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International Journal of Psychophysiology xx (2005) xxx – xxx
INTERNATIONAL JOURNAL OF PSYCHOPHYSIOLOGY
www.elsevier.com/locate/ijpsycho

Synchronized brain activity during rehearsal and short-term memory disruption by irrelevant speech is affected by recall mode

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Received 22 February 2005; received in revised form 20 September 2005; accepted 6 October 2005

Abstract

EEG coherence as a measure of synchronization of brain activity was used to investigate effects of irrelevant speech. In a delayed serial recall paradigm 21 healthy participants retained verbal items over a 10-s delay with and without interfering irrelevant speech. Recall after the delay was varied in two modes (spoken vs. written). Behavioral data showed the classic irrelevant speech effect and a superiority of written over spoken recall mode. Coherence, however, was more sensitive to processing characteristics and showed interactions between the irrelevant speech effect and recall mode during the rehearsal delay in theta (4–7.5 Hz), alpha (8–12 Hz), beta (13–20 Hz), and gamma (35–47 Hz) frequency bands. For gamma, a rehearsal-related decrease of the duration of high coherence due to presentation of irrelevant speech was found in a left-lateralized fronto-central and centro-temporal network only in spoken but not in written recall. In theta, coherence at predominantly fronto-parietal electrode combinations was indicative for memory demands and varied with individual working memory capacity assessed by digit span. Alpha coherence revealed similar results and patterns as theta coherence. In beta, a left-hemispheric network showed longer high synchronizations due to irrelevant speech only in written recall mode. EEG results suggest that mode of recall is critical for processing already during the retention period of a delayed serial recall task. Moreover, the finding that different networks are engaged with different recall modes shows that the disrupting effect of irrelevant speech is not a unitary mechanism.

Keywords: EEG coherence; Gamma; Theta; Irrelevant speech effect; Short-term memory

1. Introduction

In the present study we investigated verbal short-term rehearsal and its disruption by irrelevant speech. Numerous behavioral studies have revealed the distracting effect of auditorily presented (and to be ignored) material on short-term retention of verbal items with normal speech having the most influential effect, compared to other materials such as music or noise (e.g. Baddeley and Salamé, 1986; Boyle and Coltheart, 1996; Buchner et al., 1996; Colle and Welsh, 1976; Ellermeier and Hellbrück, 1998; LeCompte et al., 1997; LeCompte and Shaibe, 1997; Pring and Walker, 1994; Salamé and Baddeley, 1982, 1989). Several psychological theories on the nature of the irrelevant speech effect exist at present (Baddeley, 2003; Jones and Macken, 1993; Jones et al., 1992; Neath, 2000). Baddeley (2000), for example, proposes that the effect is located at the stage of phonological rehearsal and that it is, thus, confined to speech. Jones et al. (1992), on the other hand, postulate the changing state hypothesis according to which the effect is not speech-specific but operates on a more general level involving the disruption of the serial order of to-be-remembered items.

Neuroimaging studies have been carried out to determine structures related to short-term rehearsal. Several brain areas were consistently found to be involved in rehearsal across different studies, that is premotor cortex, supplementary motor cortex, left prefrontal cortex and cerebellar regions (Davachi et al., 2001; Hanakawa et al., 2003; Henson et al., 2000; Paulesu et al., 1993; Smith and Jonides, 1998). The activity of some of these areas seems to be susceptible to distraction of rehearsal using articulatory suppression (Gruber, 2001) or is sensitive to other aspects of articulatory rehearsal, like phonological similarity (Chein and Fiez, 2001). Gisselgard et al. (2003)

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0167-8760/$ - see front matter © 2005 Published by Elsevier B.V.
doi:10.1016/j.ijpsycho.2005.10.001

investigated the neural structures involved in the irrelevant speech effect using PET and found that this effect is correlated with a distributed suppression of components of the verbal working memory network, particularly in left frontal and temporal brain regions.

Imaging studies provide useful information about anatomical structures but they are still limited when it comes to the temporal dynamics of neural activity or when dynamic cooperations of brain areas are considered. There is increasing evidence that synchronous neural oscillations are closely related to dynamics of cognitive processes (Niebur et al., 2002; Nunez, 2000; Salinas and Sejnowski, 2001; Singer, 1994; Ward, 2003). Although there are several problems in interpreting EEG activity, such as volume conduction or the inverse problem, promising methods of analysis have been developed to tap into neurocognitive networks. In particular, spectral analyses are increasingly used to reveal properties of synchronous activations in the frequency domain. In the present study EEG coherences were calculated as a measure of synchronization. Coherence (ranging from 0 to 1) provides evidence of the degree of stability of phase relations between two simultaneously recorded EEG signals (Lachaux et al., 2002; Nunez et al., 1997; Schack et al., 1999; Singer, 1999).

