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Hippocampal-Cerebellar involvement in enhancement of performance in word-based BRT with the presence of background noise: an initial fMRI study

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Abstract

Background noise may impose deleterious effects on cognitive processing. However, noise below the threshold level may increase the ability to detect stimuli via stochastic resonance mechanisms (SR). The present study investigates whether task performance is deteriorated or enhanced by 5-dB SNR and, if the task performance is enhanced, whether this facilitation in performance points to a particular neural area that serves to attenuate noise and/or increase effective task performance. The areas of interest are the cerebellum and hippocampus due to their roles in working memory (WM) and their links with attention. Fifteen healthy young Malay adults performed three tasks during fMRI scanning: listening to babble noise (N), WM task in quiet (WMQ), and WM task in noise (WMN). Activated regions during N are bilateral STG and MTG. Both WM tasks produced similar activation in a network of areas in the frontal, temporal and parietal lobes. However, the two tasks demonstrated marked differences in the left hippocampus, right posterior cerebellum, and bilateral anterior cerebellum. Moreover, the results obtained from the behavioral task demonstrated that participants responded better in the presence of noise. These results support the hypothesis that the left hippocampus, right posterior cerebellum, and bilateral anterior cerebellum may be involved in attenuating noise and/or increasing attention to task performance, which could be due to SR mechanisms operating in the presence of noise. These results collectively suggest leftward asymmetries during the tasks with the right posterior cerebellum, bilateral anterior cerebellum, and left hippocampus providing compensatory attention processes, at least in the context of this study.

Keywords: fMRI, phonological working memory, cerebellum, hippocampus, stochastic resonance mechanism.

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Introduction

Cognitive processing is easily disturbed by incompatible environmental stimulation, which distracts attention from the main tasks. This is assumed to be due to the competition for attentional resources between the distracting (noise) and the target stimuli (Soderlund et al., 2010). Noise is typically conceived as being detrimental to the complex cognitive performance and

the negative effects of noise on cognitive processing especially in attention, working memory (WM), and language have been established by many researchers (Dos Santos Sequeira, Specht, Hamalainen, & Hugdahl, 2008; Kozou et al., 2005). It is also known that different types of background noise affect cognitive performance in different ways. For example, background noise in meaningful word-based contexts (e.g., babble noise and cocktail party noise) is more detrimental than other types of background noise (e.g., traffic, aircraft and highway) (Kujala & Brattico, 2009; Sorqvist, 2010).

However, there are reports of contradictory findings where moderate amounts of auditory noise will improve the cognitive performance. A recent computational model is based on the concepts of stochastic resonance (SR), postulating that noise can enhance the detectability of an input signal (Moss, Ward, & Sannita, 2004; Rousseau & Chapeau-Blondeau, 2004; Yamamoto et al., 2002). SR is a proposed mechanism where the presence of random interference (moderate auditory noise) up to a finite level of intensity enhances sensitivity to external stimuli by increasing attention (Yamamoto et al., 2002). Enhancement

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to the detection level is postulated to be due to the system resonating at a particular noise level (Rousseau & Chapeau-Blondeau, 2004). Previous studies have reported that the human central nervous system is able to utilize the noise-enhanced sensory information so that the sensitivity of sensory neurons on weak signals is optimized by adding noise (Yamamoto et al., 2002). However, noise beyond the optimal level may decrease the detectability of information or stimuli (Moss et al., 2004).

The present investigation focuses on the cerebellum and hippocampus due to their known associations with attention during cognitive processing (Alexander, Gillingham, Schweizer, & Stuss, 2011; Marvel & Desmond, 2010; Bledsoe, Semrud-Clikeman, & Pliszka, 2009; Teder-Salejari, Pierce, Courchesne, & Hillyard, 2005; Kujala et al., 2004; Gottwald, Mihajlovic, Wild, & Mehdorn, 2003). In order to assess cognitive performance and interference of background noise in the present study, a word-based backward repeat span task (word-based BRT) was used. This task was adapted from Light & Anderson (1985) and was designed to investigate WM capacity (Morra, 1994; Henry & Millar, 1991). A word-based instead of digit-based task was chosen because of the known roles of speech processing in WM (Light & Anderson, 1985; Baddeley, 1992, 2003a,b). The use of word-based stimuli also enabled us to standardize the number of syllables used, given that syllables tend to vary in number across words. This is important due to the fact that the performance of phonological WM may decrease string lengths exceeding a storage capacity limit (Baddeley, 2000; Baddeley, Allen, & Vargha-Khadem, 2010).

