gyrus, pars triangularis Right	0.008926	0.348117	-2.68
Superior Frontal Gyrus Right	Supramarginal Gyrus, anterior division Right	0.002079	0.349274	-3.18
Middle Temporal Gyrus, temporooccipital part Left	Planum Temporale Right	0.019935	0.372122	2.38
Planum Temporale Left	Middle Temporal Gyrus, temporooccipital part Left	0.014008	0.392212	2.51
Middle Temporal Gyrus	Heschl's Gyrus Left	0.028837	0.412489	2.23
Supramarginal Gyrus, anterior division Right	Superior Frontal Gyrus Right	0.027188	0.415228	-2.25
Inferior Frontal Gyrus, pars triangularis Right	Supramarginal Gyrus, anterior division Left	0.009632	0.539398	-2.65
Heschl's Gyrus Left	Middle Temporal Gyrus, temporooccipital part Left	0.016339	0.686256	2.45
Inferior Frontal Gyrus, pars triangularis Right	Supramarginal Gyrus, anterior division Right	0.045236	0.971217	-2.03

Note. Positive T values mean that older adults had a higher strength of connectivity than younger adults in those regions. Negative T values mean that younger adults had a higher strength of connectivity than older adults in those regions.

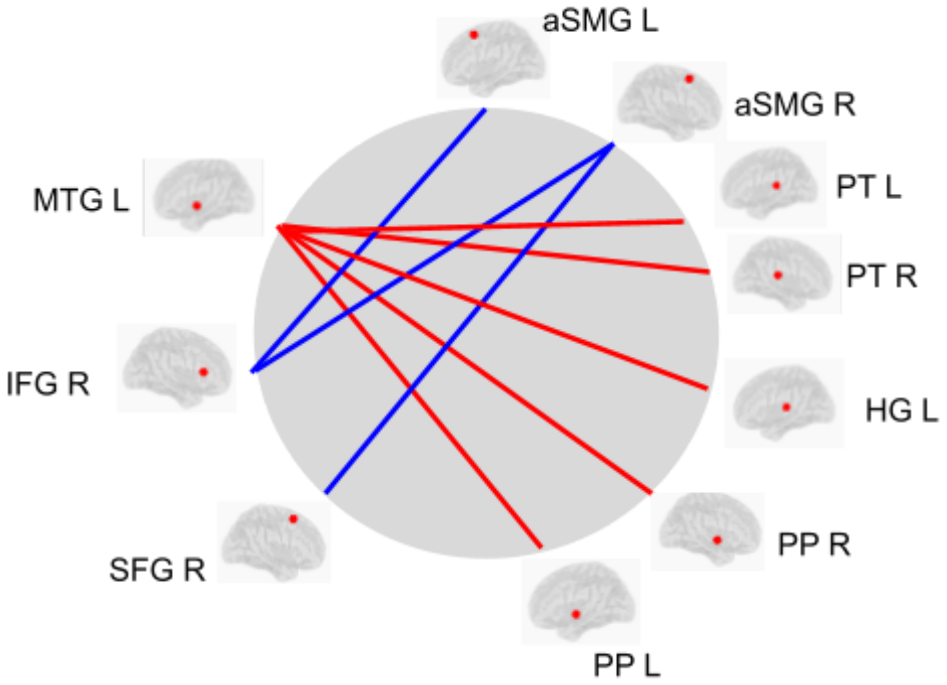


Figure 4

Brain connectivity differences associated with hypothesis 1.

Note. The red means the strength of connectivity is greater in older adults than younger adults. The blue means the strength of connectivity is greater in younger adults than older adults. MTG = middle temporal gyrus, IFG = inferior frontal gyrus, SFG = superior frontal gyrus, PP = planum polare, PT = planum temporale, SMG = supramarginal gyrus. R = right and L = left.