Oscillatory activity, particularly of the theta and gamma rhythm, is closely related to memory processes such as encoding, rehearsal, and retrieval. This holds for the oscillatory activity per se (e.g. Gruber et al., 2004; Herrmann et al., 2004; Tallon-Baudry et al., 1999) and also for the coherence between different regions of the brain (e.g. Sarnthein et al., 1998; Weiss et al., 2000): Induced gamma band activity was reported in visual short- and long-term memory tasks (Gruber et al., 2004; Tallon-Baudry et al., 1999), and increase in evoked gamma band activity when sensory input has to be related to stored representations (Herrmann et al., 2004). Theta coherence was shown to be a predictor of successful memory encoding of words (Weiss et al., 2000) and, furthermore, theta coherence increases between frontal and posterior electrodes during a working memory task compared to a perception control task (Sarnthein et al., 1998). Miltner et al. (1999) showed that gamma coherence was involved in association learning. During memory formation rhinal-hippocampal changes of phase synchronization were found in gamma (Fell et al., 2001) and these memory-related gamma changes are correlated with theta coherence (Fell et al., 2003). Evidence of a gamma–theta correlation during short-term memory processing comes from Schack et al. (2002) as well. These findings suggest that theta and gamma may also be indicative of short-term rehearsal and its disruption.

In a previous experiment (Kopp et al., 2004) we intended to find EEG coherence patterns in short-term rehearsal as participants performed a delayed serial recall paradigm. Lists of five words were presented visually, then had to be retained over a period of 10 s and then had to be recalled aloud. Participants were enabled to rehearse the verbal items in one condition (*quiet*), i.e. the retention period was marked by silence, and were prevented from rehearsal by presentation of irrelevant speech in another condition (*speech*). Initial evidence was found that the neural basis of the irrelevant speech effect consists in the reduction of long-lasting synchronization of gamma activity in the underlying phonological rehearsal network.

The present study aimed to further investigate the neural basis of the irrelevant speech effect. We especially considered the influence of recall mode (*spoken* vs. *written*) on short-term rehearsal in the same delayed serial recall paradigm (see Fig. 1). Previous results in literature concerning recall mode are not consistent. There are studies indicating that short-term retention of verbal items is not affected by recall mode (Gardiner et al., 1977; Locke and Fehr, 1972; Rönnberg and Nilsson, 1987). In contrast, some authors report a superiority of written recall over spoken recall in verbal short-term memory performance (Craik,

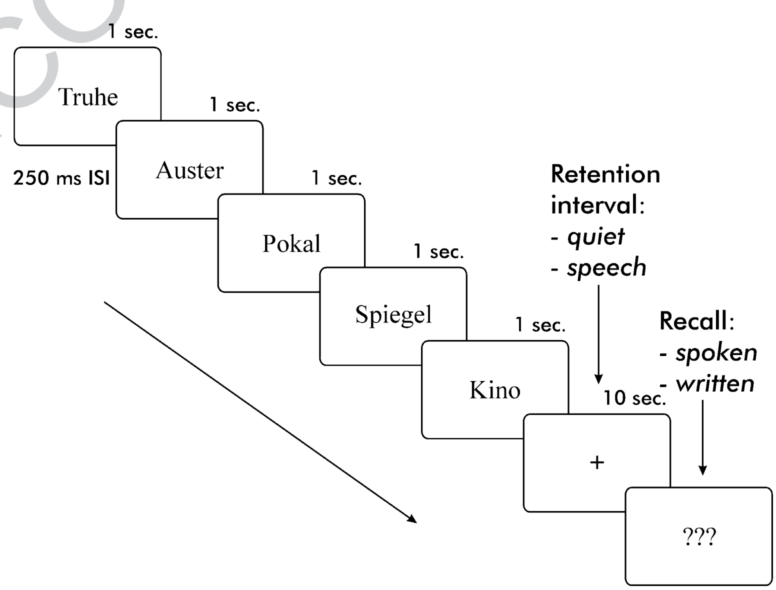

Fig. 1. Delayed serial recall paradigm. Lists of five words were presented sequentially at a rate of 1 s per item with an inter-stimulus interval of 250 ms. Items had to be retained over an interval of 10 s and had to be recalled subsequently. The tasks were performed in a 2×2 block design with the factors *distraction* (silence vs. presentation of irrelevant speech during the 10-s retention interval) and *recall mode* (spoken vs. written recall).