As suggested earlier, the deleterious effects of noise on cognitive performance is assumed to be due to inability of individuals to discriminate between noise and target stimuli. The idea of a SR mechanism is relatively new in neurological science, especially in relation to the WM system. Moreover, WM tasks have not been studied in young Malay adults, although their everyday spoken language might be influenced in yet-unknown ways by levels of background noise in the environment. The aim of this study was to identify the areas in the brain that are activated when normal hearing participants are required to listen to babble noise and perform word-based BRTs in quiet and in 5-dB SNR. Our key hypothesis was that if 5-dB SNR is within the range of enhancement effects, we should see (1) better performance in the WM task in noise as compared to in quiet, and (2) evidence of differential subcortical activation on these two conditions, taking into account that with 5-dB SNR, the hippocampus and cerebellum might increase attention, thereby enhancing the speech signals via SR mechanisms as suggested by previous researchers (Moss et al., 2004; Rousseau & Chapeau-Blondeau, 2004). If our level of noise is beyond that which produces enhancement effects, we should see (1) interference on the WM task in noise as compared to the same task in quiet, and (2) we would infer that a cerebellar/hippocampal-based resonance mechanism is not at play, but rather interference effects might produce increased demands on prefrontal cortical processes.

Materials and methods

Participants

Fifteen right-handed (Oldfield, 1971) Malay male participants with ages ranging from 20 to 29 years (mean age: 27 years, SD 1.60) were recruited to participate. All were native Malay speakers and reported no history of psychiatric or neurological disorders and no current use of any psychoactive medications. From self-report assessment, all participants had normal hearing and no history of long-time exposure to loud noises. After full explanation of the nature and risks of the study, informed consent was obtained according to the protocols approved by the Institutional Ethics Committee (IEC) of Universiti Kebangsaan Malaysia. (Reference no: UKM 1.5.3.5/244/ NN-075-2009).

Data Acquisition

Functional MRI scans were conducted in the Department of Radiology, UKM Medical Centre using a 1.5 tesla magnetic resonance imaging (MRI) system (Siemens Avanto) equipped with functional imaging options and echo planar imaging capabilities. A radiofrequency (RF) head coil was used for signal transmission and reception. Prior to each functional imaging scan, a MRI structural scan was obtained using T1*-weighted multiplanar reconstruction (MPR) spin-echo pulse sequence with the following parameters: TR = 1240 ms, FOV = 250 mm \times 250 mm, flip angle = 90°, matrix size = 128 \times 128, and slice thickness = 1 mm. Functional images were then acquired using a gradient echo-echo planar imaging (GRE-EPI) pulse sequence. Each whole brain acquisition consisted of 21 axial slices covering the whole brain volume including cerebellum. The following parameters were used during the study: acquisition time (TR) = 2 s, echo time (TE) = 50 ms, field of view (FOV) = 192 \times 192 mm, flip angle (α) = 90°, matrix size = 128 \times 128 and slice thickness = 5 mm with 1.25 mm gap. A sparse imaging paradigm was used to avoid the interference of scanner sound with the stimulus (Hall et al., 1999).

Development of Stimulus and Babble Noise

The stimuli consisted of a series of natural speech words produced by a Malay male adult voice and were digitally recorded (Sony digital voice editor), stored and edited (Adobe Audition 2.0) and played with an intensity level of 55 dB. The babble noise stimulus was originally recorded from five volunteers reading difference passages simultaneously and edited so that the intensity level was 50 dB. For the working memory task in noise (WMN), the speech stimuli were embedded within the babble noise. Thus, the signal-to-noise ratio (SNR) of speech information was 5 dB throughout the presentation.

Experimental Paradigm

Auditory stimuli were presented binaurally during the study. There were 120 trials in total with trials of 16-s duration. There were four different conditions: (i) 20

trials of listening to noise (N), (ii) 20 trials of performing the WM task in 5-dB SNR (WMN), (iii) 20 trials of performing the WM task in quiet (WMQ), and (iv) 60 trials of rest with no stimuli, thereafter referred to as quiet (Q). The sequence of conditions was fixed: N-Q-WMN-Q-WMQ-Q-N, because reaction times are faster when using fixed sequences (Hazeltine, 2002). Total scan time was 32 min per participant.

In order to construct an experimental trial for WMQ and WMN conditions, a total of 40 (2-syllable and 3-syllable) verbs and nouns that were unrelated familiar Malay words were randomized, producing 40-trial sets. Five consecutive stimuli each with 0.6-s duration separated by 0.5-s silent gap comprised a 5-s stimulus train. During a trial, the stimuli were presented at the 6th second and lasted approximately 5 s. For WMQ and WMN conditions, participants were given 5 s to repeat backward aloud all the words that were presented. The scans were acquired 5 s after the stimulus and continuously through the recall (retrieval) phase of the WM task.

fMRI and behavioral procedures

Before performing the fMRI scans, instructions about the task were explained in detail to the participants. In order to avoid systematic behavioral confounds, all participants were familiarized with the task using a training program outside of the scanner (containing trials that were identical to those used during scanning). During the fMRI scan, participants were instructed to focus on the tasks given and to remain still. During scanning, participants lay comfortably in a supine position with an adjusted head holder restricting head movement. Auditory stimuli were presented through earphones. During scanning, each individual participant's scores were recorded manually by an experimenter in the console room (i.e., number of correct backward repetition trials).