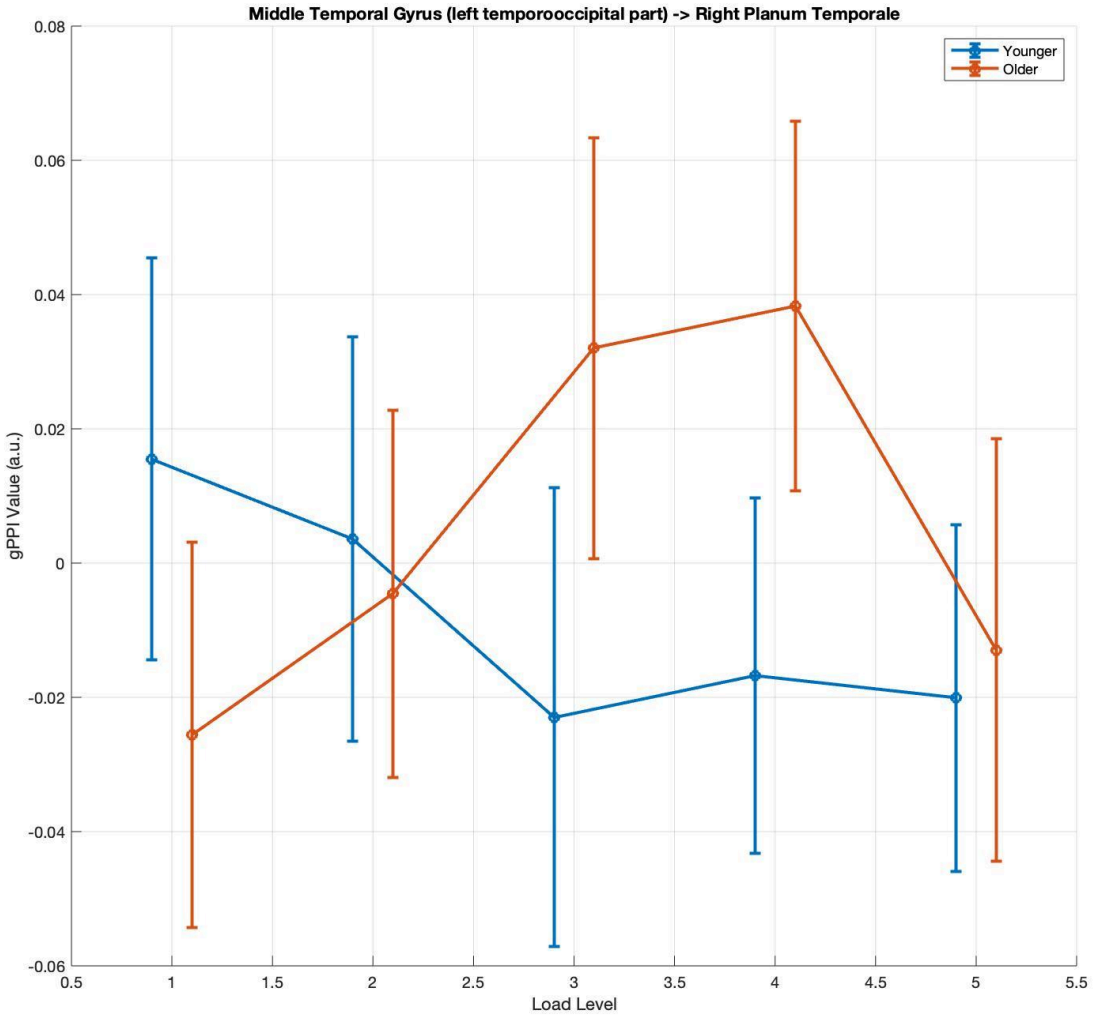


Figure 5

Younger adults compared to older adults for the strength of connectivity within the middle temporal gyrus and the right planum temporale.