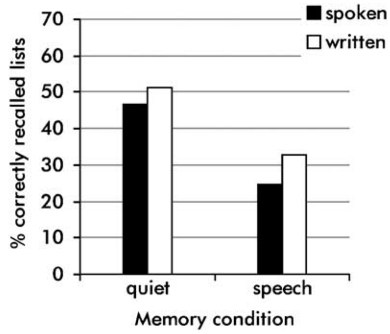

Fig. 2. Behavioral performances. Percentages of correctly recalled lists showed a pronounced irrelevant speech effect both in spoken and in written recall. No interaction was found.

1970; Murray, 1965). These contradictory findings leave open, whether mode of memory recall influences memory performance effectively, and if so, which step of processing is involved. Authors reporting differences in memory performance due to recall mode attribute them to the recall process. For example, Craik (1970) who found a superiority of written recall performance hypothesized that writing down the answers allows simultaneous rehearsal of the last items that are then better recalled. Brimer and Mueller (1979) assume that participants review their written outputs and could use them as retrieval cues to access unrecalled items. Using online measures makes it possible to investigate periods before recall (encoding, rehearsal). The aim of this study was to find synchronization patterns during short-term rehearsal of verbal items and distraction of rehearsal by irrelevant speech under conditions of *spoken* and *written* recall. According to classic findings on working memory (e.g. Baddeley, 2003) recoding of visually presented items into a phonological form is supposed to be an obligatory step and is necessary anyway for the spoken recall mode. In contrast, participants are not forced to recode visual stimuli when written recall is required. In spite of this, it might be assumed that, due to short-term memory characteristics and the important role phonology might play in reading (see e.g., Frost, 1998), recoding should occur in the written recall condition as well. However, as mentioned above, some studies found differences in short-term memory performance as a consequence of varying recall mode. Note that even when behavioral performance does not differ between these two conditions it might be possible that brain activity shows different patterns suggesting different rehearsal strategies during the retention phase. If EEG coherence is sensitive to recall mode in the retention interval then differential patterns of brain activity (interactions) are predicted for the effects of irrelevant speech and recall mode on rehearsal. It is expected that results of the previous study (Kopp et al., 2004) are replicated in the respective conditions of the present study, that is a reduction of gamma synchronization at left frontal-central sites from *quiet* to *irrelevant speech* in the *spoken* conditions.

2. Materials and methods

2.1. Participants

Participants were 21 healthy volunteers (14 women), aged 18–32 years, native speakers of German. They were free of positive neurological histories and had normal or corrected-to-normal vision. Participants were paid or participated as part of their basic studies in psychology.

Table 1
Individual characteristics and memory performances

#	Handedness	Digit span (Digit span group)	% correctly recalled lists in *quiet spoken*	% correctly recalled lists in *speech spoken*	% correctly recalled lists in *quiet written*	% correctly recalled lists in *speech written*	Irrelevant speech effect in *written*	Performance in *quiet written* ("baseline" memory condition)
1	Right	8 (high)	60	50	86.7	73.3	Weak	High
2	Ambidextrous	5 (low)	53.3	26.7	33.3	40	No	Low
3	Right	6 (low)	13.3	3.3	53.3	16.7	Strong	Low
4	Right	5 (low)	26.7	16.7	16.7	10	Weak	Low
5	Right	5 (low)	33.3	13.3	30	6.7	Strong	Low
6	Right	8 (high)	90	76.7	86.7	90	No	High
7	Right	5 (low)	6.7	0	10	6.7	Weak	Low
8	Right	8 (high)	90	70	90	70	Strong	High
9	Right	7 (low)	36.7	13.3	43.3	16.7	Strong	Low
10	Right	8 (high)	70	43.3	70	40	Strong	High
11	Right	8 (high)	36.7	20	60	53.3	Weak	High
12	Left	7 (low)	90	33.3	90	50	Strong	High
13	Right	8 (high)	60	36.7	50	43.3	Weak	Low
14	Right	6 (low)	6.7	0	3.3	0	Weak	Low
15	Right	8 (high)	40	6.7	76.7	36.7	Strong	High
16	Right	7 (low)	70	53.3	43.3	46.7	No	Low
17	Right	8 (high)	16.7	10	10	6.7	Weak	Low
18	Right	8 (high)	60	33.3	56.7	56.7	No	Low
19	Right	6 (low)	26.7	3.3	40	13.3	Strong	Low
20	Right	9 (high)	76.7	6.7	96.7	6.7	Strong	High
21	Right	6 (low)	16.7	3.3	26.7	3.3	Strong	Low

