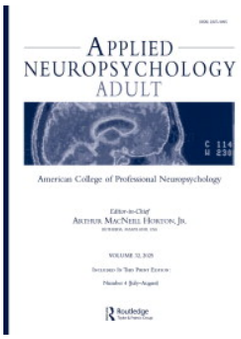

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Can short-term memory capacity change resting brain behavior? Findings from neuropsychological assessment and dynamic causal modeling

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ABSTRACT

This study aimed to investigate different short-term memory capacities (STMC) on resting brain of healthy individuals particularly the neuropsychology and connectivity behaviors. The outcomes may serve as a baseline for clinical diagnosis of memory decline due to aging and mental disorders. It was hypothesized that resting brain of low and typical STMC individuals behaves differently. Thirty-nine healthy young male adults were recruited from local universities. They were categorized as typical or low STMC based on their scores in the Malay Version of the Auditory-Verbal Learning Test (MVAVLT). A resting-state functional magnetic resonance imaging (rs-fMRI) was conducted and data were analyzed using statistical parametric mapping (SPM) and dynamic causal modeling (DCM). Nine neuropsychological assessments were significantly higher ($p < 0.05$) in typical STMC participants compared with low STMC participants. Four activation clusters survived the contrast "Low > Typical" uncorrected at set and cluster levels threshold ($p_{FWE} < 0.05$). A causal model containing these clusters as nodes found that there is no preference on negative or positive connectivity among typical and low STMC groups. Nevertheless, implementing a reduced connection scheme revealed more significant connections for the low STMC group. To conclude, the low STMC participants scored lower in all neuropsychological assessments, but a higher activation profile with more areas being connected effectively as compared with the typical STMC group. The results suggest a higher resting neural activity and communication among certain brain areas in low STMC individuals that the brain could have executed as a compensation strategy.

KEYWORDS

Causal; connectivity; fMRI; memory; parametric; resting-state

Introduction

Short-term memory capacity (STMC) refers to an individual's ability to temporarily hold and access small amounts of information when an external stimulus is no longer present (Yue & Martin, 2021). Although numerous studies have explored STMC, only a few have examined its influence on the resting brain's behavior. Understanding this relationship could significantly aid in diagnosing memory decline in individuals.

STMC varies across individuals (Cowan, 2008), with differences in both the amount of information retained and the duration it remains accessible. STMC classifications often distinguish between "good" and "poor" memory capacity based on retention within a specific time frame (Jonides et al., 2008). Information in short-term memory (STM) is typically retained for 20 to 30 seconds before being either consolidated into long-term memory (LTM), lost, or replaced (Goldstein, 2011).

STM plays a key role in everyday activities, including learning, information processing, attention, following instructions, and processing speed, all of which impact an individual's quality of life (QoL) (Fernández et al., 2024; Goldstein, 2011; Jamaluddin et al., 2009). Research shows that individuals with higher STMC tend to report better QoL (Fernández et al., 2024). Previous studies have examined STMC differences in typical and low-STMC individuals, including comparisons between normal individuals and those with schizophrenia (Jamaluddin et al., 2009), often using task-based functional MRI (tb-fMRI) (Yue & Martin, 2021). However, fewer studies have explored STMC effects on resting-state (rs) fMRI. In this study, we bridge this gap by examining neuropsychological assessment results alongside dynamic causal modeling (DCM) of rs-fMRI data, contributing insights that complement findings from tb-fMRI studies.

STMC is influenced by factors such as age (Vakil et al., 1998), sex (Hill et al., 2014), education, and task type

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This article has been corrected with minor changes. These changes do not impact the academic content of the article.

(Van der Elst et al., 2005). Many studies report on STMC variability (Magalhães & Hamdan, 2010; Unsworth & Engle, 2007; Vakil & Blachstein, 1993), with findings showing that schizophrenic patients with low STMC perform worse in the Malay Auditory Verbal Learning Test (MVAVLT) compared to normal participants (Jamaluddin et al., 2009). In addition, the low STMC group scored lower in a backward word repeat test (BWRT), a test measuring auditory working memory (AWM) performance, indicating a close relationship between STMC and AWM (Othman et al., 2020a; Oztekin & McElree, 2010). Positive correlations have been observed between STMC and memory-related brain activation in tb-fMRI, including the number of activated voxels (NAV) and percentage of signal change (PSC) (Othman et al., 2020a).

Differences in STMC also impact rs-fMRI findings, as shown by higher cortical activations in the left lingual gyrus, bilateral middle temporal gyrus, left calcarine, left superior frontal gyrus, and left precuneus for low-STMC individuals, with a significant increase in the percentage amplitude of fluctuation (PerAF) in these regions (Gafoor et al., 2021). This suggests that higher resting-state activations in low-STMC individuals may reflect reduced neural adaptability. Accordingly, effective connectivity (EC) between activated brain regions should correlate with rs-fMRI activation and PerAF, potentially showing stronger connections in low-STMC individuals. However, existing evidence correlating EC with resting-state activation remains limited, highlighting the need for further research.

The human brain operates through interconnected networks of excitatory and inhibitory neurons that maintain balanced activity patterns (Kajiwara et al., 2021). Connectivity between two neuronal regions may be excitatory or inhibitory, depending on the neuronal state and the influence of one region over another (Abdul Hamid et al., 2023; Husbani et al., 2021; Mohd Nawi et al., 2020). While excitatory neurons propagate activity, inhibitory neurons provide regulatory feedback (Sukenik et al., 2021). Research indicates that inhibitory neurons are proportionately fewer than excitatory neurons in the cortex (Kajiwara et al., 2021). Prior studies with university students, for instance, have shown that untrained groups predominantly exhibit excitatory connections, while trained groups show a balanced distribution of excitatory and inhibitory connections (Abdul Hamid et al., 2023). The present study examines whether similar differences occur in resting-state connectivity patterns associated with STMC and whether low STMC may be linked to an increased proportion of excitatory connections.

This study aims to expand understanding of the brain's resting state by comparing NAV and EC between typical and low STMC groups and correlating these findings with neuropsychological assessments. Based on prior findings, we hypothesized that the resting brain in low STMC individuals would exhibit a different connectivity profile than in typical STMC individuals, with low STMC participants showing higher NAV and more extensive connectivity in a resting network, favoring excitatory over inhibitory connections. This research may serve as a foundational baseline for investigating early indicators of memory decline.

For data analysis, DCM was applied to rs-fMRI time series to model underlying EC (Almgren et al., 2018). This study used spectral DCM (spDCM), which leverages on a generative model of cross-spectral density to capture neural fluctuations (Friston et al., 2014a; 2014b). Compared to traditional stochastic DCM, spDCM requires lower computational complexity, making it more suitable for analyzing spectral second-order data (Razi et al., 2015).

Materials and methods

Participants

Thirty-nine healthy young male adult participants were recruited from local universities in Klang Valley, Malaysia with an age range between 18 and 24 years. Only male participants were recruited to control for the effects of gender on STMC (Hill et al., 2014). The average age and its standard deviation are 21.28 ± 1.59 years. The participants were all native-Malay speakers and were all right-handed as assessed using the Edinburgh Handedness Inventory (Oldfield, 1971). All participants were confirmed to be right-handed with an average laterality index of 82.14 (in the range of 5th right). None of the participants ever had otitis media, cognitive disorder, or neurological abnormality. From the self-report assessment, none of the participants had a musical background, which is important as musicians have been shown to have a greater ability to perceive speech than non-musicians (Du & Zatorre, 2017). The pure tone audiometric (PTA) test assessed participants' normal hearing sensitivity for both ears. Participants' absolute hearing threshold was equal to or less than 20 dB HL at octave frequencies between 250 and 8000 Hz. Participants were briefed about the study's aims and procedures before obtaining their written informed consent. They were allowed to withdraw from this study on their own will if they would not be able to proceed. Human ethics and consent to participate were adhered in accordance with the Declaration of Helsinki. All participants were not meant to be differentiated by any other variable except short-term memory capacity. Variables such as academic background, age, race, sex, hearing levels, and handedness were kept as constant as possible. The participants were also free from the use of psychoactive medications and had no magnetic resonance imaging (MRI) contraindications such as metallic implants, and surgical and aneurysm clips. This study was approved by the Institutional Ethics Committee of the Universiti Kebangsaan Malaysia (UKM/PPI/111/8/JEP-2017-117) and the Malaysia Medical Research and Ethics Committee (NMRR-17-56-33800).

