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Updating working memory in aircraft noise and speech noise causes different fMRI activations

BJØRN SÆTREVIK1 and PATRIK SÖROVIST2,3

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The present study used fMRI/BOLD neuroimaging to investigate how visual-verbal working memory is updated when exposed to three different background-noise conditions: speech noise, aircraft noise and silence. The number-updating task that was used can distinguish between "substitution processes," which involve adding new items to the working memory representation and suppressing old items, and "exclusion processes," which involve rejecting new items and maintaining an intact memory set. The current findings supported the findings of a previous study by showing that substitution activated the dorsolateral prefrontal cortex, the posterior medial frontal cortex and the parietal lobes, whereas exclusion activated the anterior medial frontal cortex. Moreover, the prefrontal cortex was activated more by substitution processes when exposed to background speech than when exposed to aircraft noise. These results indicate that (a) the prefrontal cortex plays a special role when task-irrelevant materials should be denied access to working memory and (b) that, when compensating for different types of noise, either different cognitive mechanisms are involved or those cognitive mechanisms that are involved to different degrees.

Key words: Executive functions, updating, substitution, cognitive conflict, cognitive control, noise, frontal-parietal network, fMRI.

Patrik Sörqvist, Department of Building, Energy and Environmental Engineering, University of Gävle, SE-801 76 Gävle, Sweden. Tel: + 46 26 64 85 42; e-mail: patrik.sorqvist@hig.se

INTRODUCTION

The detrimental effects of noise on performance and behavior are well documented (Clark & Sörqvist, 2012; Klatte, Bergstrom & Lachmann, 2013; Smith, 2012; Szalma & Hancock, 2011). For instance, studies have shown that aircraft noise (Hygge, 2003; Hygge, Boman & Enmarker, 2003; Sörqvist, 2010), road traffic noise (Hygge et al., 2003; Ljung, Sörqvist & Hygge, 2009) and background speech (Sörqvist, Halin & Hygge, 2010) impair school- and office-related tasks such as writing (Sörqvist, Nöstl & Halin, 2012), reading comprehension (Sörgvist et al., 2010a) and remembering (Sörqvist, 2010). Aircraft noise (Hygge, 2003) and background speech (Sörqvist, 2010) stand out as the two most detrimental types of noise (Clark & Sörqvist, 2012). However, the effects of these two noise sources have rarely been directly compared in the same experiment. A notable exception is a study by Sörqvist (2010) that indicated that background speech impairs memory of written materials to a greater degree than aircraft noise does. Yet the reasons why background speech is more detrimental than aircraft noise remain unclear. In the current article, we explore the possibility that background speech may be more detrimental than aircraft noise due to its increasing processing demands on a mediating cognitive control system (Miller & Cohen, 2001).

Background sound can impair cognitive functioning by capturing attention (i.e., diverting attention from the desirable information source) or – as background speech is automatically processed and analyzed – by competing with the processes applied to performing the focal task (Hughes, 2014). One process that appears to be particularly sensitive to disruption by

background sound is serial rehearsal (Macken, Phelps & Jones, 2009). For example, any sound that changes acoustically over time impairs immediate memory of item sequences if the task emphasises serial rehearsal and the retention of order between the to-be-recalled items (Marsh, Hughes & Jones, 2008). Higherorder cognitive tasks are not process-pure, but rely on the interplay of several individual executive processes (Miyake, Friedman, Emerson, Witzki & Howerter, 2000; Sörqvist, Halin, and Hygge, 2010; Sörqvist, Ljungberg & Ljung, 2010). One of those executive processes is called "updating" and can be defined as the processes of "modifying the current status of a representation of schema in working memory (WM) to accommodate new input" (Morris & Jones, 1990, p. 112). This modification includes at least two processes: first, the representations in WM are changed by adding new information to the memory set; and second, the representations are changed by suppressing previous information from the memory set. We will refer to both the addition of newly relevant items and the suppression of no longer relevant items as "substitution processes" (Sörqvist & Sætrevik, 2010). Conversely, a new stimulus that is considered to be irrelevant may be rejected rather than leading to a change in the WM representation. We call the cognitive processes involved in this operation "exclusion processes." Our distinction between substitution processes and exclusion processes is similar to the distinction between maintenance and updating modes made by Oberauer and colleagues (Ecker, Lewandowsky & Oberauer, 2014; Ecker, Lewandowsky, Oberauer & Chee, 2010; Kessler & Oberauer, 2014). They argue that updating a subset of information held in WM involves switching between maintenance and updating modes, and they suggest that updating is a

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¹Department of Psychosocial Science, University of Bergen, Bergen, Norway

²Department of Building, Energy, and Environmental Engineering, University of Gävle, Gävle, Sweden

³Linnaeus Centre HEAD, Swedish Institute for Disability Research, Linköping University, Linköping, Sweden

two-component process of suppressing or removing outdated information and encoding new information in its place. Whilst our term "substitution processes" covers such two-component processes, our term "exclusion processes" applies to processes involving maintenance of an intact WM representation while suppressing/removing information that is denied access to the WM representation, information that is immediately discarded on the basis of an evaluation criterion at its presentation.