Data Analysis

Paired *t*-tests were used to analyze behavioral data (in terms of accuracy) on the word-based BRT in quiet and in noise. fMRI data were analyzed using MATLAB 7.4-R2008a (MathWorks Inc., Natick, MA, USA) and Statistical Parametric Mapping (SPM8) (Functional Imaging Laboratory, Wellcome Department of Imaging Neuroscience, Institute of Neurology, University College of London, UK; <http://www.fil.ion.ucl.ac.uk/spm>). The first two volumes of the functional scans were discarded. The functional scans were pre-processed using movement correction, 12-parameter nonlinear normalization into the MNI-reference state as implemented in SPM8, and smoothing (FWHM = 8 mm).

The fMRI data were analyzed according to the general linear model as implemented in SPM8. Three regressors were included in the design: (i) WMQ, (ii) WMN, and (iii) N. The regressors were convolved using the hemodynamic response function. The activated brain regions during the retrieval phase in WM tasks were examined using (i)

WMN, (ii) WMQ, (iii) N, (iv) WMQ > WMN, and (v) WMN > WMQ > N. The contrasts were computed for each participant in the first level fixed effects analysis. Contrast images were then entered into the second level group random-effects analysis. A cortical brain region is regarded as significantly activated only if a minimum cluster size of 10 voxels is reached at $P_{FWEcorr} < 0.001$ (cluster level). All voxels or clusters with *t*-values higher than 3.5 were included in region of interest analysis (ROI) using WFU PickAtlas (Maldjian et al., 2003).

The laterality index (LI) was calculated using the following formula:

$$LI = (V_L - V_R) / (V_L + V_R)$$

where V_L is the number of the activated voxels in the left hemisphere, and V_R is the number of activated voxels in the right hemisphere. LI values could range from -1 to 1, with -1 to 0 indicating right hemisphere dominance and 0 to 1 indicating left hemisphere dominance (Seghier, 2008).

Results

Behavioral scores

Participants scored significantly better (more accurately) during the word-based backward repeat task (word-based BRT) in 5-dB SNR as compared to the same task in quiet (Table 1). This was verified using a paired *t*-test revealing a significant difference between behavioral scores in the word-based BRT in quiet and in noise conditions ($p < 0.027$, $t = -2.475$, $df = 14$).

Table 1. Demographic and performance data obtained from 15 participants

Participants	
N	15
Age (range)	20 – 29
Age (mean ± SD)	27.0 ± 1.6
Years of education (mean ± SD)	14.9 ± 8.1
Word-based BRT (WMQ), accuracy rate (% ± SD)	46.3 ± 30.0
Word-based BRT (WMN), accuracy rate (% ± SD)	53.7 ± 4.2

Abbreviations: WMQ = working memory task in quiet, WMN = working memory task in noise.

fMRI results

Listening to babble noise (N)

Table 2 depicts details of the activation characteristics shown in Figure 1(a) including the number of activated voxels (NOV), coordinates of maximum intensity, *p*-values and the respective areas. Significant activation in bilateral superior temporal gyrus (STG) (left $t = 32.82$, right $t = 22.5$) and middle temporal gyrus (MTG) (left $t = 27.43$, right $t = 12.12$) were observed. Result shows rightward asymmetries in both regions.

Table 2. Anatomical area, brain hemisphere, t-value, coordinates of maximum intensity (x,y,z) and number of activated voxels obtained from group analysis (n = 15, $p < 0.05$) during listening to babble noise (N) minus quiet condition (baseline)

Anatomical Area	Hemisphere	t-value	Coordinate (x, y, z mm)	NOV
STG	R	22.5	62,-10,-2	1829
	L	32.82	-58,-20,4	1649
MTG	R	12.12	68,-34,0	906
	L	27.43	-58,-20,0	861

Abbreviations: NOV = number of activated voxels, STG = superior temporal gyrus, MTG = middle temporal gyrus, L = left, R = right.

Working memory task in quiet (WMQ) and working memory task in noise (WMN)

Comparing between WMQ and WMN conditions, all regions of interest (ROIs) commonly associated with the retrieval phase in WM demonstrate higher BOLD activation in the WMQ condition except bilateral STG (WMQ; left $t = 25.07$, right $t = 22.69$, WMN; left $t = 31.11$, right $t = 24.48$), hippocampus (WMQ; right $t = 4.91$, WMN; left $t = 5.22$, right $t = 5.83$), anterior cerebellum (WMQ; left $t = 8.42$, right $t = 11.82$, WMN; left $t = 9.98$, right $t = 12.08$) and right posterior cerebellum (WMQ; left $t = 5.71$, right $t = 12.47$, WMN; left $t = 5.17$, right $t = 12.75$) as in Table 3, Figure 1(b) and Figure 1(c). The extent of activation in these regions

Table 3. Anatomical area, brain hemisphere, t-value, coordinates of maximum intensity (x,y,z) and number of activated voxels (n = 15, $p < 0.05$) obtained from Working Memory task in Quiet (WMQ) minus quiet (baseline) condition and the Working Memory task in Noise (WMN) minus quiet (baseline)