STM capacity measurement

All participants completed the Malay Version of the Auditory-Verbal Learning Test (MVAVLT) to systematically assess short-term memory capacity (STMC) (Jamaluddin et al., 2009; Othman et al., 2020a). The test was chosen as the test of STMC because it contains elements of recall and recognize. Furthermore, the time for the participants to

recall and recognize falls in the STMC processing range. Clear instructions were provided in Malay, following the procedure outlined in prior studies (Jamaluddin et al., 2009). The MVAVLT includes three parts: Part A, Part B, and Part C.

In Part A, participants were instructed to listen, memorize, and recall as many words as possible from a 15-word list (List A), as shown in Table 1. Words were read aloud at approximately one-second intervals, and participants responded without a time limit. This procedure was repeated across five trials (A1 to A5), with the first trial (A1) ending when participants could no longer recall additional words. The word order remained consistent across trials, and each trial had a maximum score of 15, yielding a cumulative score of up to 75 across all five trials.

In Part B, participants were introduced to a new list of 15 words (List B; see Table 1). Words from List B were presented in the same manner as in Part A, though only one trial (B1) was conducted. Immediately following trial B1, participants were asked to recall words from List A in a free recall format (trial A6). After this immediate recall, participants took a 20-minute break. Upon returning, they were again asked to recall words from List A for a delayed recall (trial A7).

Part C was a recognition task. Participants were presented with a list of 30 words, consisting of the 15 words from List A mixed with 15 distractor words (Table 1). Participants were instructed to identify words from List A by responding "yes" or "no" to each word presented. Each of these trials—B1, A6, A7, and the recognition trial—had a maximum score of 15.

The entire MVAVLT session took approximately 30 to 45 minutes to complete, including the 20-minute break.

Table 1. List of Malay words and their English translations used in MVAVLT as explained in the text.

Part A	Part B	Part C
Siku/*Elbow*	Mangkuk/*Bowl*	Cermin*/*Mirror*
Harimau/*Tiger*	Monyet/*Monkey*	Tukul/*Hammer*
Kapak/*Axe*	Kasut/*Shoe*	Pisau/*Knife*
Katil/*Bed*	Lembu/*Cow*	Lilin*/*Candle*
Kapal/*Ship*	Jari/*Finger*	Beca*/*Trishaw*
Telinga/*Ear*	Baju/*Shirt*	Kapak/*Axe*
Anjing/*Dog*	Semut/*Ant*	Jam/*Clock*
Tukul/*Hammer*	Cawan/*Cup*	Bulan*/*Moon*
Kerusi/*Chair*	Tebuan/*Bee*	Kapal/*Ship*
Kereta/*Car*	Itik/*Duck*	Penyu*/*Turtle*
Mata/*Eye*	Topi/*Hat*	Ayam/*Chicken*
Ayam/*Chicken*	Kaki/*Foot*	Kaki*/*Foot*
Pisau/*Knife*	Cerek/*Kettle*	Anjing/*Dog*
Jam/*Clock*	Tikus/*Mouse*	Meja*/*Table*
Basikal/*Bicycle*	Tangan/*Hand*	Harimau/*Tiger*
		Bibir*/*Lips*
		Pokok*/*Tree*
		Siku/*Elbow*
		Hidung*/*Nose*
		Kerusi/*Chair*
		Lori*/*Lorry*
		Mata/*Eye*
		Ikan*/*Fish*
		Telinga/*Ear*
		Basikal/*Bicycle*
		Ular*/*Snake*
		Bangku*/*Stool*
		Bas*/*Bus*
		Katil/*Bed*
		Kereta/*Car*

Participants were classified into typical and low STMC groups based on their cumulative scores from trials A1 to A5. Those scoring within the upper half of the MVAVLT range (scores of 38 to 75) were categorized as typical STMC, while those scoring in the lower half (scores of 1 to 37) were categorized as low STMC. Scores from trials B1, A6, A7, and the recognition trial were not used for classification but were analyzed to further explore performance differences between the two groups (Othman et al., 2019, 2020a, 2020b).

rs-fMRI scan

Participants were instructed to keep their heads still and remain calm during the rs-fMRI scans. They were also required to clear their mind and not be in a state of "daydreaming" or "mind wandering" throughout the scanning session and fix their vision on an "X" symbol that they see on the coil mirror. The image of the symbol was reflected from a non-magnetic screen situated in front of the scanner. The symbol was projected onto the screen by an LCD projector located outside the magnet room at the control panel. Participants were continuously monitored so that they would not fall asleep during the scan because the resting brain is very much different from the sleeping brain (Nguyen et al., 2018). The rs-fMRI scans were performed using a 3-tesla Siemens Magnetom Verio at Universiti Kebangsaan Malaysia Medical Center (UKMMC). The data from the first few scans were not acquired by the MRI system to ensure signal stabilization by eliminating the effects of drift (Mohd Nawi et al., 2020) and to allow the participants to familiarize themselves with the scanner noise (Esménio et al., 2019). Functional T2*-weighted images of the brain were acquired for 9 minutes and 33 seconds using a gradient-echo echo-planar imaging (GRE-EPI) pulse sequence. The imaging parameters include echo time (TE) = 29 ms, repetition time (TR) = 2 s, flip angle (α) = 75°, slice thickness = 3.5 mm, slice gap = 1.05 mm, field of view (FOV) = 240 mm, matrix size = 64 × 64, voxel size = 3.75 × 3.75 × 4.55 mm and the number of scans = 158. In addition, structural T1-weighted multi-planar reconstruction (MPR) images of the brain were also acquired for screening purposes. The imaging parameters were repetition time (TR) = 1900 ms, echo time (TE) = 2.35 ms, flip angle = 9°, voxel size = 1.0 × 1.0 × 1.0 mm and matrix size = 256 × 256. The state of consciousness of the participants throughout the scan was verified after the completion of the scan. All participants confirmed that they had followed the instructions given to them before scanning and had given their cooperation as required by the study.

Spatial processing

For each participant, the first 8 functional scans were removed from data analysis. The remaining 150 functional scans were analyzed using Statistical Parametric Mapping (SPM12) (Functional Imaging Laboratory (FIL), Wellcome Trust Center for NeuroImaging (WTCN), Institute of Neurology (ION), University College London (UCL), United

Kingdom – www.fil.ion.ucl.ac.uk/spm/) which operates on MATLAB R2021b (The Mathworks, Inc. USA) platform. The functional images in each measurement were randomly and manually checked for any artifacts that could be caused by magnetic field distortion. The images were then entered into a slice-timing module for slice-timing correction. They were then realigned using a 6-parameter affine transformation in translational (x, y, and z) and rotational (pitch, roll, and yaw) directions to reduce the effects on the overall signal intensity that may be caused by participant movements. After realigning the data, a mean image of the series was used to estimate some warping parameters that mapped it onto a template conformed to a standard anatomical space (EPI template provided by the Montreal Neurological Institute-MNI). The normalization procedure used a 12-parameter affine transformation. The images were then smoothed using an 8-mm full-width-at-half-maximum (FWHM) Gaussian kernel. Unwanted responses caused by aliased biorhythms, cardiac effects, and other oscillatory signal variations were removed using a high-passed filter.

General linear model

The human brain has been found to exhibit low-frequency signal fluctuation (LFF) when it is at rest. This LFF is the combination of many frequencies ranging from 0.01 to 0.08 Hz (Cordes et al., 2001). The LFF detected during the resting state is associated with internally and externally oriented consciousness (Vanhaudenhuyse et al., 2011). Thus, to model the LFF, a combination of mathematical functions such as sine and cosine functions of different frequencies that show a resemblance to LFF, can be used (Di & Biswal, 2014a). The functions, also known as the Fourier basis set (Glaser & Friston, 2004), can be incorporated into the general linear model (GLM) as shown by the design matrix in Figure 1a. This Fourier basis set with N_s = 47 as regressors is thought to be suitable to model brain responses during resting state which is assumed to oscillate between 0.01–0.08 Hz (Cordes et al., 2001; Di & Biswal, 2014a). The standard cutoff brain frequency at rest is 0.008 Hz, removing any other low-frequency fluctuations caused by breathing, cardiac effects, and aliased biorhythms (Esménio et al., 2019) that could still be present after high-passed filtering. Thus, the GLM for the LFF for this study ranged from 0.008 to 0.1 Hz. The incorporation of the N_s = 47 basis set into the GLM can be construed as trying to harvest or model as many low-frequency signals as possible from the resting brain.