Hypothesis 2

Consistent with the second hypothesis, the gPPI analysis revealed that functional connectivity changed with increasing cognitive demand, independent of age in various brain regions. The brain connections implicated in the second hypothesis differed from the first hypothesis and they remained significant after applying the FDR correction. The posterior cingulate gyrus emerged as an area of particular interest, with connections to various other

regions, such as the precuneus cortex, the supramarginal gyrus and the inferior frontal gyrus (see Table 3). Specifically, the most significant connectivity changes were observed between the posterior cingulate gyrus and precuneus cortex, with the strength of connectivity decreasing as cognitive load increased, $t(80) = -7.00$, $p < .05$. Additionally, there were significant changes seen between the fusiform cortex and the occipital cortex, $t(80) = -3.78$, $p < .05$. There were significant positive changes seen between the supramarginal gyrus and the posterior cingulate cortex, with the strength of connectivity increasing as cognitive load increased, $t(80) = 6.95$, $p < .001$.

Table 3

Changes in Functional Connectivity Linearly Between the 5 Loads, Independent of Age

Originating Region	Second Region	p-unc	p-FDR	T Values (df = 80)
Posterior Cingulate Gyrus	Precuneus Cortex	p<0.001	p<0.001	-7.00
Inferior Frontal Gyrus	Right cerebellum	p<0.001	0.00018	-4.94
Right temporal Occipital Fusiform Cortex	Right Superior Lateral Occipital Cortex	0.00030	0.05100	-3.78
Posterior supramarginal gyrus	Posterior cingulate gyrus	p<0.001	p<0.001	6.95
Posterior cingulate gyrus	Inferior frontal gyrus	p<0.001	0.00350	3.79
Precuneous cortex	Posterior supramarginal gyrus	p<0.001	0.00177	4.42
Middle temporal gyrus, temporooccipital part Right	Posterior cingulate gyrus	p<0.001	p<0.001	5.30
Precuneous cortex	Inferior frontal gyrus	p<0.001	0.005690	3.69
Precuneous cortex	Middle temporal gyrus, temporooccipital part Right	p<0.001	0.011271	3.51
Anterior, right supramarginal gyrus	Posterior cingulate gyrus	p<0.001	p<0.001	5.30

Negative T values means the strength of connectivity decreased as cognitive load increased.

Positive T values means the strength of connectivity increased as cognitive load increased.

Discussion

Consistent with the first hypothesis, there were differences in functional connectivity between the younger and older age groups. Additionally, there were significant load-dependent changes in functional connectivity across various brain regions independent of age, as consistent with the second hypothesis.

Hypothesis 1

The findings from the gPPI analysis demonstrated a statistically significant age-by-load interaction in the strength of functional connectivity during the delayed match-to-sample task. Multiple brain regions demonstrated significant age-related differences in connectivity with increasing cognitive demand, when using uncorrected p-values. The middle temporal gyrus emerged as a significant region of connectivity in the results, with connections to various other areas of the brain. The temporal gyrus has been seen in prior research as relevant for linguistic processing, including letter recognition (Lochy et al., 2018). The left side of the temporal gyrus, which was a notable area in the current results, responds to individual letters (Lochy et al., 2018). The temporal gyrus is also part of the visual word form area, which responds to both word and non-word visual stimuli, and may therefore be engaged during tasks such as the delayed match-to-sample task (Li et al., 2024). One of the most significant connections was between the MTG and the planum polare. Older adults exhibited significantly stronger connectivity between the planum polare and the middle temporal gyrus as cognitive load increased, than their younger counterparts. On the other hand, younger adults showed stronger connectivity between the supramarginal gyrus and the inferior frontal gyrus with increased cognitive load, than the older adults.