Updating appears to underpin higher-order cognitive capabilities such as problem solving (Friedman, Miyake, Corley, Young, DeFries & Hewitt, 2006), reading comprehension (Carretti, Cornoldi, De Beni & Romano, 2005; De Beni, Palladino, Pazzaglia & Cornoldi, 1998; Palladino, Cornoldi, De Beni & Pazzaglia, 2001) and reasoning (van der Sluis, de Jong & van der Leij, 2007). As such, studying this particular executive function yields insights into the basic functioning of a broad spectrum of human behavioral processes. In the context of the debate concerning functional differences between noise effects, studying the effects of noise on updating processes may help clarify why speech is more detrimental to higher-order cognitive capabilities, such as prose memory, than aircraft noise (Sörqvist, 2010). For example, a possible explanation of the difference could be that these two types of noise interfere differently with WM-updating processes or interfere with different processes. The impairment of cognitive control of updating processes may act as a mediating mechanism that is responsible for the effects of noise on prose memory (and other higher-order cognitive tasks).

Using start behavioral measures to study updating processes is inherently difficult, as behavioral responses not only involve several cognitive processes but also tend to be complicated by other processes the brain is undertaking simultaneously (Ecker et al., 2010; Miyake et al., 2000; Sörqvist, Ljungberg & Ljung, 2010). One method that can be used to overcome these problems is to examine the latency cost associated with substitution and exclusion/maintenance processes (Kessler & Oberauer, 2014). For example, Ecker, Lewandowsky and Oberauer (2014) used a modified updating paradigm wherein the to-be-updated information was cued before the new memoranda were presented. Longer cue-target intervals led to faster updating, reflecting a deliberate removal of information from WM.

Another method that can be used to study specific updating processes in isolation is to use imaging techniques to measure the neural correlates involved when processing different tasks. By comparing the activated correlates to those found in other studies to be associated with basic cognitive functions (e.g., inhibition or cognitive conflict), one can identify which cognitive mechanisms are involved in WM updating in a way that would be difficult to establish from behavioral responses alone. Further, subtraction logic can be applied to discern which additional cognitive processes are involved in some WM tasks but not in others. Two different conditions in a WM task may involve the same mechanisms for perceiving, comparing and responding to stimuli, but they may also involve different additional mechanisms, for example, to counteract noise distraction. Using neuroimaging to show which areas are involved in such additional processes may give more information than differences in response choice or latency would. A final argument for the use of neuroimaging in examining memory is that in some cases, slight changes in a WM task (e.g., different background noises) may not be discernible in terms of behavioral-response accuracy or latency, yet the cognitive mechanisms behind the performance may differ between the two conditions. Neuroimaging may reveal that different brain regions are involved, while the two conditions would appear similar if one were only examining behavioral measures.

Some of the traditional "updating tasks" suffer from methodological limitations according to a number of independent researchers (see Palladino & Jarrold, 2008; Ruiz, Elosua & Lechuga, 2005). For example, in a running memory task frequently employed to measure updating processes - the participants view a sequence of visual items. The length of the sequence is unknown to the participants, and their task is to recall the most recent items (e.g., four items) when the sequence ends. The task is purposefully designed to require continuous updating of WM content throughout the sequence. Yet, it has been shown that participants ignore the items in the first part of the sequence, because this is a more successful strategy in fulfilling the task's requirements (see e.g., Palladino & Jarrold, 2008). In a previous investigation (Sörqvist & Sætrevik, 2010), we used the "number-updating task" (introduced by Carretti, Cornoldi & Pelegrina, 2007) to measure substitution processes, which addresses some of these problems. In our version of the numberupdating task, sequences of two-digit numbers are presented visually one at a time (e.g., the sequence 47, 23, 58, 49, 63, 30, 52, 41, 67, 45). The instructions ask the participants to remember the three numbers with the lowest arithmetic value presented so far. When starting a new list, the first three numbers in the sequence will necessarily be the lowest so far and must be retained (in the example above, 47, 23 and 58). In response to each subsequent number presented, the participants should either replace one of the items in their WM with the presented number (which involves "substitution processes") or maintain the previous WM content without including the presented number (which involves "exclusion processes"). Substitution processes (i.e., to add a new number and suppress an old number) are needed when the presented number is lower than one of the three numbers currently held in memory (e.g., when 49 is presented fourth in the sequence above). We call this condition a "substitution" trial. Exclusion processes (i.e., to maintain the memory set intact) are needed when the presented number is higher than the three numbers held in memory (e.g., 63, the fifth number in the sequence above). We call this condition a "no substitution" trial. The processes involved in comparing the presented number with the numbers in one's WM are assumed to be stable across the two types of trial.