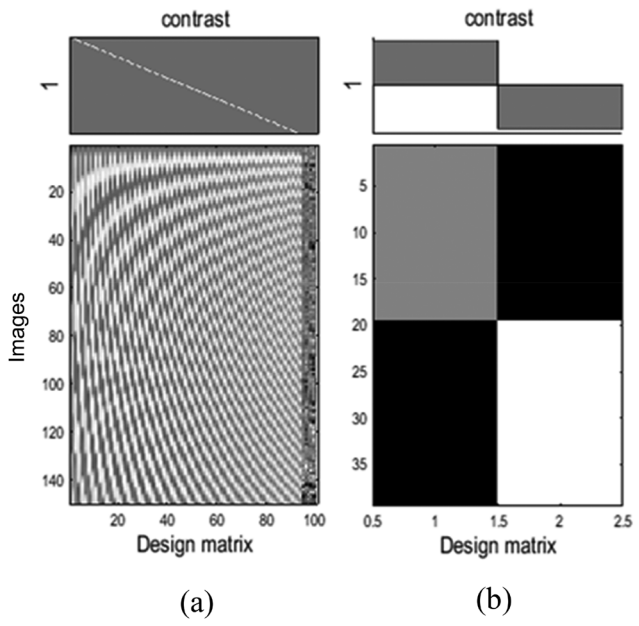

Figure 1. Design matrix used for (a) individual subject and (b) group differential analyses.

Concerning the design matrix shown in Figure 1a, columns 1 to 94, denoted as parameters, represent the 47 Fourier basis set mentioned before with their 90° phase delay oscillating at 0.008 Hz to 0.1 Hz in the step of 0.002 Hz. Column 95 to column 100 represent the movement-related parameters. The last column (column 101) represents the effects that may be caused by other factors. This is known as first-level analysis (Zeidman et al., 2019a). The horizontal lines in the design matrix, denoted as images, are the number of scans. In this design matrix, the 150 rs-fMRI functional scans for each of the participants were incorporated. The design matrix shown in Figure 1a was then estimated and the images of the parameter estimates for the model known as ESS image (ESS.img) was obtained for individual participants using the F statistics. The ESS image obtained from the individual-subject analysis was then entered into a second-level differential group analysis (Zeidman et al., 2019b) conducted using an independent sample t-test to compare the typical and low STMC groups of participants. The design matrix used is shown in Figure 1b. The area, sub-area, anatomical functions, voxel value, and peak coordinates of the activations for comparisons of low STMC > typical STMC and typical STMC > low STMC, thresholded at corrected and uncorrected p values are recorded and tabulated. The confirmation of the areas of activation, if any, was obtained from a region-of-interest (ROI) analysis using a MATLAB-based WFU Pick Atlas toolbox (Wake Forest University, North Carolina, USA).

EC analysis

The following connectivity analyses were conducted based on the methods described by Ashburner et al. (2018). A GLM containing the time-corrected, realigned, normalized, and smoothed images was specified for each participant and a design matrix was constructed as shown in Figure 2a. This first design matrix in connectivity analysis steps was then estimated and used in extracting the time series signals from cerebrospinal fluid (CSF) and white matter (WM) of a 6-mm radius node centered at (0, −40, −5) and (0, −24, −33) respectively. For participants who did not show an acceptable amplitude of LFF for WM at the respective coordinates, alternative coordinates of (-40, −51, 10) located in the superior longitudinal fasciculus were chosen. The extracted signals from CSF and WM were then used as regressors to construct the second design matrix as shown in Figure 2b.

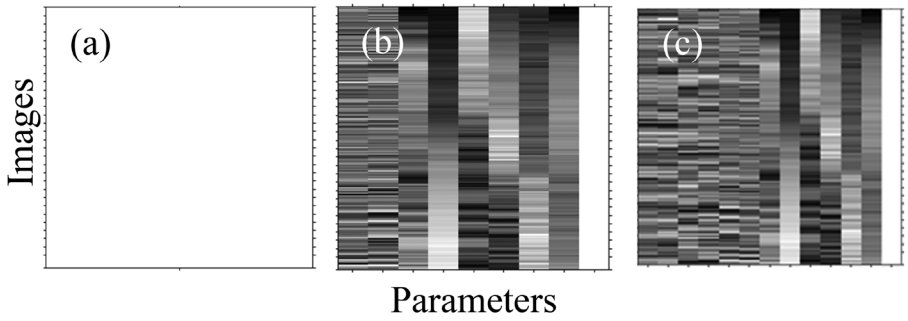

Figure 2. Single subject design matrix used for obtaining endogenous random fluctuations.

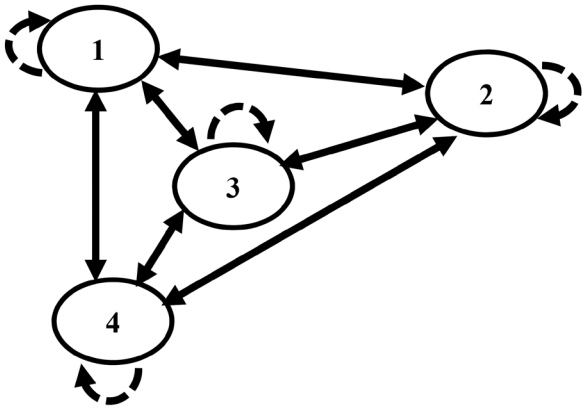

Figure 3. Example of a fully connected model containing four nodes. Solid arrows represent bidirectional intrinsic connectivity (i.e., "from" and "to") while dashed arrows denote self-connection.

Note that the first two columns of the design matrix in Figure 2b are the signal fluctuations during rest from CSF and WM, respectively. The six subsequent columns represent movement-related parameters while the last column represents global or other effects that may exist. This new design matrix was then estimated. The design matrix in Figure 2b was later used to extract signals from the selected 8-mm radius node of the significantly activated regions obtained from the differential analysis mentioned earlier. Differential analysis will result in regions that are significantly actively higher either in typical or low STMC groups. The conditions for the regions to be selected as nodes for connectivity analysis are that they must be significantly activated and survive peak, cluster, and set levels of inference. EC models will be constructed using these nodes.

The time series signal extracted from the selected nodes was entered into the third design matrix, together with the extracted signals from CSF and WM, six realigned parameters, and global effects. Note that the newly constructed design matrix shown in Figure 2c was taken from the analysis of the current results and displayed here for reference. This design matrix was then estimated. After estimation, the time series signals extracted from each selected node were then used in specifying and constructing a full-connected dynamic causal model. This was done using DCM (DCM12.5). The same model will be used for all participants in both groups. An example of a full-connected model comprising four nodes is shown in Figure 3. The models were then estimated using spDCM to obtain the intrinsic and self-connectivity values for every participant as described in a previous communication (Razi et al., 2015). In the estimation process, the endogenous fluctuation of activity within the nodes was first recorded and analyzed to generate complex cross spectra. The time-invariant covariance of the random fluctuations between nodes was then estimated to obtain the cross-spectrum density. The EC among coupled neuronal responses was subsequently estimated using a neuronally plausible power-law model (Friston et al., 2014a).

The output will be the model shown in Figure 3 with the values of intrinsic- and self-connections. The validity of the analytical technique used has been explained in a previous work (Razi et al., 2015). The estimated models from each participant were then entered into Bayesian Parameter Averaging (BPA) to obtain the average EC values (Stephan et al. 2009). From the averaging results, the connection that has a posterior probability value of less than 0.9 will be discarded. In the Bayesian framework, a connection is considered significant if its posterior probability value is equal to or larger than 0.9 (Penny et al., 2004). The same goes for connections that have a value of less than 0.1 which can be considered as trivial connections. This step will result in a model with reduced connections because there will be connections that will be removed from the model. This is done separately for both groups of participants.

Brain activation and DCM results obtained from both low and typical STMC groups will be compared to explore changes brought about by the difference in STMC. The outcomes will then be triangulated with findings from neuropsychological assessment.

Results

The Malay Version Auditory Verbal Learning Test (MVAVLT) results

Among the 39 participants who completed the MVAVLT, 20 were classified as having typical STMC (scores of 38 to 75), while 19 were categorized as having low STMC (scores of 1 to 37). Table 2 presents the results for each group. Preliminary assumptions for normality and homogeneity of variances were checked using the Shapiro-Wilk and Levene's tests, respectively. Both tests were non-significant for all trials ($p > 0.05$), confirming that

the data met the assumptions of normality and equal variances. To examine differences between groups, independent samples t-tests ($p < 0.05$, 95% CI, two-tailed) were conducted, comparing the mean scores of typical STMC participants to those of low STMC participants. Results showed that the typical STMC group scored significantly higher ($p < 0.05$) across all trials compared to the low STMC group, indicating a robust difference in performance between the two groups.