The planum polare (PP), which was identified as a relevant region in connectivity for older adults, is a component of the auditory cortex (Moerel et al., 2014). While the delayed match-to-sample task is visual, viewing letters can recruit auditory regions in the brain due to

phonological processing (Chan et al., 2014; Baddeley & Hitch, 1974). This evidence suggests that auditory regions may contribute to language-related processing even in visually driven tasks like the delayed match-to-sample task. Additionally, there is little research on whether the PP is relevant in working memory on its own, however, evidence suggests it's functionally connected with other networks. For example, in resting-state functional connectivity analyses, the PP was found to be significantly connected to both language and visual networks (Pascual et al., 2015). Particularly, the PP showed significant connectivity with the middle temporal gyrus, which plays a role in both of these networks (Petrides, 2023). These results suggest that the planum polare may not be acting on its own but rather functionally interacting with the MTG. There may be additional coordination required to perform well on the delayed match-to-sample task. As cognitive demands increase, differences in the connectivity patterns between older and younger adults may reflect differences in the neural resources included to support task performance. As consistent with prior work, higher cognitive demands generally require the recruitment of additional brain networks (Newton et al., 2010; O'Connell & Basak., 2018).

In addition to the PP and MTG connectivity, the gPPI analysis revealed that the connection between the left supramarginal gyrus (SMG) and the right inferior frontal gyrus (IFG) was stronger in younger adults than older adults as cognitive load increased. While these individual connections were not significant following FDR correction, the direction of the effect may be consistent with the possibility that younger adults maintained stronger functional connections between regions involved in phonological processing under conditions of increased cognitive demand.

The SMG has shown involvement with phonological inputs and outputs by holding temporary storage of verbal or symbolic information for working memory tasks (Paulesu et al., 1993). Consistent with this role, Yue and Martin (2021) found that phonological

representations could be decoded specifically in the left SMG during the delay period of a short-term memorization task. The SMG has been associated with the phonological loop, a working memory model for processing verbal information (Baddeley & Hitch, 1974; Deschamps et al., 2020). In particular, the SMG may function as part of the visual processing component of the loop, contributing to phonological recognition (Sliwinska et al., 2012).

The SMG was functionally connected to the inferior frontal gyrus (IFG), which has been implicated in previous research on cognitive demand. One study testing the delayed match-to-sample task, found increased activation in the prefrontal cortex as participants completed the task, including activation in the inferior frontal gyrus (Daniel et al., 2017). Another study looking at proactive interference, relevant for delayed recognition tasks, found increased activation in the IFG (Feredoes & Postle., 2010). When the IFG was damaged, errors increased in tasks on delayed letter recognition, demonstrating its importance in working memory (Feredoes et al., 2006).

Importantly, the SMG and IFG have been shown to functionally interact during various types of processing tasks. For instance, these regions have shown increased functional connectivity during comprehension tasks (Smirnov et al., 2014), as well as during language processing and cognitive control (Bulut, 2022). As consistent with the current directional pattern, the SMG and IFG are a part of the verbal working memory network, as they work together during the memory retention and the rehearsal phases of tasks (Yue & Martin, 2022). Derya and Wallraven (2024) found reduced connectivity in older adults between the posterior network and prefrontal cortex, which included the SMG and IFG. They also found increased connectivity in younger adults, specifically the visual and default mode networks. These findings indicate that older and younger adults may rely on different neural coordination for various cognitive processes, particularly as cognitive demands increase.

The present findings highlight the importance of cognitive load in shaping functional connectivity differently across older and younger adults. The significant age-by-load interaction suggests that changes in connectivity associated with increasing cognitive demand differed between the two age groups. Older and younger adults demonstrated increased connectivity strength in distinct brain networks, with older adults showing greater connectivity in temporal and auditory regions, while younger adults showed stronger connectivity in frontal-parietal regions. This pattern is consistent with previous research demonstrating age-related differences in functional connectivity in the brain. Oschmann & Gawryluk (2020) investigated age-related changes in functional connectivity in resting-state networks and found reduced connectivity in the fronto-parietal network with age, as consistent with the current results. Similarly, younger adults are found to exhibit stronger connectivity than older adults within the fronto-parietal network during cognitively demanding tasks (Patil et al., 2021).