In our previous study (Sörqvist & Sætrevik, 2010), fMRI recordings indicated that the dorsolateral prefrontal cortex (DLPFC), the posterior medial frontal cortex and the parietal cortex were more activated by "substitution" trials than in "no substitution" trials, whereas the anterior medial frontal cortex was more activated by "no substitution" trials than by "substitution" trials. This pattern of activation was explained as being a result of cognitive conflict detection (Miller & Cohen, 2001). At the outset of a trial, participants are prepared to substitute WM content if the currently presented item fits the criteria. For "no substitution" trials, substitution must be inhibited, as the stimulus

does not fit the criterion, which may cause a higher degree of cognitive conflict than that caused by "substitution" trials. Stated differently, the participants must avoid responding with the prepared - and thus activated - substitution response to irrelevant stimuli in "no substitution" trials. Consistent with our findings, previous neuroimaging studies have associated cognitive conflict detection within the anterior prefrontal cortex (PFC), whereas behavioral outputs that are consistent with the prepared responses have been associated with the involvement of the DLPFC (e.g. Miller & Cohen, 2001; Ridderinkhof, Ullsperger, Crone & Nieuwenhuis, 2004). Moreover, the PFC is activated when exclusion of task-irrelevant items from WM is necessary (McNab & Klingberg, 2008; Sætrevik & Specht, 2009; Vogel, McCollough & Machizawa, 2005). Based on these findings, we argue that "no substitution" trials activate a distinct cognitive mechanism responsible for excluding potentially, but not currently, relevant stimuli, which is associated with the anterior PFC.

In the current experiment, we used an fMRI protocol to compare the cortical activities associated with substitution and exclusion processes in three background-noise conditions: silence, speech and aircraft noise. The main aim was to study the neural underpinnings of updating processes as carried out in the presence of the two background-noise sources. A secondary aim was to replicate the findings of our previous study, which had only eight participants and was the first neuroimaging study using the number-updating task (Sörqvist & Sætrevik, 2010), in a similar experimental setup with greater statistical power.

METHOD

Participants

A total of 18 participants, 8 males and 10 females, were recruited for this experiment. They were healthy, right-handed adults with a mean age of 24.3 years (ranging from 20 to 28). The participants had not performed the number-updating task prior to taking part in the experiment. All reported to be of normal hearing and to have Norwegian as their native language. They received an honorarium of 200 NOK (about 26 EUR) for their participation.

Materials

The participants were outfitted with noise-isolating headphones so that the stimuli were clearly distinguishable from the scanner's noise. Sound pressure levels (SPL) were pilot tested to ensure stimuli sounds were clearly discernable in the scanner environment.

The aircraft noise was created by recording the sound of passing aircraft nearby an airport. The speech noise was created by recording a Norwegian male actor reading a meaningful, correctly structured, fictitious story with non-salient content. Longer, unnatural pauses, which were a consequence of the recording procedure, were adjusted to maintain a normal, conversational speech pattern. The recordings were digitalised and edited to 40 seconds' duration. The respective volumes of the two sounds were made equivalent with computer software and were played back in mono at approximately 70 dB(A) SPL.

Visual stimuli (double-digit numbers) were presented as white text on a black background, in Arial type and font size 72. Each participant wore MRI-compatible glasses on which the numbers were displayed in a 600×800 pixel resolution.

The experiment presented 12 different lists of numbers. The instructions clarified that each presented number should be compared to preced-

ing numbers in the current list, but not with numbers from previous lists. Each list consisted of 10 two-digit numbers, varying pseudo-randomly between 15 and 99. All numbers were between two and six values distant from another number in the list. The arithmetic distance between the lowest and the highest number in a list varied between 30 and 36. These limitations were intended to prevent participants from using heuristic task strategies (e.g., excluding numbers that appeared vastly larger than the previous numbers). Each list was preceded by the symbol ## to signal the onset of a new list. Thereafter, the 10 numbers in the list were presented sequentially with a display time of 2 s and an interstimulus interval (ISI) of 1 s. Participants were equipped with a response clicker with a thumb and an index finger button. The participants were instructed to respond to each number with a response indicating "substitution" if the presented number was one of the three lowest numbers presented so far in the present list or with a response indicating "no substitution" if the presented number was higher than the three lowest numbers presented

Procedure

The number-updating task used in the present study was adopted from Carretti et al. (2007) and was identical to the task used in a previous study (Sörqvist & Sætrevik, 2010). Subsequent to the first three numbers, which by necessity were "substitution" trials, each stimulus list was designed to require three "substitution" and four "no substitution" responses. Numbers were presented one at a time for 2 s on screen, with a 1 s ISI between each number. Three null events were distributed in each list for comparison of neural task activation. During these, the screen remained blank but the noise condition continued. Four lists were presented in silence, four lists with aircraft noise in the background and four lists with speech in the background. The order of the noise conditions was randomised between participants.