Differential brain activation

This study presents and discusses brain activation patterns based on group differential analysis. Notably, both the typical and low STMC groups showed distinct areas of peak activation intensity. For the low STMC group, the cluster with the maximum intensity voxel (p_{FWE} = 0.05) was located in the left cerebral white matter, primarily within the frontal and limbic lobes, specifically in the cingulate gyrus at coordinates (-22, −24, 46). In contrast, for the typical STMC group, the maximum intensity voxel was observed at coordinates (-36, −58, 02), also within the left cerebral white matter but mainly in the temporal lobe. The activated areas included the sub-gyral region, left middle temporal gyrus, left middle occipital gyrus, left ventricle, and extranuclear areas. Although significant activation was noted in both groups in the precuneus and posterior cingulate cortex (PCC), these areas did not show peak intensities as high as in our previous studies on the default mode network (DMN) using rs-fMRI (Husbani et al., 2021; Mohd Nawi et al., 2020).

Group differential random-effects (RFX) analysis was conducted using a contrast of typical STMC > low STMC. However, no cluster of voxels survived the corrected (p_{FWE} = 0.05) or uncorrected ($p = 0.001$) thresholds. For the low STMC > typical STMC contrast, no cluster of voxels survived the corrected threshold (p_{FWE} = 0.05), but several cluster of voxels indicated significant differences at the uncorrected threshold ($p < 0.001$), as shown in Figure 4a (Gafoor et al., 2021).

The design matrix and the contrast used to generate the activation clusters in Figure 4a are shown in Figure 4b. Based on the automated anatomical labeling (AAL) atlas, these activated clusters are the left lingual gyrus (LLG), left thalamus (LTH), right middle temporal gyrus (RMTG), cuneus (CUN), left superior frontal gyrus (LSFG), left temporal pole (LTMP), left pre-cuneus (LPCU), and left cerebellum (LCE). The exact location of these regions on axial brain images are given in Figure 5 and the details about the statistics, coordinates, and names of these activated regions are summarized in Table 3.

Table 2. Malay Version Auditory Verbal Learning Test (MVAVLT) scores for the typical and low STMC groups.

MVAVLT trials	Descriptive statistics Typical STMC Mean ± SD	Low STMC Mean ± SD	Independent samples *t*-test Mean differences	*p* Value
A1	7.80 ± 1.01	4.60 ± 0.94	3.20	< .001
A2	8.70 ± 1.17	5.50 ± 1.00	3.20	< .001
A3	9.45 ± 1.36	5.95 ± 1.09	3.50	< .001
A4	10.70 ± 1.30	6.80 ± 0.70	3.90	< .001
A5	12.10 ± 0.83	8.00 ± 0.80	4.05	< .001
Total A1-A5*	48.70 ± 4.73	30.85 ± 3.08	17.85	< .001
B1	8.85 ± 1.42	5.45 ± 1.47	3.40	< .001
A6; Immediate Recall	11.45 ± 1.82	7.75 ± 1.41	3.70	< .001
A7; Delayed Recall	11.20 ± 1.61	7.05 ± 1.32	4.15	< .001
Recognition Recall	13.45 ± 1.15	12.35 ± 1.27	1.15	< .003

*Index used to classify participants into typical and low STMC groups.

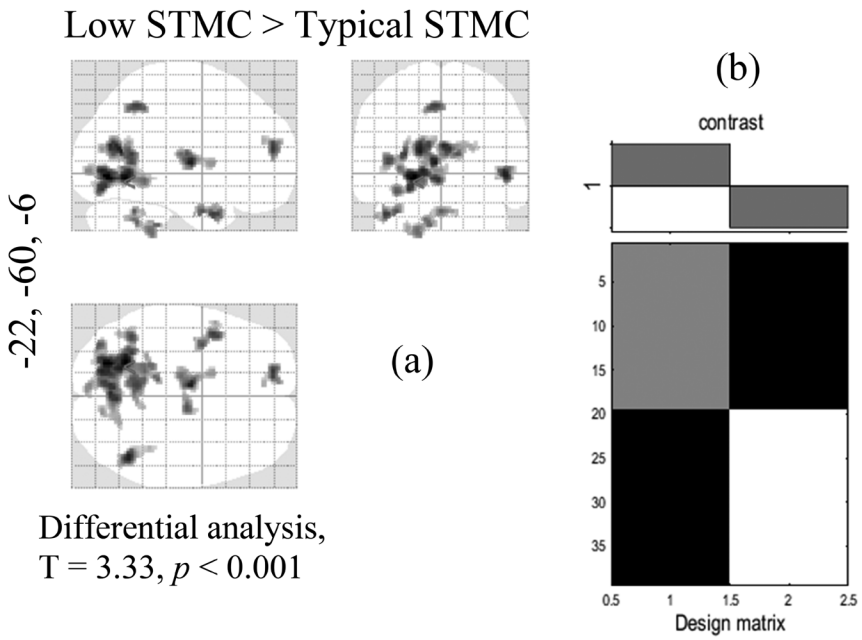

Figure 4. Statistical parametric maps obtained from group differential RFX for contrast Low STMC > Typical STMC showing activation clusters that are significantly (uncorrected threshold, $p < 0.001$) activated.

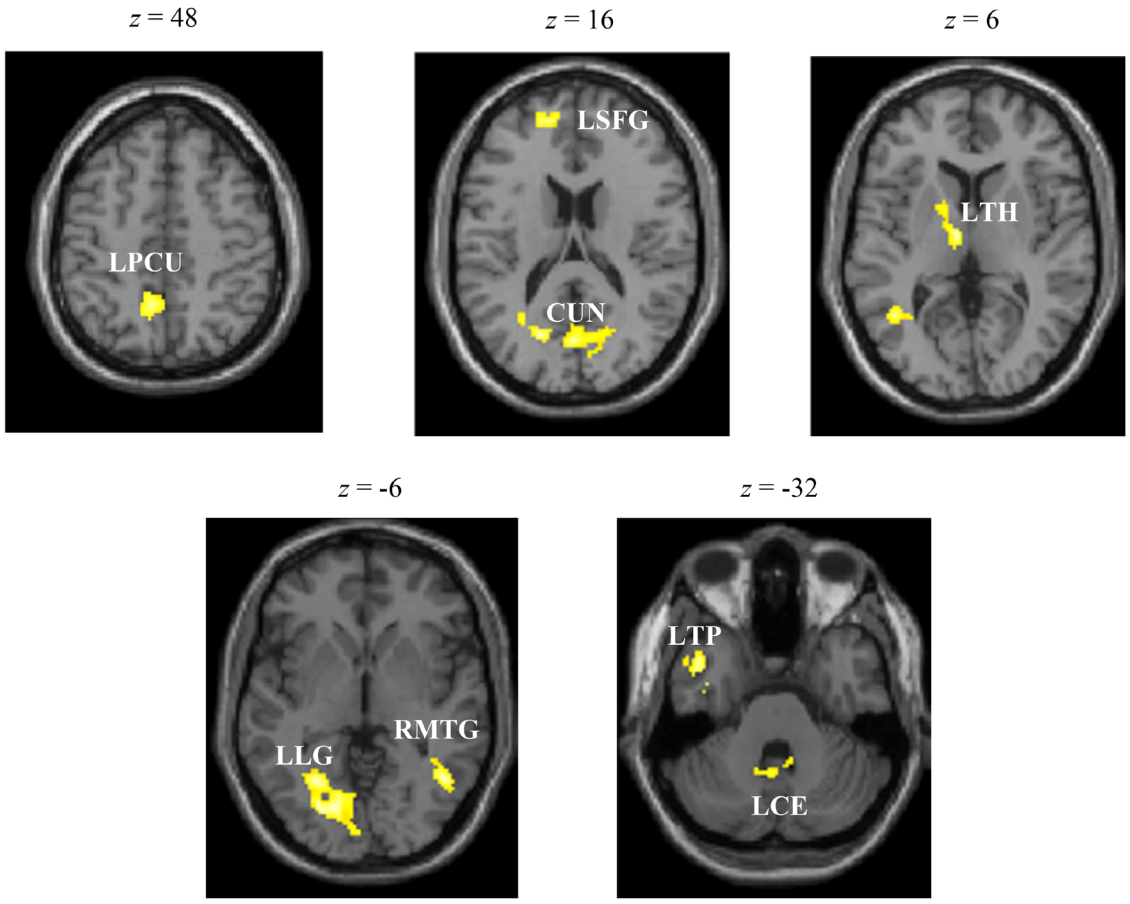

Figure 5. Descending T1 axial neurological brain images showing the eight activated clusters at different *z*-coordinate.

Table 3. Statistics (adjusted for search volume) of the activated regions obtained from group differential RFX for contrast Low STMC > Typical STMC at set-, cluster- and peak-level ($p < 0.001$ uncorrected). Also shown are the maximum intensity coordinates and the name of the regions based on automated anatomical labeling (AAL).