WMQ minus QUIET					WMN minus QUIET		
Anatomical Area	Hemisphere	t-value	Coordinate (x, y, z mm)	NOV	t-value	Coordinate (x, y, z mm)	NOV
STG	R	22.69	64,14,-4	2109	24.48	64,-14,-4	2114
	L	25.07	-60,-20,2	1839	31.11	-58,-20,2	1871
PCG	R	15.1	50,-6,34	1006	15.9	50,-6,34	971
	L	14.62	-54,-8,30	1311	14.86	-52,-8,30	1280
MTG	R	16.61	64,16,-8	1103	17.09	64,-16,-8	958
	L	24.31	-60,-18,0	1294	29.37	-58,-20,0	1208
Lingual Gyrus	R	7.51	8,-90,-4	115	8.35	10,-82,-14	115
	L	7.33	-8,-86,-16	254	8.94	-8,-86,-16	181
SPL	R	7.44	34,-64,54	235	6.62	34,-64,54	130
	L	9.74	-30,-66,52	445	9.46	-30,-64,50	410
IFG (tri)	R	6.05	42,18,4	141	4.84	42,18,4	8
	L	11.24	-52,16,-2	484	12.96	-52,16,-2	206
MFG	R	9.12	38,42,24	623	8.9	38,42,24	365
	L	8.52	-46,10,36	583	8.55	-34,52,20	523
Precuneus	R	7.65	6,-70,48	208	6.76	6,-68,48	116
	L	7.55	-6,-70,48	346	7.07	-6,-46,72	279
Post-CG	R	17.02	52,-8,30	729	17.91	52,-8,30	669
	L	16.93	-56,-8,24	1279	15.99	-54,-10,26	1166
Hippocampus	R	4.91	16,-28,-8	6	5.83	16,-28,-8	11
	L	—	—	—	5.22	-16,-34,10	33
Anterior Cerebellum	R	11.82	26,-58,-28	314	12.08	22,-60,-26	327
	L	8.42	-30,-58,-30	231	9.98	-32,-58,-32	354
Posterior Cerebellum	R	12.47	26,-62,-28	1714	12.75	24,-62,-28	2088
	L	5.71	-28,-38,-46	12	5.17	-28,-38,-46	11

Abbreviations: WMQ = working memory task in quiet, WMN = working memory task in noise, NOV = number of activated voxels, STG = superior temporal gyrus, MTG = middle temporal gyrus, PCG = precentral gyrus, SPL = superior parietal lobes, IPL = inferior parietal lobes, IFG (tri) = inferior frontal gyrus (triangularis), MFG = middle frontal gyrus, Post-CG = postcentral gyrus, L = left, R = right.