While many of the individual connections were not significant following FDR correction for multiple comparisons, the connectivity cluster identified remained significant. These findings may reflect broader trends within networks of the brain rather than isolated connectivity regions. Therefore, the results may be best interpreted at the network level, rather than attributing the observed effects to any single connection, suggesting that older and younger adults may have differed in how their functional networks responded to increasing cognitive demands. Additionally, there was still an observed pattern of older adults demonstrating increased connectivity in more sensory-related regions, like the temporal and auditory areas of the brain. Prior research has examined the idea of a compensatory process associated with ageing. The compensatory mechanism refers to the increasing of neural activity in the brain when faced with high cognitive demands (Cabeza et al., 2018). As seen in other forms of cognition, older adults tend to recruit additional brain regions to compensate

for the decline of others, showing a shift in how neural resources are used. A longitudinal study by Deschwanden et al. (2025) found dedifferentiation of brain regions and more widespread connectivity in older adults over the course of 7 years. Dennis & Cabeza (2011) found that older adults recruited additional brain regions when completing tasks on implicit and explicit learning, while younger adults showed more differentiation of the brain. The changes in the brain associated with ageing are considered heterogeneous, so some connections may increase while others decrease, depending on the task (Chen et al., 2016; Cabeza, 2002). These findings suggest that ageing is associated with changes in reliance on particular brain networks. With increased age, the brain shifts away from fronto-parietal networks towards temporal and sensory-related regions when participants complete tasks requiring varying task demand.

Hypothesis 2

Connectivity also differed based on cognitive load, independent of age, in different regions than the ones implicated in hypothesis 1. Connectivity decreased with higher load levels in various areas such as the posterior cingulate gyrus and precuneus cortex. These regions are associated with the default mode network, which is most active at rest and generally linked to self-reflection and mental exploration (Azarias et al., 2025). In contrast, connectivity increased in other areas, such as the supramarginal gyrus and the posterior cingulate gyrus.

The delayed-match-to-sample task included five cognitive loads, with task difficulty increasing with each level. Functional connectivity showed changes across load conditions, with the strongest effects observed at higher levels of task demand. Some of the relevant clusters were the default mode network and the visual processing network. As task difficulty increased, the connectivity within regions of the default mode network decreased, for instance, the connection between the posterior cingulate gyrus and the precuneus cortex was

especially relevant, T(80) = -7.00. These regions have been observed in the literature as an important connectivity area within the default mode network (Fransson & Marrelec, 2008). The posterior cingulate gyrus has a few different functions, allowing for communication within the default mode network and supporting memory retrieval (Leech & Sharp, 2013). The precuneus cortex similarly supports cognition and is functionally connected with the posterior cingulate during resting state (Zhang & Li, 2011). The connectivity between these regions is strongest at rest and reduces as individuals engage in cognitive tasks, as consistent with the current results (Utevsky et al., 2014). These results demonstrate reduced functional connectivity within the default mode network as task demand increased. The suppression of more internal modes of processing may be done to prioritize higher-level cognition as task demand goes up.

Another relevant cluster identified was the visual processing network. A significant decrease in connectivity was observed between the lateral occipital cortex and the lateral visual network, T(80) = -3.78. The lateral occipital cortex plays an important role in object recognition and identifying and comparing visual stimuli (Grill-Spector et al., 2001). The temporal occipital fusiform cortex has been linked to processing the perception of shapes, objects and visual patterns (Perszyk, 2021). The current study noted that the connectivity between these regions decreased as cognitive load increased. This pattern may demonstrate a change in neural resources away from visual processing networks towards more complex cognitive processes as a way of handling tasks of higher demand. Previous literature has suggested that as working memory demands increase, brain activity becomes more strongly concentrated in the fronto-parietal control networks, while the connectivity within other areas decreases, as consistent with the current findings (Finc et al., 2020). This reduced connectivity around the visual region may reflect a change in the distribution of resources

within the brain, relying less on visual analysis and more on higher-level cognitive processing.