Cluster	*p* set-level	$p_{FWE\text{-}corr.}$ cluster-level	$p_{uncorr.}$ peak-level	*t* peak-level	*NAV* (*k* = 100)	Peak mm mm mm	Regions
1*	< 0.001	< 0.001	< 0.001	5.40	1215	−22 −60 −6	LLG
2*	< 0.001	0.012	< 0.001	4.94	253	−6 −10 6	LTH
3	< 0.001	0.062	< 0.001	4.92	164	46 −58 −2	RMTG
4*	< 0.001	0.022	< 0.001	4.76	219	0 −72 18	CUN
5	< 0.001	0.117	< 0.001	4.63	133	−16 52 16	LSFG
6	< 0.001	0.153	< 0.001	4.59	120	−44 6 −32	LTMP
7	< 0.001	0.127	< 0.001	4.56	129	−6 −52 48	LPCU
8*	< 0.001	0.033	< 0.001	4.27	197	−2 −54 −30	LCE

k = Extent threshold; *FWE* = Family-wise Error; corr. = Corrected; uncorr. = Uncorrected; *NAV* = Number of activated voxels; * = Significant at peak, cluster and set levels.

Dynamic causal modeling

The LLG is the region with the highest height and spatial activation. Out of the eight clusters of activation that survived the height and spatial threshold ($p < 0.001$; $k = 100$), only four clusters are significant at set and cluster levels. Those clusters are assigned to LLG, LTH, CUN, and LCE. These clusters were used as nodes in the construction of a full-connected model in connectivity analysis for both typical and low STMC groups as shown in Figure 3. Concerning Figure 3, CUN = Node 1, LTH = Node 2, LLG = Node 3, and LCE = Node 4. Tables 4 and 5 show the connections between the nodes as well as within the respective node (self-connection) for typical STMC (20 participants) and low STMC (19 participants) individuals. The averages were shown at the bottom of each respective table for comparison. The average values (AVG) were obtained from Bayesian parameter averaging (BPA). Data represented in italic bold-face font are not significant which means that the values are relatively small with the posterior probability of less than 0.9.

Concerning Tables 4 and 5, for any one participant, 16 connections are being investigated including four self-connections. There are more significant connections than insignificant connections for any one of the participants. For any one connection, more participants show significant connections than insignificant connections. There is only one participant from the typical STMC group

Table 4. Connectivity values between nodes in typical STMC subjects. Self-connections are represented by CUN – CUN, LCE – LCE, LLG – LLG and LTH – LTH.

	CUN-CUN	LCE-CUN	LLG-CUN	LTH-CUN	CUN-LCE	LCE-LCE	LLG-LCE	LTH-LCE	CUN-LLG	LCE-LLG	LLG-LLG	LTH-LLG	CUN-LTH	LCE-LTH	LLG-LTH	LTH-LTH
subject_001	−0.1285	−0.5664	0.6246	−0.5937	***0.0438***	***0.1002***	−0.5575	0.6718	−0.3603	***−0.0292***	***−0.1172***	−0.4658	0.2362	−0.2959	−0.4984	***0.0125***
subject_002	−0.0835	***−0.0300***	1.3053	−0.9158	0.0491	0.7568	−0.0912	−0.1257	−0.0922	−0.1493	***−0.0791***	−1.2205	0.3061	0.1548	−0.1069	***−0.0367***
subject_004	***0.0341***	−0.914	1.0572	0.2593	0.3046	−0.3566	−0.1345	0.2952	−0.0645	−1.1243	0.3007	0.2976	0.0623	−0.808	0.1595	0.4884
subject_005	0.1808	−0.8003	0.8011	***0.0775***	0.3773	−0.6034	***0.0401***	***0.0618***	***0.0322***	−1.3823	−0.1336	0.1504	0.1481	−0.4219	−0.1550	0.5506
subject_006	−0.2466	−0.1082	1.0076	−0.1765	−0.0461	0.3593	−0.0953	−0.8041	−0.3957	−0.6437	−0.5750	−0.1922	***0.0129***	0.7709	−0.3312	−0.2572
subject_007	0.313	−0.0631	0.6873	0.1584	0.2266	***−0.0926***	−0.9803	−0.6032	−0.3325	0.2409	−0.4035	0.3223	***0.0033***	0.4455	***−0.0168***	0.4120
subject_012	0.3376	0.3074	0.2161	−0.2418	−0.3387	−0.1954	−1.1722	−0.2626	0.8277	0.2817	−0.3954	***−0.0253***	0.129	***−0.0084***	0.2644	0.4593
subject_013	−0.1082	0.1126	0.0888	***0.0052***	***0.0034***	−1.1327	−0.2067	0.7325	−0.4078	−0.2541	−0.9253	−0.3657	0.0543	−0.8398	0.1528	−0.2854
subject_016	***0.0400***	−0.8966	***0.0949***	−0.5942	0.2335	−0.2221	0.2125	0.7678	0.2279	−0.5186	0.5075	−0.6627	0.2703	0.6192	0.3488	***−0.0453***
subject_021	***0.0079***	−0.9874	0.8040	***0.0695***	0.3667	−0.6193	−0.0942	0.0960	−0.1387	−1.1382	−0.2809	0.2451	0.2681	−0.5913	−0.2682	0.3871
subject_022	***0.0355***	−0.8197	0.6059	0.4774	0.4799	−0.4910	−0.0556	***−0.013***	***0.0540***	−0.9028	0.3815	0.1817	***0.0592***	−0.9902	−0.2301	0.1042
subject_025	0.1683	***−0.0816***	0.3656	0.2752	0.2017	0.1821	0.2126	0.1778	0.5153	0.4241	***−0.1184***	0.2511	−0.7619	−0.8942	−1.0498	−0.4021
subject_026	−0.4482	−0.2719	0.4751	−0.2769	−0.1101	−0.5356	0.5308	0.2779	−0.1027	−0.2531	−0.3819	0.2350	0.259	−0.4471	−0.2873	−0.5344
subject_028	−0.5309	−0.4501	0.2273	−0.7857	0.5959	***0.0782***	−0.9781	−0.3014	−0.0984	0.3185	−0.3555	−0.2547	0.1932	0.2466	0.2215	***−0.0900***
subject_029	***−0.0322***	0.4528	0.1143	−0.1077	0.3444	−0.3002	−0.1828	−0.7599	−0.0894	−0.8241	***0.0994***	***−0.0565***	0.2398	0.8038	−0.5420	0.1053
subject_032	***−0.0304***	−0.8010	1.0291	***−0.0097***	0.3630	−0.3211	−0.1263	0.2497	−0.1533	−1.3694	***−0.0026***	−0.2436	***0.0151***	−0.1903	0.1009	0.6149
subject_034	−0.1614	***0.0800***	0.9993	−0.9875	−0.0754	0.8558	0.1509	0.2304	−0.1238	−0.2422	−0.2067	−1.3967	0.3031	−0.1894	−0.0790	***−0.1134***
subject_036	−0.3749	−1.1806	0.2639	***0.0002***	0.2942	−0.3076	***0.0134***	0.4557	−0.2905	−0.3583	0.1450	0.3110	0.5491	−0.5471	−1.1031	***−0.0541***
subject_037	***−0.0713***	−0.9141	0.5174	0.2357	0.5576	−0.2310	−0.3222	−0.1427	−0.0704	−0.5392	0.5281	0.3954	−0.2278	−0.4735	−0.4659	−0.5410
subject_039	0.1881	***0.0347***	0.3378	0.5758	−0.1718	−0.3239	−0.3723	−0.2245	***−0.0010***	0.5429	−0.2941	0.2228	−0.1772	0.7825	0.5349	−0.6466
AVG	−0.4495	−0.2072	0.5090	0.0638	0.0503	−1.0592	0.0377	−0.0204	−0.2127	0.0807	−0.8995	0.0187	0.0213	−0.0552	−0.0056	−0.7445

Insignificant connections are in italic-bold.
CUN = Cuneus, LTH = Left thalamus, LLG = Left lingual gyrus, LCE = Left cerebellum.

Table 5. Connectivity values between nodes in low STMC subjects. Self-connections are represented by CUN – CUN, LCE – LCE, LLG – LLG and LTH – LTH.