Immediately before the participants entered the scanner, they performed a short training session on a laptop computer during which they used the same response buttons as they would use in the scanner to become acquainted with the task requirements. All participants reported that they were confident that they could complete the task before starting the experiment proper.

The experiment consisted of 12 ON blocks, during which tasks and background noises were presented, and 12 OFF blocks, during which no tasks or noises were presented. The experiment had a total duration of 16 m, 48 s. Each ON block lasted for 42 s, and one list of stimuli was presented in each ON block. At the beginning of each ON block, the symbols ## were displayed for 1 s prior to the onset of the numbers and aircraft or speech background noise. Each list had 10 trials and three null events, both lasting 3 s, resulting in a 39 s duration for each list. After the last number of the list, the symbols -- were shown for 1 s, overlapping with the end of the 40 s of background noise, and for an additional 1 s while waiting for scanner synchronization. Each 42 s ON block was followed by a 42 s OFF block, during which a fixation mark, +, was presented without any noise.

A 3.0T GE Tesla Signa Excite MRI scanner was used for BOLD image acquisition. A T1-weighted MPRAGE sequence was used for initial 3D body scanning. Thereafter, 336 BOLD-sensitive echo-planar image (EPI) volumes were acquired with a repetition time (TR) of 3 s. An EPI volume consisted of a set of 25 slices based on a 64×64 voxel matrix, with $3 \times 3 \times 5$ mm cubic voxels. The DICOM images were converted to the NIfTI image format using the dcm2nii software (McCausland Centre, Columbia, SC, http://www.mccauslandcenter.sc. edu/mricro/mricron/dcm2nii.html). The EPI images were further preprocessed and analyzed using the Statistical Parametric Mapping software (SPM5 - Wellcome Department of Cognitive Neurology, London, www.fil.ion.ac.uk), running in MatLab version 6.5.1. (Mathworks Inc., Natick, MA, www.mathworks.com). The preprocessing steps involved realignment and unwarping of all subsequent EPI volumes to the first volume of the time series to correct for head movements, normalisation to the Montreal Neurological Institute (MNI) stereotaxic space, resampling to a voxel size of $2 \times 2 \times 2$ mm and smoothing with an 8 mm full-width-at-half-maximum kernel. The EPI images were individually

Table 1. Clusters of voxels significantly more activated in the contrasts of interest

Contrast Name 1 Substitution > no-substitution *** 2 No-substitution > substitution *** 3 Task in speech noise > task in sircraft 6 Task in aircraft noise > task in sircraft 5 Task in sneech > Task in aircraft 5	substitution *** substitution ***	t-threshold	Cluster	size	>	Z	t-value		Anatomical localization	Brodmann area
	substitution *** substitution ***	7.154						,		
	substitution **		_	429	-2	12 5	1 15	6.64	Superior motor area	6, 32
	substitution **				8-			5.49		
	substitution **		2	992			_	6.59	Left precentral, left frontal inferior operculum	48, 44, 6
	substitution **						_	5.99		
	substitution **							5.61		
	substitution **		3	547	-36 -		_	5.92	Left inferior parietal lobule, left postcentral gyrus	40
	substitution **				-48	-38 52	9.56	5.54		
	substitution **				-35	-32 52	9.04	5.4		
	substitution **		4	303		-58 44	11.11	5.92	Right angular gyrus, right superior occipital gyrus	7
	substitution **					-72 42	2 8.53	5.25		
	substitution **		5	4				5.43	Right supramarginal gyrus, right inferior parietal lobule	40
	substitution **		9	162	26	6 54	4 8.87	5.35	Right frontal middle gyrus, right frontal superior gyrus	~
	substitution **				30	5 52		5.29) }	
	substitution **							5.05		
		7.154	1	557	-2	54 4	1	6.72	Anterior cingulum, medial superior frontal gyrus	10, 32
					-2	45 24	4 8.2	5.15		
			2	136	0	-24 42		5.26	Middle cingulate	23
					4-	-15 40	8.55	5.25		
	Task in speech noise > task in silence *	3.965	1	1091	-46	-32	6 6.43	4.52	Left superior temporal gyrus	21, 41, 48
					-54	-26	2 6.29	4.46		
					- 09-	-14 -2		4.08		
			2	424		-14 -2	5.41	4.07	Right superior temporal gyrus	22, 48
					- 29	-2 -10) 4.2	3.43		
	Task in aircraft noise > task in silence *	3.965	1	201	-46	-30	6 6.13	4.4	Left superior temporal gyrus	21, 48, 22
					-34	-38 14	4.91	3.82		
					-48 -	-18	0 4.02	3.33		
	Task in speech > Task in aircraft noise *	3.965	1	225		-14 -2		4.14	Left middle temporal gyrus	22, 21
					-50 -	-30		3.63		
6 Task in aircraft no	Task in aircraft noise > task in speech noise	1.74	1	320	9			2.55	Anterior cingulum	24
					4-	0 38		1.92		
					9-	8 36		1.83		
			2	233	2	-14 24		2.19	Right postcentral gyrus, right supramarginal gyrus	48, 43
					- 09	-16 32		2.19		
					48	-16 22	2 2.23	2.06		
			3	201	18	-56 -26		2	Right cerebellum 6	37, 19
					10	-60 - 14	1 2.09	1.95		
					14	-42 -36	5 2.05	1.92		
7 Substitution in spe	Substitution in speech noise > substitution in	3.965	_	785	40	-26 66	5 7.09	4.77	Right precentral gyrus, right postcentral gyrus	4, 6
aircraft noise *						-26 58		4.38		
						-28 76	5 5.08	4.37		
			2	975	- 9	-14 48	8 6.78	4.66	Middle cingulate, supplemental motor area	23, 4
					8-	-28 50) 5.56	4.57		
					5			3.77		