Subgroups based on strength of irrelevant speech effect in condition *written* were formed in an attempt to explain gamma coherence. Digit spans and performances in condition *quiet written* were classified to explain coherence patterns in theta. Handedness might play an important role in left-hemispheric coherence patterns in beta.

2.2. Tasks and procedure

We used a delayed serial recall paradigm (see Fig. 1). Verbal material consisted of 120 word lists of five disyllabic concrete German nouns with four to seven letters. Concreteness was rated before the experiment by six independent raters, and abstract nouns were excluded from the lists. All word lists were matched in word frequency and semantic relatedness. We used semantically unrelated words within one list, rated and adjusted by eight independent people. No words were repeated across lists.

The five words of each list were presented sequentially on the center of a PC screen at the rate of one word per second with an inter-stimulus interval of 250 ms. This relatively fast presentation rate was supposed to prevent participants from establishing elaborated rehearsal strategies. A 10-s retention interval followed the words. In this interval participants saw only a fixation cross on the screen. At the end of the interval three question marks prompted participants to recall items in the correct order. After recall participants continued with the next trial.

This basic paradigm varied block by block in a 2 (*distraction*) × 2 (*recall mode*) design. Factor *distraction* differed during the 10-s retention interval: Condition *quiet* had no distracting material and enabled participants to subvocally rehearse items whereas in condition *speech* participants were presented with irrelevant speech via headphones. This irrelevant speech consisted of 10-s digitalized radio recordings of texts (topics from sciences, art, news etc.) without background music or noise. Speech was considered to be unattended due to instruction but causing the classic irrelevant speech effect by disturbing short-term storage. Factor *recall mode* varied between *spoken* recall, where participants had to say item lists aloud as the three question-marks appeared, and *written* recall, where participants had to write down the to-be-remembered items on a sheet of paper.

Four experimental blocks (*quiet spoken*, *speech spoken*, *quiet written*, and *speech written*) were tested with 30 trials and 3 practice trials per condition. Each trial in the spoken conditions lasted about 25 s and each trial in the written conditions lasted about 35 s. Total experimental time was about 90 min. Block order was counterbalanced across participants in terms of recall mode: 11 participants performed the spoken conditions first, 10 participants performed the written conditions first.

A

Gamma	2-4 s			6-8 s		
	Distract	Recall Mode	Distract x Recall Mode	Distract	Recall Mode	Distract x Recall Mode
Fp1-Fp2						
F7-F3						
F7-Fz	*	*	*	*	*	*
F3-Fz	*	*	*	*	*	*
F3-F4						
Fz-F4	*					
Fz-F8						
F4-F8						
T3-C3				*	*	*
T3-Cz						
C3-Cz	*	*	*	*	*	*
C3-C4	*	*	*	*	*	*
Cz-C4	*	*	*	*	*	*
Cz-T4						
C4-T4						
T5-P3		*			*	
T5-Pz						
P3-Pz		*				
P3-P4						
Pz-P4						
Pz-T6						
P4-T6						
O1-O2						
Fp1-F7						
Fp1-F3				*	*	*
Fp1-Fz						
Fp1-F4						
Fp2-F3						
Fp2-Fz						
Fp2-F4						
Fp2-F8						
F7-T3						
F7-C3						
F7-Cz						

	2-4 s			6-8 s		
	Distract	Recall Mode	Distract x Recall Mode	Distract	Recall Mode	Distract x Recall Mode
F3-T3						
F3-C3	*	*	*	*	*	*
F3-Cz	*	*	*	*	*	*
F3-C4						
Fz-T3						
Fz-C3	*	*	*	*	*	*
Fz-Cz	*	*	*	*	*	*
Fz-C4					*	
Fz-T4						
F4-C3						
F4-Cz	*			*		
F4-C4						
F4-T4						
F8-Cz						
F8-C4						
F8-T4						
T3-T5						
T3-P3	*	*	*			
T3-Pz						
C3-T5	*	*	*	*	*	*
C3-P3	*	*	*	*	*	*
C3-Pz	*					
C3-P4						
Cz-T5						
Cz-P3	*	*	*	*	*	*
Cz-Pz	*			*		
Cz-P4						
Cz-T6						
C4-P3						
C4-Pz						
C4-P4						
C4-T6						
T4-Pz						
T4-P4						