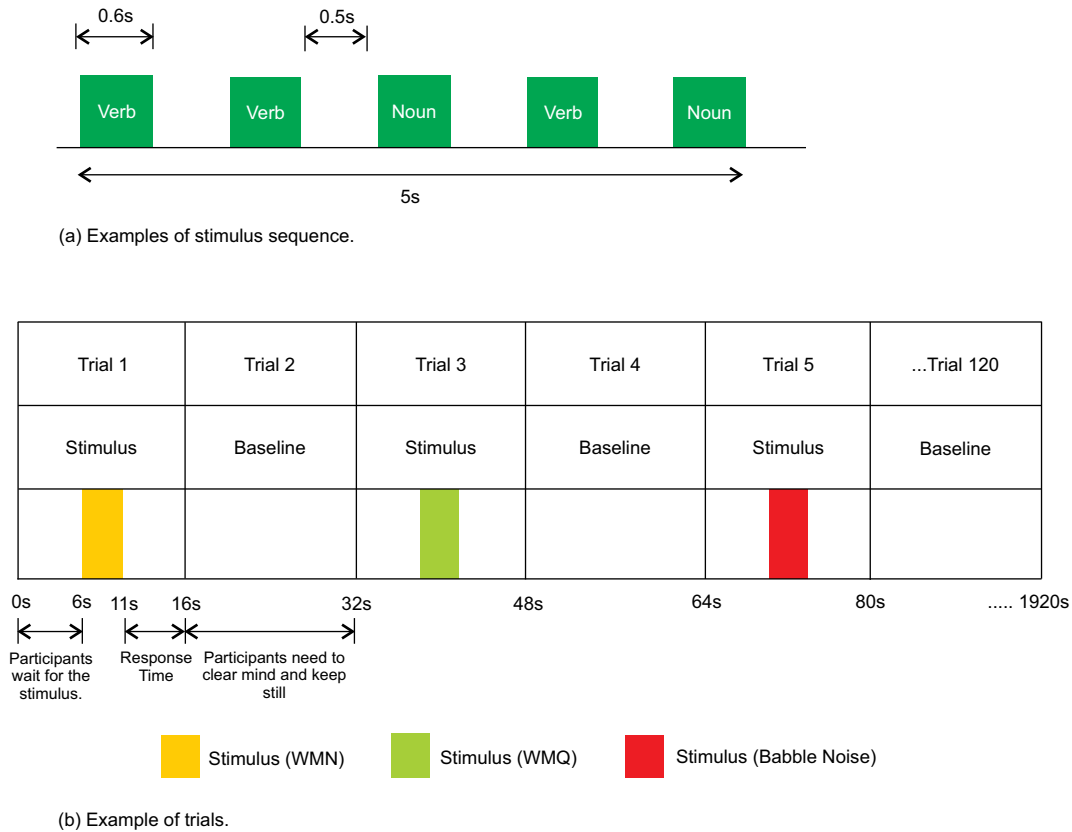


Figure 1. (a) Illustration of stimulus train use in the present study. (b) Illustration depicting sequences of stimulus in four different conditions: WMN; WMQ; Babble Noise; Baseline (Quiet). The sequence of the conditions was fixed; WMN-baseline-WMQ-baseline-Babble Noise-baseline. Total duration of each trial is 16s. During stimulus trials, stimuli were presented at the 6th second, and lasted approximately 5s.

during WMN is further supported by the contrast WMN > WMQ (Table 4, Figure 2(a) and Figure 2(b) and the double subtraction analysis, WMN > WMQ > N (Table 5 and Figure 3). Notably, previous studies using digit

BRT do not report such activation (Zhou et al., 2006; Sun et al., 2005).

Behavioural scores in relation to fMRI results

Correlations between behavioral scores on the WMQ and WMN tasks (separately) and fMRI activation in eight ROIs were examined for both right and left sides of STG, PCG, hippocampus, and cerebellum to assess a possible relationship between behavior and brain activity. Correlations ranged from -0.174 to 0.395 for the WMQ condition and between -0.232 and 0.325 for the WMN condition, but none were statistically significant ($p > 0.05$). In the WMQ condition the correlation shown for the left STG was the highest (0.395) and for the WMN condition the correlation shown for the left cerebellum was the highest (0.325), but even those were not statistically significant.

Discussion

The main purpose of this study was to examine the areas of the brain that are activated in the three listening conditions while focusing on our specific aims of examining whether the 5-dB SNR is within the range to cause enhancement effects through a stochastic resonance (SR) mechanism or beyond the range to produce interference.

Table 4. Anatomical area, brain hemisphere, t-value, coordinates of maximum intensity (x,y,z) and number of activated voxels are obtained from the group analysis ($n = 15$, $p < 0.001$) comparing the Working Memory task in Noise (WMN) minus Working Memory task in Quiet (WMQ) as shown in Figure 3

WMN > WMQ				
Anatomical Area	Hemisphere	t-value	Coordinate (x, y, z mm)	NOV
STG	L	7.01	-54,-22,4	562
Cerebellar Vermis	R	4.53	0,-44,-8	95
STG	R	4.44	50,-20,2	131
Cerebellum	R	3.9	2,-86,-28	22
Cerebellum	L	3.83	-8,-40,-24	22
Cerebellum	R	3.79	10,-38,-22	30
Hippocampus	L	3.62	-12,-36,10	43

Abbreviations: WMQ = working memory task in quiet, WMN = working memory task in noise, NOV = number of activated voxels, STG = superior temporal gyrus, L = left, R = right.