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Contrast	Name	t-threshold	Cluster	Cluster size	X	Z	t-value	z-value	Anatomical localization	Brodmann area
			3	1054	-16 -88 20 -84	-88 18 -84 28	6.7	4.62	Left superior occipital gyrus, left middle	19, 18
								4.06	occipitat gytas, cancas	
			4	599	50			4.53	Right superior temporal gyrus, right middle temporal gyrus	42, 41, 22
						32 18		4.15		
					40	-22 20		3.85		
			5	547	- 62	-8 -14		4.45	Right middle temporal gyrus, right superior temporal gyrus	21, 20
					58	4 0	5.6	4.16		
					52	-4 -22		4.1		
			9	463	-58	-6 -14		4.32	Left middle temporal gyrus	21
					-62	-12 -8	5.63	4.17		
					·- 99-	-26 2	5.21	3.97		
∞	Substitution in aircraft noise > substitution	3.965	1	1017	14 –(-66 -30		5.35	Right cerebellum 6, right cerebellum 8	37 and inferior
	in speech noise *				22 —:	-56 -34	5.43	4.52		
					15 –8	-84 -26	5.64	4.18		
			2	3487	-38	-46 46	8.37	5.2	Left inferior parietal gyrus, left superior	40, 7, 2
					-14 -(-66 62	7.88	5.05	parietal gyrus, left precuneus	
					-26 -(-66 54		4.86		
			3	1201	30	-72 54		4.88	Right superior parietal gyrus, right inferior	7, 40
					36 –	-50 44		4.75	parietal gyrus, right angular gyrus	
					4	-42 48	6.82	4.67		
			4	1141		-6 74		4.76	Left superior frontal gyrus, left precentral gyrus,	9
					-26 -	-4 54	6.51	4.55	supplemental motor area	
					-5	10 58		4.39		
			5	1064	-50	10 44		4.63	Left precentral gyrus, left middle frontal gyrus	6, 44, 9
					4-	0 32		4.61	and left inferior frontal triangularis	
					-48	22 36		4.33		
			9	794	28	2 58		4.6	Right superior frontal gyrus, right middle frontal gyrus	6,8
					56	16 62		4.15		
					22	14 54	5.41	4.07		
			7	249	-28 –(-68 -36		4.51	Left crus cerebellum	(none)
			∞	209	-14	0 14		4.14	Left caudate, left thalamus	(none)
			6	350	. 94	38 34		4.09	Right middle frontal gyrus	45, 46, 44
					46	24 36		3.87		

Contrasts marked with ** (contrast 1 and 2) were familywise error corrected, p < 0.05, voxel threshold = 100. Contrasts marked with * (contrast 3, 4, 5, 7 and 8) are uncorrected, p < 0.005, voxel threshold = 200.

modeled according to the three background-noise conditions and by whether they were from the first three trials in a list, "substitution" trials or "no substitution" trials. EPI images from error trials with the wrong response were not included in the analyses. Single subject *t*-tests were done between "substitution" and "no substitution" trials, between each of the noise conditions and silence, and between "substitution" trials under both background-noise conditions. The resulting individual contrast images served as input for subsequent random-effects analyses, using one-sample *t*-tests.