	2-4 s			6-8 s		
	Distract	Recall Mode	Distract x Recall Mode	Distract	Recall Mode	Distract x Recall Mode
T4-T6						
T5-O1						
P3-O1						
Pz-O1						
P4-O1						
P3-O2						
Pz-O2						
P4-O2						
T6-O2						
Fp1-T3						
Fp1-C3						
Fp1-Cz						
Fp2-Cz						
Fp2-C4						
Fp2-T4						
F7-T5						
F7-P3						
F3-T5						
F3-P3						
F3-Pz						
Fz-P3				*	*	*
Fz-Pz						
Fz-P4						
F4-Pz						
F4-P4						
F4-T6						
F8-P4						
F8-T6						
T3-O1						
C3-O1						
Cz-O1						
Cz-O2						
C4-O2						
T4-O2						

Fig. 3. Summary of statistical analyses in (A) gamma (35–47 Hz), (B) theta (4–7.5 Hz), (C) alpha (8–12 Hz), (D) beta (13–20 Hz) at all electrode pairs, and in periods between 2–4 and 6–8 s. An asterisk indicates significance of an effect: main effect *distract*, main effect *recall mode*, interaction *distract* and *recall mode*.

B

Theta	2-4 s			6-8 s		
	Distract	Recall Mode	Distract x Recall Mode	Distract	Recall Mode	Distract x Recall Mode
Fp1-Fp2						
F7-F3	*	*	*	*	*	*
F7-Fz		*				
F3-Fz		*				
F3-F4						
Fz-F4						
Fz-F8						
F4-F8						
T3-C3						
T3-Cz						
C3-Cz						
C3-C4						
Cz-C4						*
Cz-T4						
C4-T4	*	*		*	*	*
T5-P3						
T5-Pz						
P3-Pz						
P3-P4						
Pz-P4						
Pz-T6						
P4-T6						
O1-O2						
Fp1-F7		*				
Fp1-F3		*			*	
Fp1-Fz						
Fp1-F4						
Fp2-F3						
Fp2-Fz						
Fp2-F4						
Fp2-F8						
F7-T3						
F7-C3						
F7-Cz	*	*	*	*	*	*

	2-4 s			6-8 s		
	Distract	Recall Mode	Distract x Recall Mode	Distract	Recall Mode	Distract x Recall Mode
F3-T3						
F3-C3		*	*		*	
F3-Cz	*	*	*	*	*	*
F3-C4	*	*	*	*	*	*
Fz-T3						
Fz-C3	*	*	*	*	*	*
Fz-Cz				*	*	*
Fz-C4	*	*	*	*	*	*
Fz-T4	*					
F4-C3						
F4-Cz					*	
F4-C4		*			*	*
F4-T4						
F8-Cz						
F8-C4						
F8-T4					*	
T3-T5						
T3-P3						
T3-Pz						
C3-T5						
C3-P3						
C3-Pz						*
C3-P4	*					*
Cz-T5						
Cz-P3						
Cz-Pz						
Cz-P4						
Cz-T6	*	*	*	*	*	*
C4-P3		*				
C4-Pz			*			
C4-P4						
C4-T6	*	*	*	*	*	*
T4-Pz						
T4-P4	*	*	*	*	*	*

	2-4 s			6-8 s		
	Distract	Recall Mode	Distract x Recall Mode	Distract	Recall Mode	Distract x Recall Mode
T4-T6	*	*	*	*	*	*
T5-O1						
P3-O1						
Pz-O1						
P4-O1						
P3-O2						
Pz-O2				*	*	*
P4-O2						
T6-O2	*					
Fp1-T3						
Fp1-C3	*	*	*	*	*	*
Fp1-Cz	*	*	*	*	*	*
Fp2-Cz						
Fp2-C4						
Fp2-T4						
F7-T5						
F7-P3						
F3-T5						
F3-P3	*	*	*	*	*	*
F3-Pz	*	*	*	*	*	*
Fz-P3	*	*	*	*	*	*
Fz-Pz	*	*	*	*	*	*
Fz-P4	*	*	*	*	*	*
F4-Pz	*	*	*			
F4-P4	*	*	*		*	
F4-T6	*					
F8-P4						
F8-T6						
T3-O1						
C3-O1						
Cz-O1						
Cz-O2						
C4-O2					*	
T4-O2	*					

Fig. 3 (*continued*).