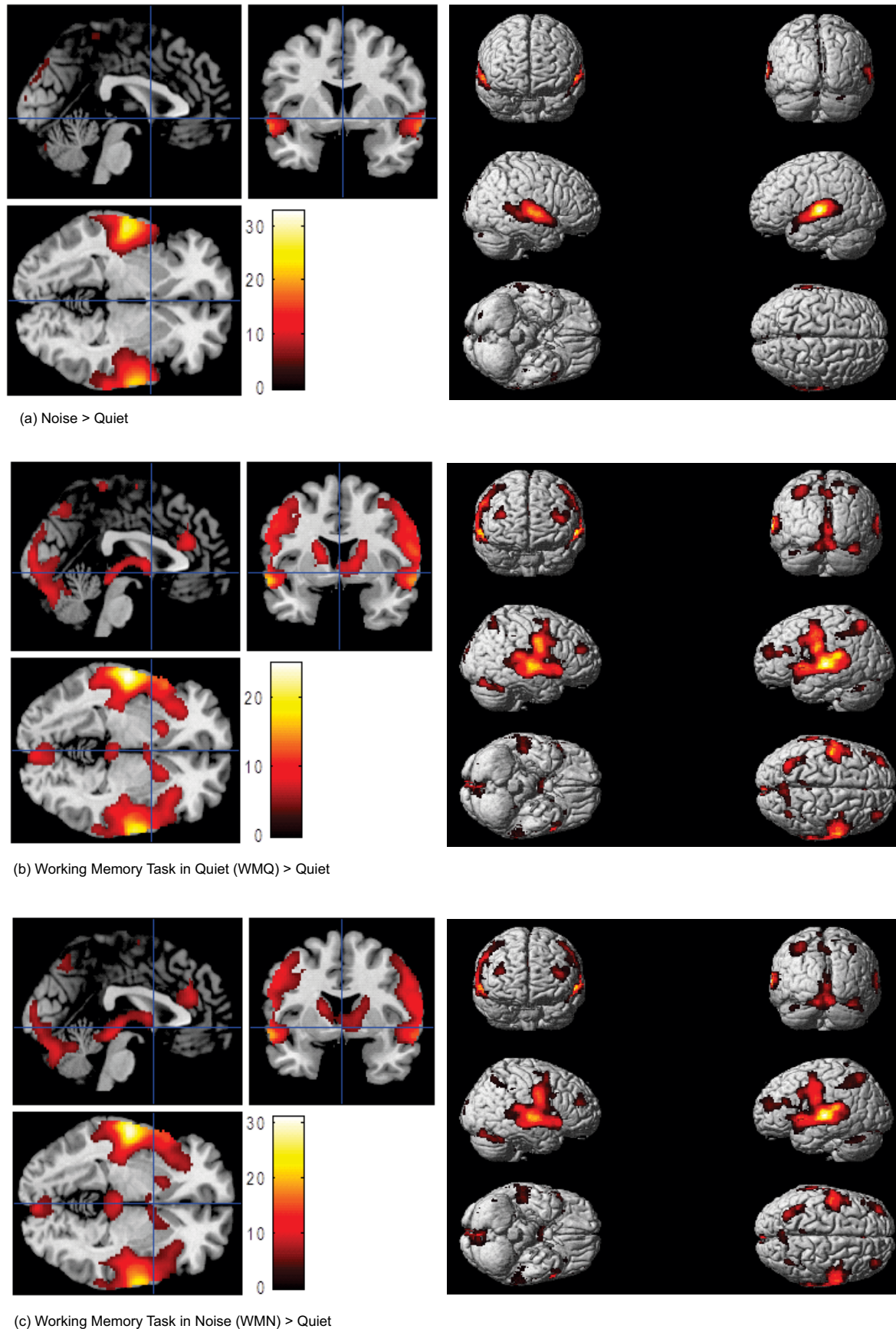


Figure 2. Statistical parametric maps (SPMs) obtain from group analysis ($n = 15$, $p < 0.05$) showing brain activation associated with (a) $N > Q$, (b) $WMQ > Q$ and (c) $WMN > Q$, overlaid onto structural brain images, shown for transverse, sagittal, and coronal slices (left side of figures), and using a whole brain map (right side of figures). The t-values for the activated voxels are scaled to the colours as shown. [Note: left side of the brain is on the left: neurological conventions].

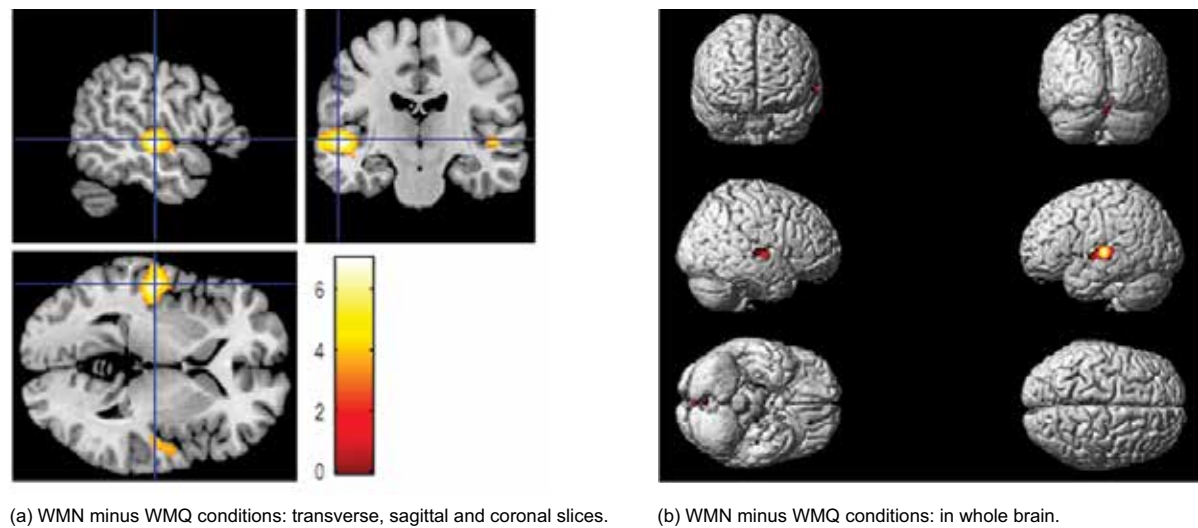


Figure 3. Statistical parametric maps (SPMs) obtain from the group analysis ($n = 15$, $p < 0.001$) showing WMN > WMQ. Arrow shows the higher maxima intensity; superior temporal gyrus (-54,-22, 4). The t-values for the activated voxels are scaled in colours (red to white) as shown. [Note: left side of the brain is on the left, neurological conventions].