	CUN-CUN	LCE-CUN	LLG-CUN	LTH-CUN	CUN-LCE	LCE-LCE	LLG-LCE	LTH-LCE	CUN-LLG	LCE-LLG	LLG-LLG	LTH-LLG	CUN-LTH	LCE-LTH	LLG-LTH	LTH-LTH
subject_003	−0.5516	−1.3670	0.0191	0.0279	***0.0102***	−0.4194	0.4694	0.7172	0.2462	−0.2079	0.6588	***−0.0184***	0.2961	−0.3052	***0.0360***	0.2291
subject_008	0.1026	−0.7548	0.5394	0.3781	0.3369	−0.7074	0.0554	***−0.0017***	−0.0675	−1.4129	***−0.0471***	***0.0355***	−0.1332	−0.3807	0.3379	0.3357
subject_009	0.1105	***−0.0667***	0.7983	0.7378	−0.0297	0.8427	−0.1238	−0.1676	−0.2175	−0.1172	−0.406	1.3336	−0.3518	***0.0048***	***−0.0094***	−0.6328
subject_010	0.1990	−0.8022	0.8080	0.2269	0.4184	−0.3465	−0.3309	0.3585	−0.3424	−1.4069	−0.3805	0.2034	−0.1631	−0.7487	***0.0294***	0.3680
subject_011	−0.1714	1.0287	0.4367	0.7874	−0.4020	−0.7126	0.1861	0.0885	−0.1090	***0.0326***	0.5360	0.3957	−0.0605	1.1459	***−0.4455***	0.3025
subject_014	−0.4550	−1.8307	0.4731	−0.4699	−0.0308	−1.0246	0.8070	0.3757	0.0927	−0.5121	0.2613	***0.0242***	0.3833	−0.2441	−0.4273	0.1850
subject_015	0.2729	−0.7328	0.2671	−0.5625	0.5251	−0.3235	***0.0591***	0.6177	0.1402	−0.7917	0.3243	−0.4894	0.2919	0.7513	0.2758	0.1994
subject_017	−0.1583	−0.8106	0.8884	0.5702	0.2517	***0.0281***	−0.7756	0.1109	−0.3837	***−0.0334***	−0.3029	0.2058	−0.1068	−0.9600	0.3332	0.1152
subject_018	−0.3020	−1.4792	***0.0023***	0.2420	−0.0980	−0.3439	0.5615	0.7692	0.3196	−0.7452	0.4972	***−0.0291***	0.1362	−0.3993	0.1473	0.2911
subject_019	0.0712	−0.7488	0.9480	0.4100	0.2533	***−0.023***	−0.0966	0.2216	−0.1306	−1.2562	−0.1980	***0.0631***	***0.0262***	−0.7252	0.4003	0.1814
subject_020	0.1452	0.2166	1.2317	0.5502	−0.0068	0.8441	0.1459	0.4114	−0.3397	−0.3397	−0.7355	−0.0338	***0.0086***	−0.5984	0.1070	0.0729
subject_023	−0.4703	−0.2943	0.5538	−0.0142	0.0429	0.4214	0.0933	0.2548	−0.0099	−0.1861	−0.0551	−0.5086	0.2011	0.2031	−0.1871	−0.4486
subject_024	0.2675	***−0.0524***	0.5666	−0.4690	−0.0695	0.2271	−0.4523	0.2170	−0.4560	0.3750	***−0.1176***	−0.7048	0.5276	−0.4094	−0.6354	−0.1487
subject_027	0.2763	−0.2526	***−0.0493***	0.1203	***0.0303***	***−0.0287***	0.2447	0.3108	0.3422	0.1920	0.4714	0.1579	−0.1214	−0.5883	−0.3183	***−0.0052***
subject_030	***0.0337***	−0.8709	0.6294	0.6054	0.4279	−0.3252	−0.1751	**0.0467**	***−0.0199***	−0.808	0.4042	0.0855	−0.1009	−1.1346	0.3542	***0.0148***
subject_031	−0.2343	***0.0181***	0.8055	***0.0116***	0.2048	−0.1294	0.1766	−0.3456	−0.1464	0.1399	−0.7085	−0.7898	0.0953	0.9375	0.2352	−0.1583
subject_033	−0.4098	0.2125	1.0273	−0.8726	−0.0555	0.4783	***0.0806***	***−0.0078***	−0.0416	***0.0819***	−0.1754	−0.8886	0.4138	−0.0918	***−0.0524***	−0.1763
subject_035	0.2331	0.3640	1.1185	0.9134	−0.1096	0.7986	−0.1663	0.2220	−0.1629	0.5261	***−0.0177***	0.9674	−0.4258	0.6254	0.2171	−0.2849
subject_040	−0.1332	−0.4965	1.1652	0.1398	0.2130	***0.0091***	***0.0392***	***−0.0425***	−0.2034	−1.3791	−0.5433	−0.2241	−0.0212	***0.0608***	0.3202	0.5554
AVG	−0.3067	−0.2082	0.8564	0.1542	0.0180	−0.4914	0.0300	0.1197	−0.1846	−0.3345	−1.6624	−0.0556	0.0476	0.1346	0.0007	−0.3118

Insignificant connections are in italic-bold.
CUN = Cuneus, LTH = Left thalamus, LLG = Left lingual gyrus, LCE = Left cerebellum.

(subject_026) and one participant from the low STMC group (subject_023) that has all connections significant.

The average connectivity values for typical and low STMC groups obtained from BMA (see the bottom row of Tables 4 and 5) are all significant. All the self-connections in both groups are negative. For the typical STMC group, 5 intrinsic connections are negatives and 7 connections are positives. For the low STMC group, 4 intrinsic connections are negative while 8 are positive. Excluding self-connections, it can be said that there are more positive connections than negative connections in both groups. Similarly, both the typical and low STMC groups is not so different in the ratio of positive and negative connections. Thus, this small differences is insufficient for a conclusion to be made on the preference of each group for negative or positive connection. Figures 6 and 7 show the full-connected model for both groups which were constructed based on the average values shown in Tables 4 and 5.

Figure 8 shows a reduced connection model for the typical STMC group while Figure 9 represents the low STMC group. A reduced model is a model with connectivity values between nodes equal to or larger than 0.1 while connections with connectivity values smaller than 0.1 are considered trivial. The cutoff used in this study to exclude trivial connections is larger than that reported by Razi et al. (2015) which was 0.05. It is assumed that a higher threshold is suitable in this study due to data inhomogeneity caused by the small number of participants. By implementing this threshold, the difference in connectivity structure between typical and low STMC groups becomes obvious. While the typical STMC group exhibits only 3 significant connections, the low STMC group has more significant intrinsic connections which are 7. All self-connections in both groups survived the threshold.

Discussion

Neuropsychological assessment

As shown in Table 2, performance in both groups across the five trials (trials A1 to A5) indicated an increase in the number of recalled words. The differences in average scores between groups on each of the five trials were statistically significant ($p < 0.05$). These results indicate that participants in typical STMC were able to maintain, on average, three more words during the first trial and four additional words during the last trial as compared with participants in the low STMC group. Normative data from previous studies (Jamaluddin et al., 2009) suggest that healthy young adults (age range 20 to 39 years) typically recall six to seven words in trial A1 and twelve to thirteen words in trial A5, consistent with the results for the typical STMC group.

The increase in recalled words from trial A1 to A5 reflects auditory verbal learning capacity (Mitrushina et al.,

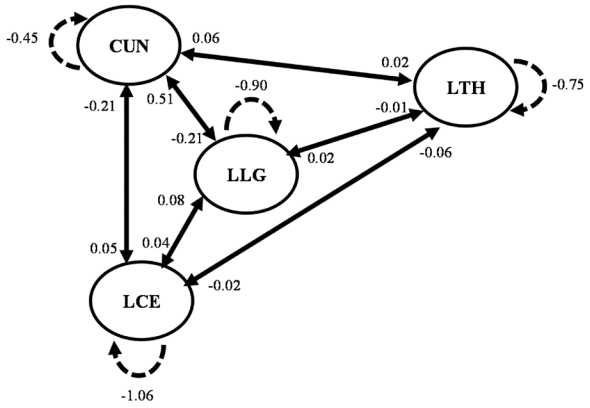

Figure 6. Full connectivity model for typical STMC group.

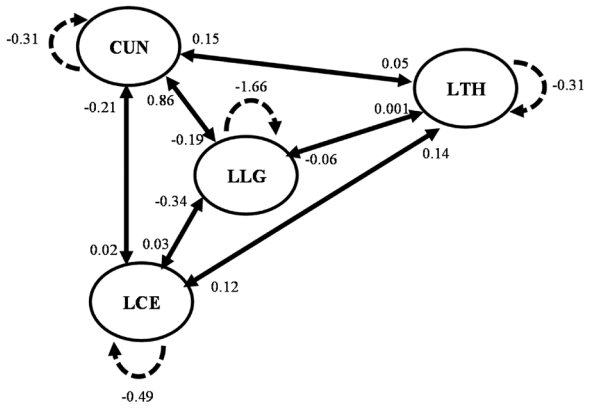

Figure 7. Full connectivity model for low STMC group.