Before the experiment a forward digit span task (see e.g. Wilde et al., 2004) was performed to measure working memory capacity: The experimenter read lists of single-digit items aloud at a rate of 1 s per item. Immediately after the last item the participant had to repeat the list in the correct order. The test began with a series of three items presented for recall and continued to a maximum of nine items. There were two trials at each series length. Failure to reproduce both trials of a series length lead to termination of the test and digit span was defined as the maximum of items of one list the participant was able to recall. A differential analysis of EEG coherence data due to working memory capacity required the formation of participant groups: Participants with a digit span of five, six, or seven were classified as having a low working memory capacity and participants with a digit span of eight or nine were classified as having a high working memory capacity.

Since we were aware of the difficulty to relate coherence results to behavioral data we decided to interview participants after the experiment about their rehearsal strategies (phonological rehearsal, visual rehearsal, formation of associations etc.) and obtained subjective reports on task difficulties between the four experimental conditions.

2.3. EEG acquisition and analysis

EEG was recorded using 19 Ag–AgCl electrodes according to the 10–20 system, horizontal and vertical EOG, and the nose as reference. Impedances were less than 5 kÙ. The band pass was set between 0.5 and 50 Hz, with a 50 Hz Notch filter switched on. EEG signals were recorded and digitalized by a Synamps 32-channel amplifier (Neuroscan Inc.) with a sample rate of 250 Hz throughout the experiment.

To compute coherence we used a procedure developed by Schack (Schack et al., 1999). A model-based parametric approach based on autoregressive moving average models (model orders $p=15$ and $q=5$) with time-varying parameters (for details see also Schack and Krause, 1995). The most important difference to the classic coherence calculation is that the problem of nonstationarity of EEG signals is avoided. The procedure is adaptive as the model parameters are adjusted at every sample point and thus the calculation is closer to process dynamics.

We calculated the duration of high coherence, i.e. the sum of all periods of coherence levels above the threshold of 0.7, reflecting long-lasting high synchronization between associated

C

Alpha	2-4 s			6-8 s				2-4 s			6-8 s				2-4 s			6-8 s		
	Distract	Recall Mode	Distract x Recall Mode	Distract	Recall Mode	Distract x Recall Mode		Distract	Recall Mode	Distract x Recall Mode	Distract	Recall Mode	Distract x Recall Mode		Distract	Recall Mode	Distract x Recall Mode	Distract	Recall Mode	Distract x Recall Mode
Fp1-Fp2							F3-T3							T4-T6						
F7-F3	*			*	*	*	F3-C3							T5-O1						
F7-Fz	*	*	*				F3-Cz							P3-O1						
F3-Fz		*					F3-C4							Pz-O1						
F3-F4							Fz-T3							P4-O1						
Fz-F4							Fz-C3	*	*	*			*	P3-O2						
Fz-F8							Fz-Cz	*	*	*			*	Pz-O2						
F4-F8					*		Fz-C4				*	*	*	P4-O2						
T3-C3							Fz-T4				*	*	*	T6-O2						
T3-Cz							F4-C3	*	*	*				Fp1-T3	*	*	*	*	*	*
C3-Cz							F4-Cz							Fp1-C3						
C3-C4							F4-C4					*	*	Fp1-Cz						
Cz-C4							F4-T4				*	*	*	Fp2-Cz				*	*	*
Cz-T4							F8-Cz							Fp2-C4	*	*	*			
C4-T4							F8-C4							Fp2-T4	*	*	*			
T5-P3							F8-T4							F7-T5						
T5-Pz							T3-T5							F7-P3	*	*	*			
P3-Pz	*						T3-P3							F3-T5				*	*	*
P3-P4							T3-Pz							F3-P3						
Pz-P4							C3-T5							F3-Pz						
Pz-T6							C3-P3	*	*	*	*	*	*	Fz-P3	*	*	*	*	*	*
P4-T6							C3-Pz							Fz-Pz						
O1-O2							C3-P4							Fz-P4				*	*	*
Fp1-F7							Cz-T5							F4-Pz	*	*	*			
Fp1-F3							Cz-P3							F4-P4	*	*	*	*	*	*
Fp1-Fz							Cz-Pz							F4-T6	*	*	*	*	*	*
Fp1-F4							Cz-P4							F8-P4	*	*	*			
Fp2-F3							Cz-T6							F8-T6				*	*	*
Fp2-Fz							C4-P3							T3-O1						
Fp2-F4						*	C4-Pz						*	C3-O1						
Fp2-F8		*					C4-P4							Cz-O1						
F7-T3							C4-T6	*						Cz-O2						
F7-C3	*	*	*	*	*	*	T4-Pz							C4-O2						
F7-Cz	*	*	*				T4-P4							T4-O2						