RESULTS

Behavioral data

The participants' performance on responses indicating whether or not they updated their WM content had a high accuracy across trial types (overall accuracy, M = 95%, SD = 21.7%). This indicated that the task had been understood, and we can assume that the fMRI analyses can model which WM functions are performed in various trials. The response accuracy rates were comparable between the conditions (silence, M = 95.4%, SD = 20.19%; speech noise, M = 95.1%, SD = 21.5%; and aircraft noise, M = 94.6%, SD = 22.7%), and t-test comparisons were not significantly different (all p > 0.5). None of the participants stood out as having given a particularly poor performance.

fMRI data

Error trials and null events were excluded from further analysis. Subtraction t-contrasts were calculated for 8 comparisons of interest. For the contrasts comparing different task trials (substitution and no-substitution trials), the analyses used familywise error correction, an alpha level of p < 0.05 (whole-brain comparison) and a cluster-extension threshold of 100 voxels. For contrasts comparing the different noise conditions, the analyses used no correction for multiple testing, and to compensate, an alpha level of p < 0.0005 and a cluster threshold of 200 voxels were applied. The activated clusters, anatomical correlates and Brodmann areas for all eight contrasts are shown in Table 1.

The "substitution" trials activated six clusters in the medial, temporal and parietal areas, while the "no substitution" trials activated two clusters in the medial frontal and temporal areas, with the largest cluster in the anterior cingulate cortex. Thus, the WM substitution process showed more activation in the DLPFC, medial PFC and parietal areas than the "no substitution" trials (contrast 1). This is shown in Figs. 1 and 2, which are comparable to Figures 1 and 2 in Sörqvist and Sætrevik (2010). The "no substitution" trials showed more activation in the anterior medial PFC than the "substitution" trials (contrast 2).

An analysis of the noise conditions alone, showed that doing the task with speech as a background noise (while subtracting the activation of doing the task in silence) activated the bilateral but left-lateralized temporal cortex (contrast 3). Doing the task with aircraft noise as a background noise (while subtracting the activation of doing the task in silence) activated only the left temporal cortex, and to a lesser extent than background speech did (contrast 4).

A subtraction between the two noises showed an area in the left temporal lobe to be more activated by speech than by aircraft noise (contrast 5). Conversely, aircraft noise did not activate any areas more than speech did at the chosen alpha levels. Reducing the alpha level to p < 0.05 to explore sub-threshold effects revealed activation in the basal structures of the right temporal lobe and cerebellum (contrast 6).

Comparing the trials in which WM was updated under different noise conditions showed that "substitution" trials with aircraft noise in the background (while subtracting "substitution" trials with speech as a background) activated six clusters in the medial, temporal and occipital cortex (contrast 7). These activations are illustrated in Fig. 3. Conversely, "substitution" trials with speech as a background noise (while subtracting "substitution" trials with aircraft noise in the background) activated the occipital, parietal and frontal cortex (contrast 8). This is shown in Fig. 4.

DISCUSSION

"Substitution" trials activated the DLPFC, the posterior medial PFC and the parietal lobes, while "no substitution" trails activated the anterior MFC. These findings support our previous study (Sörqvist & Sætrevik, 2010), although the present study used a substantially larger sample size. Performing the task with background speech noise and aircraft noise increased activity in the temporal lobes. The increase was significant in left hemisphere for speech and was bilateral for aircraft noise, although speech noise increased activity in a larger left-hemisphere area that aircraft noise did. "Substitution" trials undertaken with speech in the background activated frontal, medial and temporal areas significantly more than "substitution" trials undertaken with aircraft noise in the background did, while the inverse activated cerebellar, parietal and frontal areas more. This indicates that the task involves different cognitive processes depending on the background noises present.

The scanner environment did not allow the participants to report their actual memory content. Instead, participants were asked to indicate when they updated their WM content by pressing a key. The behavioral data showed a performance well above chance level, indicating that the participants updated when the stimuli required them to. Thus, the participants carried out the WM operations that were expected in the task design, and the fMRI analyses can be assumed to indicate the expected memory operations.

Areas associated with updating processes

The first two contrasts examined the effect of the two types of trials in the task, while compensating for the distraction caused by the different noise conditions. The DLPFC, the posterior medial frontal cortex and the parietal lobes were activated more by the "substitution" trials (i.e., trials that involved adding a new item to the memory set and removing an old item from the memory set), whereas the anterior medial PFC was activated more by "no substitution" trials (i.e., trials in which the new item does not require a change of memory content). The areas activated by the substitution processes in the current study correspond to the frontal-parietal network that is often observed to be activated by WM paradigms that do not distinguish between

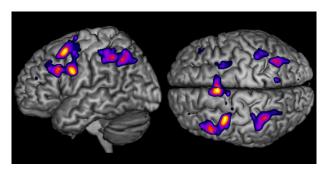


Fig. 1. Areas more activated when updating working memory content than when not updating. Activations are shown for t-values between 7.15 and 15; search depth is infinite.

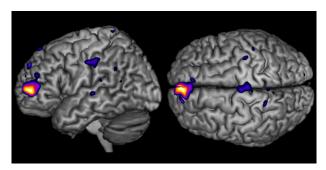


Fig. 2. Areas more activated when not updating working memory content than when updating. Activations are shown for t-values between 7.15 and 15.54; search depth is infinite.