The left middle temporal gyrus (MTG) was observed as a relevant region of connectivity in the first hypothesis, with age-related differences identified. On the other hand, the second hypothesis was more strongly associated with the right side of the middle temporal gyrus, with differences observed independent of age. This distinction between the left and right MTG may reflect hemispheric specialization during the processing of increasing cognitive demands. The left temporal cortex is more associated with language-related and verbal processing, such as semantic retrieval (Tzourio-Mazoyer et al., 2017). In contrast, the right temporal cortex has been observed in the literature as more associated with attentional control and general task processing (Geng & Vossel, 2013). As cognitive demand increases, the recruitment of the right MTG may reflect higher-level cognitive processing that occurred independently of age. However, hemispheric specialization was not directly examined in the current study, and this interpretation should therefore be considered a possible explanation for an observed pattern rather than a direct conclusion.

Limitations

There are some aspects of the current study design that could have limited its ability to detect significant relationships. One of the potential limitations is with diversity of the sample, as most participants were recruited from the University of Ottawa campus. Without a diverse enough sample, it may be difficult to generalize the findings. There may also be a self-selection bias, where individuals who volunteer for a study of this nature may be more confident in their cognitive abilities. If an individual knows they're having trouble with task management or other skills, they may be reluctant to participate. Additionally, participants' hearing ability was not assessed in the current study. With the involvement of auditory

regions such as the planum polare in the findings, variability in hearing may have influenced functional connectivity patterns.

There may also be some limitations with the study design. The delayed match-to-sample task was divided into three phases, with the colour of the letters differing between the first and final phases. In the first phase, participants were shown a set of white letters, whereas in the final phase, they were shown a blue letter. This change in colour was done to make it clear to participants that they had moved on to a new task. However, this difference could have affected participants' performance independently of the variable being studied. Differences in colour may have affected the visibility of the letters, potentially making them harder for some participants to see. Therefore, differences in performance could partly reflect the change in visual presentation.

Vision was also not tested in the current study. It is unclear whether individual differences in colour perception may have influenced participants' ability to perceive the letters. This is particularly relevant when comparing older and younger adults, as age-related changes in vision could have affected participants' performance in the delayed match-to-sample task

Future Directions

There are many different ways the current research could be expanded. To begin with, future research could look at other variables aside from age, such as level of education or physical activity. There has been some research on how education serves as a protective mechanism against cognitive decline (Floeter et al., 1997) but there is a gap in whether those results would extend to task-based functional connectivity. It would be beneficial to identify additional variables that are affecting functional connectivity, as these differences can significantly influence how the brain adapts to various tasks. Future studies could then benefit

from incorporating a longitudinal design to examine whether changes in functional connectivity are potentially reversible with lifestyle alterations.

While the current study focused solely on the changes in functional connectivity, future research could benefit from considering the behavioural performance data. Measures such as accuracy and reaction time could provide greater insight into how changes in connectivity influence cognition during tasks. This approach could aid in distinguishing between theories such as the compensatory mechanism or dedifferentiation. To provide stronger evidence for compensation, future research would need to determine whether the additional connectivity observed in older adults is associated with better behavioural performance. Response times could be analyzed in relation to the strength of functional connectivity across the different levels of load. If older adults who demonstrated greater increases in connectivity also show faster response times, this would indicate that additional connectivity may support task performance (Goldstone et al., 2018). To examine whether dedifferentiation is occurring, future research could assess whether older adults show more widespread connectivity across different functional networks than younger adults do as cognitive load increases. Greater connectivity across networks of the brain that are normally distinct may indicate reduced functional specialization, providing evidence for dedifferentiation. While stronger connectivity that is more distinct may suggest greater differentiation or more efficient recruitment of areas of the brain. The current study cannot determine whether the changes seen are beneficial or harming performance, therefore, response times could provide an important way to examine the relationship between connectivity and behavioural performance.