Fig. 3 (*continued*).

brain structures. Generally, we hypothesize that long-lasting high synchronizations are significant for rehearsal in short-term memory. In particular, Tallon-Baudry et al. (1999) found prolonged gamma activity in continuous rehearsal vs. transient memory at single electrode positions. We hypothesize that a prolongation in gamma band activity at single electrode sites (Tallon-Baudry et al., 1999) provides a basis for an increase in the duration of coherent gamma band activity between electrode sites (present study). We calculated frequency-band-specific coherence histograms for several electrode pairs. An analysis of these histograms revealed that variability of coherence values started around 0.7. In other words, with lower coherence values the histograms are relatively small and do not distinguish between different electrode pairs.

EEG coherence was analysed within the 10-s retention interval. To achieve a sufficient amount of artefact-free trials, coherence durations were computed for 2-s periods only. We chose the 2–4 and the 6–8 s periods after onset of the retention interval. That is, the first period is in the early phase of the retention interval while the second is in the late phase. Although we did not expect differences with regard to the effects of recall mode between these two phases, it should be ensured to find them if they exist. All trials in which EEG variability for the respective period exceeded a standard deviation of 50 μV were discarded as artefacts for further analysis. This criterion turned out to be suited in detecting eye-blinks and excessive muscular activity.

As we were interested in differential EEG coherence effects of recall mode on the irrelevant-speech effect, the rational for analysing the data was as follows:

From the 171 possible electrode combinations, those 102 were selected which had a distance that did not exceed 3 positions on the 10–20 system (for example, for F7 coherences were computed with Fp1, F3, Fz, T3, C3, Cz, T5, P3). This was done to achieve a balance between including electrode pairs that turned out to be promising according to previous research (Kopp et al., 2004) and not to include too many in order to avoid that Bonferroni adjustment will demand an unrealistic high degree of power.

For each of the 102 combinations, coherence was computed for the gamma (35–47 Hz), beta (13–20 Hz), alpha (8–12 Hz), and theta (4–7.5 Hz) bands. For each combination, the durations of high coherence were analysed with a 2 (factor *distraction*: *quiet* vs. *irrelevant speech*) × 2 (factor *recall*

D

Beta	2-4 s			6-8 s				2-4 s			6-8 s				2-4 s			6-8 s		
	Distract	Recall Mode	Distract x Recall Mode	Distract	Recall Mode	Distract x Recall Mode		Distract	Recall Mode	Distract x Recall Mode	Distract	Recall Mode	Distract x Recall Mode		Distract	Recall Mode	Distract x Recall Mode	Distract	Recall Mode	Distract x Recall Mode
Fp1-Fp2							F3-T3		*	*		*	*	T4-T6		*				
F7-F3							F3-C3					*		T5-O1		*				
F7-Fz							F3-Cz							P3-O1		*	*		*	*
F3-Fz							F3-C4							Pz-O1						
F3-F4							Fz-T3		*	*		*	*	P4-O1						
Fz-F4							Fz-C3					*	*	P3-O2						
Fz-F8							Fz-Cz						*	Pz-O2						
F4-F8							Fz-C4							P4-O2						
T3-C3		*	*		*	*	Fz-T4							T6-O2						
T3-Cz		*	*		*	*	F4-C3							Fp1-T3						
C3-Cz							F4-Cz							Fp1-C3		*	*		*	*
C3-C4			*		*	*	F4-C4							Fp1-Cz						
Cz-C4						*	F4-T4							Fp2-Cz						
Cz-T4							F8-Cz							Fp2-C4						
C4-T4							F8-C4			*				Fp2-T4						
T5-P3							F8-T4							F7-T5						
T5-Pz			*			*	T3-T5			*		*	*	F7-P3						
P3-Pz		*	*				T3-P3		*	*		*	*	F3-T5					*	
P3-P4							T3-Pz		*	*		*	*	F3-P3		*	*		*	*
Pz-P4							C3-T5					*	*	F3-Pz						
Pz-T6							C3-P3							Fz-P3					*	*
P4-T6		*					C3-Pz							Fz-Pz		*	*		*	*
O1-O2							C3-P4							Fz-P4						
Fp1-F7		*	*				Cz-T5							F4-Pz						
Fp1-F3			*				Cz-P3			*				F4-P4						
Fp1-Fz							Cz-Pz						*	F4-T6						
Fp1-F4							Cz-P4							F8-P4						
Fp2-F3							Cz-T6							F8-T6						
Fp2-Fz	*						C4-P3							T3-O1			*		*	*
Fp2-F4	*						C4-Pz							C3-O1		*	*			
Fp2-F8							C4-P4							Cz-O1					*	
F7-T3		*					C4-T6					*		Cz-O2			*			
F7-C3							T4-Pz							C4-O2						
F7-Cz			*				T4-P4							T4-O2						