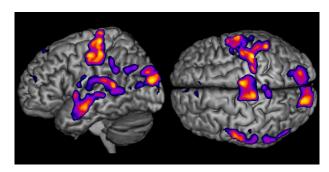


Fig. 3. Areas more activated when updating working memory content with speech in the background than when updating with aircraft noise in the background. Activations are shown for t-values between 3.97 and 7.09; search depth is infinite.

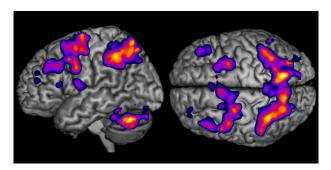


Fig. 4. Areas more activated when updating working memory content with aircraft noise in the background than when updating with speech in the background. Activations are shown for t-values between 3.97 and 8.86; search depth is infinite.

subprocesses (see e.g., Todd & Marois, 2004). This leads us to argue that the frontal-parietal network should be characterized as a 'manipulation/change' network that brings about a change to the WM representation rather than as a network used for the passive maintenance of the WM representation. This manipulation/ change network roughly corresponds to the local updating component of Kessler and Meiran's (2008) framework, which distinguished between a global updating process, which provides stability by shielding the WM contents from interference, and a local updating process, which is active when the WM representation is changed.

"No substitution" trials activated the same areas as detection of cognitive conflict has activated in previous studies (Botvinick, Cohen & Carter, 2004; Carter & Van Veen, 2007). This indicates that evaluating and not updating when presented with a new trial (i.e., maintaining WM content) involves mechanisms of attending to information that could be relevant but that is rejected (McNab & Klingberg, 2008). The current results replicate results in our previous study (Sörqvist & Sætrevik, 2010) and provide further evidence for the assumption that there are distinct cognitive mechanisms for various subprocesses in WM function, rather than an overall mechanism for the operation of WM in general (Sörqvist, Ljungberg & Ljung, 2010). These processes should be akin to the global updating processes (associated with the protection of the WM content from interference) of Kessler and Meiran's (2008) framework.

Interestingly, previous research has found a positive association between updating and anterior medial PFC activation (Collette & Van der Linden, 2002), whereas the results reported here and in our previous study (Sörqvist & Sætrevik, 2010) point in the opposite direction, as activation in this area was found to be associated with "no substitution" trials. One possible reason for this discrepancy is that some tasks referred to in earlier research as "updating tasks" may be successfully completed without actually updating WM representation, such as the "running memory task" (Palladino & Jarrold, 2008; Ruiz et al., 2005), during which the participants tend to ignore the first part of the list, thus avoiding the more difficult "updating" strategy, and instead aim for encoding the final items only. Hence, experiments using the "running memory task" may incorrectly identify the WM operation being performed, as activation has erroneously been associated with the executive function of updating.

Effects of noise

In addition to replicating the activation patterns of substituting or maintaining WM content from our previous study (Sörqvist & Sætrevik, 2010), the current study also provides neuroimaging correlates for the processing evoked by task-irrelevant background speech and aircraft noise. Doing the task in either kind of noise (subtracting the activation of doing the task in the silent condition) activated the superior temporal gyrus (bilaterally for speech noise; on left side only for aircraft noise). These areas have previously been shown to be involved in auditory processing (Buchsbaum, Hickok & Humphries, 2001; Friederici, Rüschemeyer, Hahne & Fiebach, 2003). To identify areas that are uniquely activated by doing the task in either sound condition, the activations of the two types of noise were subtracted from each other, and this showed that the left middle temporal gyrus was activated more by speech than by aircraft noise, while no areas were activated more by aircraft noise than by speech (at standard alpha levels). The differences in activation caused by the sounds themselves (i.e., regardless of the task) may be due in part to differences in frequency distribution amongst the two types of sound.

As the study aimed to compare the WM-updating processes when done in either speech or aircraft background noise, dedicated contrasts were run to subtract the "substitution" trials in the two noise conditions from each other. The results show that trials requiring updating processes undertaken with speech in the background are associated with a greater activation in the medial PFC (middle cingulate and supplemental motor area), in the right central gyrus and in bilateral temporal areas than substitution trials undertaken with aircraft noise in the background. The inverse contrast shows that "substitution" trials undertaken with aircraft noise in the background caused more activation in the occipital, temporal and anterior parietal regions than "substitution" trials undertaken with speech in the background did. Comparing these two contrasts shows that different cortical networks are activated when WM is updated in the presence of to-be-ignored background speech than in the presence of to-be-ignored aircraft noise. This indicates that different cognitive mechanisms are used to combat potential distraction by the two types of noise.