Table 5. Anatomical area, brain hemisphere, t-value, coordinates of maximum intensity (x,y,z) and number of activated voxels are obtained from the group analysis ($n = 15$, $p < 0.001$) on double subtraction; comparing the Working Memory task in Noise (WMN) minus Working Memory task in Quiet (WMQ) minus Noise (N) conditions as shown in Figure 4

WMN minus WMQ minus N				
Anatomical Area	Hemisphere	t-value	Coordinate (x, y, z mm)	NOV
Hippocampus	R	7.69	24, -8, -30	30
SFG	R	7.63	16, -12, 40	44
SFG	R	5.96	2, 30, 48	48
Cerebellum	R	5.44	20, 2, 66	11
Cerebellum	L	4.98	-4, -46, -14	67
Cerebellum	L	4.64	-10, -52, -10	37
Cerebellum	R	4.49	8, -46, -10	34

Abbreviations: WMQ = working memory task in quiet, WMN = working memory task in noise, NOV = number of activated voxels, SFG = superior frontal gyrus, L = left, R = right.

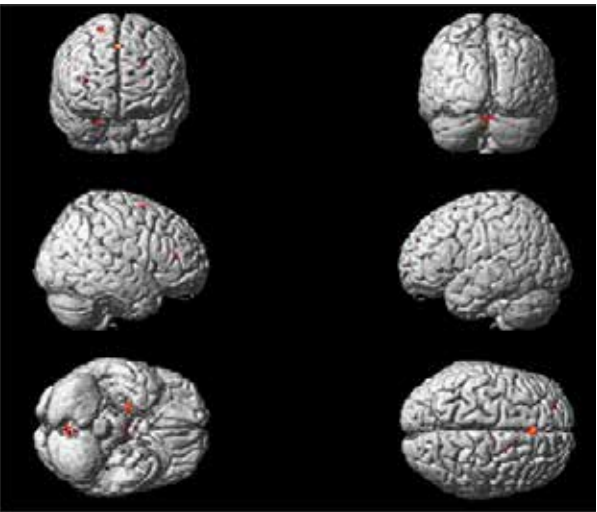


Figure 4. Statistical parametric maps (SPMs) obtain from the group analysis ($n = 15$, $p < 0.001$) showing double subtraction analysis; WMN > WMQ > N. [Note: left side of the brain is on the left, neurological conventions].

fMRI results

Listening to babble noise (N)

Compared to WMQ and WMN, N condition imposed the smallest processing demands as the participants needed only to listen to the babble noise presented binaurally. Activation of bilateral STG and MTG were expected given that auditory stimuli were used, and these regions are primarily involved in auditory processing (Burton & Small, 2006). Both areas showed rightward asymmetries, supporting the finding that the right hemisphere is relatively more sensitive than the left in the processing of nonverbal stimuli (Sequeira et al., 2008).

Comparing WMQ and WMN

Result reveals the following primary effects: 1) cortical areas with significant activation during WMQ are similar to those demonstrated in WMN. This suggests that WMQ and WMN use the same neural areas in processing both tasks. 2) In WMN, results show decreases in neural activity in all ROIs except in the cerebellum and hippocampus, which points to

interesting findings in relation to the use 5-dB SNR in word stimuli (which will be discussed later).

In both the WMQ and WMN conditions (as shown in Table 3 and Figure 1b and 1c), there was bilateral STG and MTG activation, consistent with previous studies assessing the involvement of these areas in auditory (Burton & Small, 2006; Jonides et al., 1998) and spoken word processing (Wong et al., 2009). Both tasks also activated the prefrontal cortex, specifically the MFG and IFG covering BA 47 bilaterally. These areas are suggested to play a crucial role in executive functioning during WM tasks (Jonides et al., 1998). PCG and post-CG were also activated, and these areas are important for rehearsal of verbal information (Smith et al., 2000). As we asked participants to remember words, the storage area as suggested by Shivde & Thompson-Schill (2004) was activated (SPL, IPL and precuneus) (Hodge et al., 2000). SPL and IPL covering BA 40 and BA 7 are also proposed to be involved in encoding and retrieval of verbal information (Luck et al., 2010; Sweet et al., 2008; Jonides et al., 1998). Activation in the lingual gyrus was also found, consistent with the proposal that the area is involved in information encoding (Karlsgodt et al., 2005). These tasks also activated the hippocampus and cerebellum. Traditionally, the hippocampus and cerebellum have been thought to be responsible for motor coordination and balance but recently these structures are hypothesized to be involved in executive function and attention during cognitive processing (Gottwald et al., 2003; Desmond & Fiez, 1998). We postulate that both WMQ and WMN activated the same neural areas because both tasks involved the requirements to attend to stimuli and repeat them backwards. Both tasks involved storage, rehearsal, encoding, and executive functioning (Baddeley & Wilson, 2002; Baddeley, 1986; Baddeley & Hitch, 1974), all of which depend on attention.