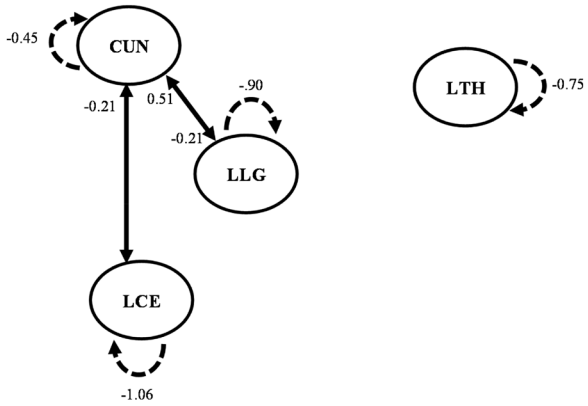

Figure 8. Reduced connection model for typical STMC group.

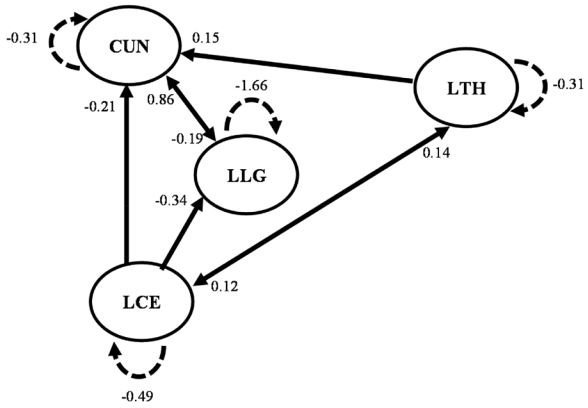

Figure 9. Reduced connection model for low STMC group.

1991; Vakil & Blachstein, 1993), with higher scores indicating stronger learning ability. The results in Table 2 show that the average score from trials A1 to A5 increases in both groups. The participants involved in this study were sampled from a healthy population and it has been shown that healthy individuals have a good ability to learn new things, although this capability decreases as age increases (Nemeth et al., 2013). On the contrary, individuals who have been clinically diagnosed with dyslexia or attention-deficit hyperactivity disorder (ADHD) have demonstrated learning deficits (Alt et al., 2017; Pedersen & Ohrmann, 2018). Our results indicate that despite STMC differences, healthy adolescents possess adequate learning capabilities.

There are several notable differences between typical and low STMC groups. First, the typical STMC group showed a higher learning rate than the low STMC group. The learning rate, which reflects an individual's learning ability, is measured by deducting the score obtained in trial A1 from that achieved in trial A5 (Vakil & Blachstein, 1993). The results in Table 2 show that the learning rate for the typical STMC group was 4.30 (12.10–7.80), whereas the learning rate for the low STMC group was 3.40 (8.00–4.60). These results indicate that the typical STMC participants were able to learn more words than the low STMC participants. A plausible explanation for these differences is that a typical STMC participant has a larger mental storage capacity than a low STMC participant. This advantage allows an individual with a larger STMC to maintain more verbal information in their minds (Vellage et al., 2019). Additionally, an individual with low STMC is weaker at keeping information in mind (Unsworth & Engle, 2007).

Secondly, the typical STMC group showed a remarkable improvement in the amount of learning as compared with the low STMC group. The amount of learning, which reflects an individual's capacity to maintain and retrieve words across trials, is measured by adding the scores obtained in trial A1 to A5 (Mitrushina et al., 1991; Vakil & Blachstein, 1993). Thus, the total score measures the STMC (Van der Elst et al., 2005). The results in Table 2 show that the accumulative score for the typical STMC group was 49 out of 75. The accumulative score for the low STMC group, on the other hand, was only 31 out of 75. These results also indicated that typical STMC participants were able to maintain and recall, on average, 18 additional words than the low STMC participants across trials A1 to A5. This finding supports, rather than contradicts, previous studies suggesting that low STMC participants are less capable of maintaining and retrieving verbal information (Oztekin & McElree, 2010; Unsworth & Engle, 2007).

It is important to note that the remaining trials were not conducted to classify participants into the two different groups of STMC. Those trials were, however, undertaken to identify other cognitive differences that may exist between the groups. The B1 trial was used to assess rates of proactive interference (Magalhães & Hamdan, 2010). Proactive interference refers to the finding that previously learned information could impair the memory of more recently learned information (Nicenboim et al., 2015). Proactive interference can be observed when participants' recall of words in list B is affected by the words presented previously in list A. The rate of proactive interference was calculated by dividing the score obtained in trial B1 by the score obtained in trial A1 (B1/A1) (Magalhães & Hamdan, 2010). The rate of interference represents susceptibility to previous activity. If the interference ratio is less than 1, an interference effect is demonstrated. But if the ratio is equal to 1, no interference effect is observed. The rate of proactive interference for typical and low STMC groups was 1.13 and 1.18, respectively. This indicates that both groups were not affected by proactive interference.

The A6 (immediate recall) trial measured an individual's ability to perform task-specific goals in the presence of retroactive interference (Magalhães & Hamdan, 2010). Retroactive interference refers to the finding that recently learned information could impair the memory of previously learned information (Brawn et al., 2018). During this trial, words from list B served as the retroactive interference. The results in Table 2 showed that participants in the typical STMC group were able to correctly recall approximately four words more than participants in the low STMC group in the presence of interference. These suggest that, in addition to having a larger mental storage capacity, typical STMC participants may also have a better ability to suppress interference (Pettigrew & Martin, 2016). Additionally, these findings support the view that items stored in the minds of low STMC participants are more likely to be displaced by interferences (Lilienthal et al., 2015; Oztekin & McElree, 2010; Tehan et al., 2018).

Trial A7 (delayed recall) measured an individual's ability to retain information previously learned (Vakil et al., 1998) and therefore, reflects short-term memory (Vakil & Blachstein, 1993). The results in Table 2 show that the typical STMC group was able to maintain an additional four words after a 20-minute delay compared with the low STMC group. This may suggest that participants with typical STMC have a better capability to retain information in the working memory. Looking from another perspective, this may also indicate that newly acquired information decays rapidly for the low STMC participants. However, this is a highly speculative conjecture, and additional investigation is warranted to confirm this perspective.

Finally, the recognition trial represents a storage factor and reflects the amount of information stored in memory (Vakil & Blachstein, 1993). The recognition trial measures recognition memory, that is the ability to recognize events (e.g., words) that have been previously encountered (Malmberg, 2008). Table 2 shows that the typical STMC group has a better recognition memory than the low STMC group. This suggests that low STMC individuals may not only have a reduced mental storage capacity but also a diminished ability to recognize previously learned items (Shen et al., 2018).

Overall, STMC significantly influenced neuropsychological performance in healthy adolescents, as measured by the MVAVLT. Typical STMC participants consistently outperformed their low STMC counterparts across trials, showing greater learning rates, better resistance to interference, and superior delayed recall and recognition abilities. These findings align with previous research indicating that low STMC

is associated with limitations in verbal information maintenance and retrieval (Oztekin & McElree, 2010; Unsworth & Engle, 2007), providing further evidence of the cognitive differences associated with varying STMC levels.

Resting-state differential brain activation

Resting-state fMRI has been successfully implemented to compare brain activation between typical and low creative groups (Beaty et al., 2014) and connectivity models of network structure (Di & Biswal, 2014a; 2014b) within a group of participants. In addition, altered brain activation in multiple brain regions in terms of the amplitude of low-frequency fluctuation (ALFF) and percent amplitude of fluctuation (PerAF) was observed in inactive patients with non-neuropsychiatric systemic lupus erythematosus (NPSLE) (Yu et al., 2019) as compared with healthy participants. The absence of differential brain activation between typical STMC and low STMC groups at a corrected (FWE) significant level of 0.05 found in this study indicates that each group's activation has little difference from each other, hence incomparable at a high cutoff. The difference however turns comparable when the statistical threshold is lowered down to an uncorrected significant level of 0.001, but only to reveal differential activation from contrast low STMC group > typical STMC group. Thus, the activated areas; LLG, LTH, RMTG, CUN, LSFG, LTMP, LPCU, and LCE are the resting brain areas that are more active in the low STMC brain than in the typical STMC brain. The functions of these brain areas have been summarized in our previous work (Gafoor et al., 2021). These findings from differential brain activation are correlated to the percentage of amplitude fluctuation (PerAF) results obtained from that study. It was found that PerAF for the eight activated areas was also higher in the low STMC group than in the typical STMC group (Gafoor et al., 2021). Thus, it can be summarized that the low STMC participants show a higher resting-state spatial and height extent of activation as compared with typical STMC participants despite having many neuropsychological disadvantages as discussed in the previous paragraphs. Concerning previous studies (Raichle, 2011; Wang et al., 2019), it can be clarified that the four among the eight activated areas in this study that have been found significant at the peak, cluster and set levels, i.e., LLG, LTH, CUN, and LCE are all DMN areas.