Beyond functional connectivity, future research could investigate how changes in brain structure, like reduced gray or white matter volume relate to functional connectivity. As described in the introduction, previous studies, such as Satake et al. (2024), have

demonstrated how structural and functional connectivity can be examined together. It would be beneficial for future research to analyze structural changes specifically during tasks with varying cognitive demands, like the delayed match-to-sample task. This would allow for a more comprehensive understanding of the differences between structural and functional connectivity. Additionally, it would offer insights into whether the compensatory mechanism observed in older adults is correlated to structural changes in the brain.

Conclusion

The current study offers insights into how ageing and cognitive load differentially influence functional connectivity within the brain. Using a generalized psychophysiological interaction (gPPI) analysis during the delayed match to sample task, the findings demonstrated that younger and older adults exhibit different patterns of connectivity under increasing task demands. Specifically, older adults showed selective changes in connectivity within the auditory-temporal network, while younger adults demonstrated a potential pattern of stronger connectivity within frontal-parietal regions. These changes may reflect age-related declines in the use of brain networks that support language processing and working memory. Additionally, ageing may involve compensatory recruitment of additional neural resources to maintain performance under increasing task difficulty.

Cognitive load, independent of age, influences connectivity across different areas of the brain, such as the default mode and the visual-temporal networks. The differences between age-related and solely task-related changes in connectivity suggest they operate through different neural mechanisms. One notable finding was the difference in connectivity across hemispheres, with the left middle temporal gyrus being more strongly associated with age-related connectivity, while the right middle temporal gyrus was more strongly implicated in cognitive load effects, independent of age. These findings provide a more comprehensive

understanding of the relationship between age, task demands of varying loads and functional connectivity.

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Appendix

Table A1

Full Table: Changes in Functional Connectivity Linearly Between the 5 Loads, Independent of Age

Originating Region	Second Region	p-unc	p-FDR	T Values (df = 80)
Posterior cingulate gyrus	Precuneus cortex	p<0.001	p<0.001	-7.00
Inferior frontal gyrus	Right cerebellum	p<0.001	0.00018	-4.94
Left middle frontal gyrus	Right cerebellum	p<0.001	0.0011	-4.27
Right temporal occipital fusiform cortex	Right superior lateral occipital cortex	p<0.001	0.05100	-3.78
Right cerebellum	Inferior frontal gyrus	p<0.001	0.0017	-4.59
Posterior cerebellum	Left inferior frontal gyrus	p<0.001	0.0021	-4.44
Middle frontal gyrus	Right cerebellum	0.003	0.0182	-3.05
Inferior frontal gyrus	Posterior cerebellum	0.001	0.0473	-3.31
Posterior supramarginal gyrus	Posterior cingulate gyrus	p<0.001	p<0.001	6.95
Frontal medial cortex	Posterior supramarginal gyrus	p<0.001	0.0023	4.46
Frontal medial cortex	Middle temporal gyrus	p<0.001	0.004	3.99
Posterior supramarginal gyrus	Subcallosal cortex	0.00257	0.0197	3.11
Middle temporal gyrus	Subcallosal cortex	0.00299	0.0295	3.06
Posterior cingulate gyrus	Inferior frontal gyrus	p<0.001	0.00350	3.79
Precuneous cortex	Posterior supramarginal gyrus	p<0.001	0.00177	4.42
Middle temporal gyrus, temporooccipital part Right	Posterior cingulate gyrus	p<0.001	p<0.001	5.30
Precuneous cortex	Inferior frontal gyrus	p<0.001	0.005690	3.69

Precuneous cortex	Middle temporal gyrus, temporooccipital part Right	$p<0.001$	0.011271	3.51
Anterior, right supramarginal gyrus	Posterior cingulate gyrus	$p<0.001$	$p<0.001$	5.30
Posterior supramarginal gyrus	Anterior middle temporal gyrus	0.0113	0.0557	2.59