The extended activation in the bilateral anterior cerebellum and right posterior cerebellum during WMN suggests greater recruitment of attention resources, probably to compensate for interference due to 5-dB SNR. This finding supports the proposal based on previous work in other domains that, in the presence of relatively low-level background noise, participants' attention to word stimuli is enhanced via SR mechanisms (Moss et al., 2004) involving a hippocampal–cerebellar system. A related possibility is that the presence of 5-dB SNR might prime the system to work better, a hypothesis supported by earlier claims that humans are thought to have the special ability to focus and pay more attention to particular sounds given in a mixture of various sounds (Sohn & Lee, 2000). Another possibility is that the cerebellum amplifies and refines the signal to facilitate correct decision making when the level of background noise is suitable within the range of the enhancement phenomenon. These possibilities, which are not mutually exclusive, are further supported by our behavioral scores indicating that participants responded better in the presence of 5-dB SNR (Table 1). The proposed involvement of the cerebellum in attention is

also supported by previous researchers in other domains (Schweizer et al., 2007; Krischen et al., 2006; Teder-Salejarvi et al., 2005; Gottwald et al., 2003; Townsend et al., 2001; Harris et al., 1999; Courchesne, 1997).

The hippocampus was also activated in the present study although the NOV (Table 3, Figure 2 and Figure 3) is small, and the involvement of the hippocampus in attention is implicated in an earlier study (Faraco et al., 2011; Toepper et al., 2010). We suggest that activation of the hippocampus in the present study is not due to the WM mechanism but rather to the role of the hippocampus as an attention controller in compensating for the effects of noise. In this manner, the hippocampus and cerebellum might work together in the presence of background noise to increase attention to relevant stimuli (i.e., the signal) via SR mechanisms. This hypothesis is supported by our fMRI results in that the left hippocampus was activated only in WMN conditions and not in the WMQ condition. Furthermore, the nature of stimuli used in the present study was not similar to that of previous studies (Lindauer et al., 2005; Karlsgodt et al., 2005) that have investigated the WM system, reporting activation of the hippocampus. Additionally, behavioral results in the present study revealed that participants performed better with noise (i.e., in WMN conditions). Thus, our study clearly differs from previous studies both in the task and in the findings, pointing to hippocampal involvement in SR mechanisms involved in attention rather than to the WM processes implicated in those previous studies. The involvement of hippocampus as an attention controller is further supported by patients with posttraumatic stress disorder (PTSD) (Lindauer et al., 2006) and ADHD (Plessen et al., 2006).

In summary, comparing the WMQ and WMN tasks of the present study, results demonstrate higher BOLD activity in the WMQ condition except in the bilateral anterior cerebellum, right posterior cerebellum, and left hippocampus. Findings of other activated areas in this study such as PCG, MTG, lingual gyrus, SPL, IFG (triangular), MFG, precuneus, and post-CG (Table 3) appear at odds with previous studies suggesting that performing a WM task in noise increases neural activity related to WM demands (Just et al., 1996; Wong et al., 2004). We propose that the differences between the present and previous studies (Just et al., 1996; Wong et al., 2004) reveal the operation of a SR mechanism in the present study. The idea of SR is relatively new in neurological science, suggesting that, in the presence of external noise up to a finite level of intensity, there is an enhanced sensitivity to the stimuli (the signal) (Moss et al., 2004). We postulate that the 5-dB SNR used in the present study was within the range to produce such enhancement effects as shown in our task. These findings also support the idea that brain functions require additional attention resources under noisy conditions. Our results are further supported by the behavioral scores demonstrating that participants performed better in the presence of noise than without it (quiet). Whether or not our participants would be hindered in performance with higher levels of noise remains to be studied, but we can

safely conclude on the basis of the present findings that they show enhancement effects with such relatively low levels of noise, thereby providing a firm foundation for future studies of this type.

The manipulation of noise in the present study is very important given that noise pollution is now one of the fast-becoming major public health issues in Malaysia (Ismail et al., 2009). Yusoff & Ishak (2005) discovered that noise level exposure experienced by the Klang Valley residents exceeded the Malaysian Department of Environment's (DOE) guidelines on a daily basis. In the next 5 to 10 years, noise levels are expected to increase and this issue will become a major concern. However, the cerebellar-hippocampus involvement as proposed in this study has not yet been conclusive and evidence is still limited especially in regard to attention and WM. Thus, future study related to this issue is needed.

Conclusions

There are a number of similarities in task and brain activation in the present study compared to other available studies. However, the present study highlights the involvement of the cerebellum and hippocampus in a SR mechanism when a BRT is performed in the presence of a low level (5-dB SNR) of background noise. The present study provides evidence that (1) the 5-dB SNR used in our study is within the range of enhancement phenomena best explained with SR mechanisms. This is supported by the behavioral scores revealing better performance in the WMN condition and is further supported by our fMRI results revealing activation in the bilateral posterior cerebellum, left anterior cerebellum, and left hippocampus, all of which are relevant in attention processes and have been implicated in SR mechanisms. However, while we speculate about possible underlying effects on SR mechanisms in association with cerebellar-hippocampal activation, it is clear that additional research is necessary to cement such claims (or refute them). The present study, therefore, provides a foundation and adds to the very limited literature on the role of the cerebellum and hippocampus in attention enhancement effects in the context of cognitive performance.

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