Instead of using a corrected significant level, the uncorrected significant level was used in the differential analysis for several reasons. Firstly, the participants from both groups were equally healthy. Thus, it can be said that the brain functions in the resting state for both low and typical STMC groups were equally working at an optimum level resulting in a relatively small difference in the group activation. Hence an undetectable brain activation difference at a corrected significant level. But with the results of neuropsychological assessments that show a significantly higher scores for typical STMC participants, it was initially thought that the results could still be related to the resting-state brain activation difference but at a less conservative threshold ($p < 0.001$ uncorrected). The activation shown in Figures 4 and 5 strongly supports this argument with significant uncorrected activation areas were only observable for contrast Low STMC > Typical STMC. Secondly, the activation areas were found to be related to the areas of the default mode network (DMN) indicating the specificity of the results. Thirdly, even though the differential brain activation reported in Figure 5 were obtained at an uncorrected significant level, they were significant at peak, cluster and set levels.

The differential brain activation results described above show that the human brain of different STMC possesses a slight difference in resting brain activity. The difference may be explained by the understanding that to maintain an equilibrium condition at rest, participants in the low STMC group would generally have a higher neural activity or enhanced cerebral alertness level and consume more energy, especially in the DMN regions (Di & Biswal, 2014a) than those in typical STMC group. In a study that investigated the effects of background noise on arithmetic performance (Proverbio et al., 2018), it was found that the introverted group of participants had a higher arousal level compared with extroverts. Thus, it is thought that this should also be true for a resting brain even though the findings by Proverbio et al. (2018) were gathered from a task-based MRI study. Further analyses provide evidence that the significantly activated areas are mostly located in the left hemisphere as opposed to the previous study (Di & Biswal, 2014a) that found the dominance of right-hemisphere endogenous connectivity among the participants. Current findings however support our previous studies that suggested the correlation of left-hemisphere alteration in brain activation with AWM processing (Othman et al., 2020b). In another report, increased activity of the pre-frontal cortex (PFC) and left hemispheric lateralization for auditory-verbal processing in no-task conditions suggest inefficient brain organization in low STMC participants (Daneman & Carpenter, 1980).

In summary, STMC differences among healthy adolescents are associated with significant changes in resting-state spatial and height extent of brain activation. This increased activation in the low STMC group may reflect compensatory mechanisms but appears negatively correlated with neuropsychological performance, highlighting the impact of STMC on resting-state brain function.

Resting-state EC

From the results of individual DCM for both groups of participants, the more significant connections for any one participant and the more participants showing significant connections for any one connection reflect the suitability of the full-connected model as the generative model that generates the resting-state data. This is further supported by the results from BPA that show that the average of all connections are significant for both groups. The full-connected model that comprised LLG, LTH, CUN, and LCE as DMN nodes seemed suitable to represent parts of the intrinsic architecture of the resting brain in the absence of experimental exogenous input, at least in the context of this work.

A connection between nodes is usually weighted, directed, and excited/inhibited (Razi et al., 2017). Weighting represents the strength of a connection while direction is related to causal. Negative connection is understood as inhibitory while positive connection is excitatory. The preference toward negative or positive connections among the typical and low STMC groups may suggest another possible brain characteristic that may be useful in differentiating between individuals with different STMC capacity or individuals with brain disorders and illnesses.

In a previous study on university students with and without creativity training, it was found that most connections between the activated regions in a resting brain are excitatory in the untrained group whereas for the trained group, there are equal numbers of excitatory and inhibitory connections with a symmetrical distribution (Abdul Hamid et al., 2023). Taken together, it can be postulated that the human brain contains systems of network in which excitatory and inhibitory connections within the network must reach a certain ratio to keep the network system in equilibrium. It is well known that in a balanced brain, the relative percentage of inhibitory neurons is much smaller than excitatory neurons (Kajiwara et al., 2021), e.g., 15–30% of inhibitory neurons are needed to maintain stable dynamics (Sukenik et al., 2021).

However, in this work, both the typical and low STMC groups did not show any preference toward excitatory (positive) or inhibitory (negative) connections, i.e., 8 +ve vs. 8 -ve for low STMC group and 7 +ve vs. 9 -ve for typical STMC group, out of the 16 connections being investigated (including all 4 self-connections that took a negative value). As far as the fully connected model is concerned (see Figures 8 and 9), both groups preferred a balanced distribution of positive and negative connections in the brain when it is at rest. This showed that STMC capacity did not influence the preference toward positive or negative connections of the model network under study as for the preference for inhibitory and excitatory neurons by the brain to achieve an equilibrium state (Sukenik et al., 2021).

A reduced-connection model excludes trivial connections based on the connectivity values. It is a way of thresholding the connections so that model for each group contains not only significant connections but also connections with a higher rate (in Hz) of communication between nodes. This cutoff was proposed due to the nature of an rs-fMRI data analysis that relies on the inconsistent fluctuation of activity in each node. The endogenous fluctuations from any two nodes were later cross-correlated to obtain a connectivity value. This means, by setting a threshold of equal or larger than 0.1 for a connectivity value to be acceptable, extremely low connectivity values with significant probability can be controlled and the optimum connectivity model for low and typical groups can be differentiated. The reduced-connection model is less complex than the full-connection model and it appears to be less complex for the typical STMC group with the low STMC group having more significant connections. This is parallel to the previous discussion on brain activation that the low STMC participants showed higher neural activity for the eight selected regions. The findings from brain activation, PerAF, and EC have clearly shown an agreement between each other. It can thus be suggested that higher brain spatial and height extent of resting-state activation in a region may influence the EC between two or more regions.

To summarize, we found evidence of significant changes in neuropsychological behaviors, resting-state brain activation, and resting-state brain EC due to the difference in STMC among healthy young adults. From the perspective of brain functional specialization and integration (Friston, 2004), it is believed that these changes are related to one another and can be triangulated to give more meaningful insights which could be the focus of future works. The current experimental findings on neuropsychological behavior, brain activation, and brain EC of a resting brain could be used to explain the uniqueness of human behavior in healthy, disordered, and deceased brains, perhaps by implementing the concept of personalized medicine to assist in the diagnosis of a disease. This study has three limitations. First, differential brain activation was only significant at an uncorrected threshold, reflecting relatively small between-group differences. However, the results were significant at the set and cluster levels. Second, the fully connected model emerged as the best fit for both groups, indicating its robustness despite the added complexity. Perhaps, future studies should compare the fully connected model tested in the present work with a model that contains connections between nodes that are gated by the activity in each node. Third, summarized on the reduced model concept that is weak.

Conclusion

In conclusion, typical and low STMC participants have been found to differ in their STMC based on their performance in their neuropsychological assessments. Typical STMC participants scored higher in all of the assessment components. The differences between the two groups were also observed for spatial (NAV) extent of brain activation particularly in LLG, LTH, RMTG, CUN, LSFG, LTMP, LPCU, and LCE areas. The MVAVLT scores achieved by both groups were negatively correlated with the NAV from which the low STMC group saw resting-state NAV that were significantly higher than the typical STMC group which were in good agreement with PerAF obtained in our previous study for the eight regions mentioned above. This reciprocity behavior showed by the NAV and PerAF could be caused by higher neural activity and alertness levels in the low STMC brain to achieve equilibrium at rest. In addition, supporting evidence was obtained from DCM analysis. The EC between nodes of significant differential analysis of activation particularly LLG, LTH, CUN, and LCE are all significant when specified as a full connectivity model. However, when the model of reduced connection was considered, the low STMC group showed more significant connections between the four nodes as compared with the typical STMC group. This again supports the argument mentioned earlier about the neural activity and alertness level of low STMC individuals. These

results suggest that individuals with lower STMC may experience higher neural activity and alertness levels at rest, possibly due to reduced neural adaptability and less efficient brain organization. The combined use of SPM and DCM effectively characterized and differentiated the brain activation and EC patterns of typical and low STMC groups. Overall, the low STMC group performed poorly in neuropsychological assessment, displayed a higher activation profile and a greater number of effective connections across regions, indicating a unique neurological behavior associated with reduced STMC.

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The authors report there are no competing interests to declare.

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Data availability statement

The data that support the findings of this study are not openly available due to reasons of sensitivity and are available from the corresponding author upon reasonable request.

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