Previous studies have indicated that background speech interferes with verbal tasks to a larger degree than non-speech sounds (see Marsh & Jones, 2010, for a review), and although background speech appears to be more detrimental than aircraft noise to updating the WM (Sörqvist, 2010), aircraft noise still stands out as a particularly potent distraction (Clark & Sörgvist, 2012; Hygge, 2003). Previous neuroimaging studies of the effects of sound on cognitive processes have identified that the DLPFC and the superior temporal gyrus are involved in the effect irrelevant sound has on reducing performance (Gisselgard, Petersson, Baddeley & Ingvar, 2003; Gisselgard, Petersson & Ingvar, 2004). More specifically, irrelevant sound decreases activation in several brain areas, including the left ventrolateral PFC, the bilateral secondary auditory cortex and the left inferior parietal cortex, and it increases activation in the DLPFC (for reviews, see Beaman, Bridges & Scott, 2007; Campbell, 2005). In these studies, the primary task was a visual-verbal serial recall task, in which participants viewed a sequence of visually presented items and were required to verbally recall the items in their order of presentation. The decreased activation found in the studies may be due to task-relevant inhibition processes that suppress these areas to protect performance from distraction, but the suppression may also have a cost, as these areas appear to be involved in complying with the recall task (for behavioral evidence in support of this spill-over effect of task-relevant inhibition, see Marsh, Beaman, Hughes & Jones, 2012). The increased activation of the DLPFC in previous studies may be a result of noise conditions that required greater effort. As our previous research indicated that substitution processes involve the DLPFC (Sörqvist & Sætrevik, 2010) and that updating is impaired by background noise (Sörqvist, Halin & Hygge, 2010), one possible explanation for this is that noise interferes with substitution processes. Moreover, the reason that speech is more detrimental to cognitive performance than aircraft noise could, at least in part, be because they have different effects on substitution processes.

Surprisingly, substitution processes undertaken with speech in the background activated a cluster in the occipital lobe significantly more than substitution undertaken with aircraft noise in the background. Occipital activation is typically associated with visual processes (Albers, Kok, Toni, Dijkerman & de Lange, 2013). It is possible that this activation reflects the involvement of visual imagery (or the visuo-spatial sketchpad) to perform the task. A phonological loop (Baddeley, 1998, 2012) may be involved in maintaining and updating WM when doing the task in silence, but this system may be more vulnerable to interference from speech noise, forcing the participant to rely more on visual imagery, which is reflected in the occipital activation.

It should be noted that there was no difference in the behavioral performance between the three conditions in the current study. This may be due to participants' increasing their mental effort when background noises were present to compensate for the interference. Although behavioral performance was high under all three noise conditions, different cortical regions were activated on "substitution" trials when different background noises were present. This could reflect that while the two types of noise did not interfere sufficiently to diminish performance, it did lead to the task being solved in a different way and to its relying on different cognitive functions. Both contrasts showed non-overlapping temporal activations that may be associated with the background noises rather than with performing the task. The activation patterns of speech differ from those of aircraft noise in two ways that may be relevant here. First, the two types of sound have different acoustic characteristics, such as frequency distribution, that may activate different brain regions (Scott, Blank, Rosen & Wise, 2000). Second, despite being taskirrelevant, the semantic referents contained in speech may automatically activate cognitive processes, and speech background noise may thus interfere with task processing (Marsh et al., 2008) in a different way than non-semantic noise. This carries the potential for cognitive conflict, and cognitive control is needed to concentrate on the intended signal rather than the distraction signal (Botvinick, Braver, Barch, Carter & Cohen, 2001: Miller & Cohen, 2001). Both of these factors may have contributed to the difference in frontal activation for WM updating in each of the two types of background noise. The noise effects of speech on task performance can be counteracted by deliberate inhibition and cognitive control of the undesired speech processing (e.g. Beaman, 2004; Halin, Marsh, Haga, Holmgren & Sörqvist, 2014; Marsh et al., 2008). In the current experiment, the background speech may have required more cognitive control and active inhibition than the background aircraft noise in order to prevent the irrelevant background speech content from interfering with the processing of the task-relevant visual-verbal number content (Marsh et al., 2012). The current finding of greater medial PFC activity during "substitution" trials with background speech present supports this proposition, as this area has been associated with excluding task-irrelevant materials from WM (e.g. McNab & Klingberg, 2008).

The current results may have implications for how to interpret differences between the effects of different types of noise on higher-order cognitive capabilities such as reading comprehension and prose memory. A possible explanation as to why background speech is more detrimental than aircraft noise for such tasks could be that they interfere with WM-updating processes differently, as verbal distractors during a verbal task require additional cognitive control. The deteriorating effect that noise has on reading comprehension in behavioral studies is due to impairment of the cognitive control function, more specifically updating processes in WM. The current experiment is a first step towards applying this kind of explanatory framework to the comparison of different noise effects. These ideas can be explored further in the context of behavioral noise studies by measuring the effects of noise on updating processes, the effects of noise on higher-level cognitive tasks (e.g., reading comprehension) and undertaking a mediation analysis of these two measures.

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