Fig. 3 (*continued*).

mode: *spoken* vs. *written*) repeated measures ANOVA. The alpha-level was set to 0.05. An alpha-error adjustment to avoid spurious effects was performed according to the method of Bonferroni (0.05/102).

3. Results

3.1. Behavioral results

Percentages of completely recalled lists per condition served as the dependent variable for behavioral performance (Fig. 2). Statistical analyses (ANOVA) revealed a significant main effect for *distraction* [$F(1,20)=26.93$; $p<.001$] with a pronounced decline of performance in *speech* compared to *quiet*, i.e. the classic irrelevant speech effect. A main effect was also found for *recall mode* [$F(1,20)=4.78$; $p<.041$] with advantages in performance for *written* compared to *spoken*. There was no interaction between *distraction* and *recall mode*.

Individuals showed considerable variability in behavioral performance. In Table 1 individual characteristics (digit span, handedness, memory performances) are presented. These data were considered later in the analysis of EEG coherences. All participants reported that *written* conditions had been easier to perform than *spoken* conditions and that *quiet* conditions had been easier to perform than *speech* conditions. Also all participants described their rehearsal strategy as phonological. Any attempts to establish more elaborated strategies, such as remembering the first letters, forming associations and stories, or forming visual patterns had to be given up already during the practice trials due to fast item presentation rate.

3.2. Coherence data

The analysis of 2-s periods (2–4 and 6–8 s after onset of retention interval) achieved the following numbers of artefact-free trials: for the 2–4 s period a mean number of trials of 27.33 (SD=2.08) in *quiet spoken*, 27.57 (SD=2.6) in *speech spoken*, 28.05 (SD=2.5) in *quiet written*, 28.43 (SD=2.62) in *speech written*, and for the 6–8 s period a mean number of trials of 27.67 (SD=2.18) in *quiet spoken*, 27.67 (SD=2.44) in *speech spoken*, 28.29 (SD=2.74) in *quiet written*, 28.38 (SD=2.56) in *speech written*.

In Fig. 3A–D statistical results are illustrated for the selected electrode pairs, frequency bands and for the 2–4 s period and for the 6–8 s period with an asterisk indicating significant data. This kind of illustration of results was chosen to provide the reader with all significant main effects and interactions and, at the same time, to avoid an overload with F and p values. Moreover, we report the range of F values for electrode pairs showing significant effects (all p values <.05) . As results are similar for the 2–4 and the 6–8 s period further figures illustrate results of the 2–4 s period exemplarily.

In Fig. 4 the duration of high coherence is presented for the gamma frequency band. Statistical analyses revealed a main effect for *distraction* [$F(1,20)$ range from 4.23 to 15.23 (2–4 s), $F(1,20)$ range from 4.34 to 14.10 (6–8 s)], a main effect for *recall mode* [$F(1,20)$ range from 4.26 to 17.99 (2–4 s), $F(1,20)$ range from 4.09 to 20.22 (6–8 s)] and a significant interaction of *distraction* and *recall mode* [$F(1,20)$ range from 4.90 to 22.14 (2–4 s), $F(1,20)$ range from 4.39 to 17.96 (6–8 s)] on coherence durations at central and left frontal and additionally at left centro-temporal and centro-parietal electrode combinations. Coherence duration decreased for *speech* compared to *quiet* at these electrode pairs, but only for the *spoken* conditions. In *written* there is no significant difference between *quiet* and *speech*. Since the latter result was contrary to our hypothesis we focused on the formation of subgroups of participants based on behavioral results, which turned out to be

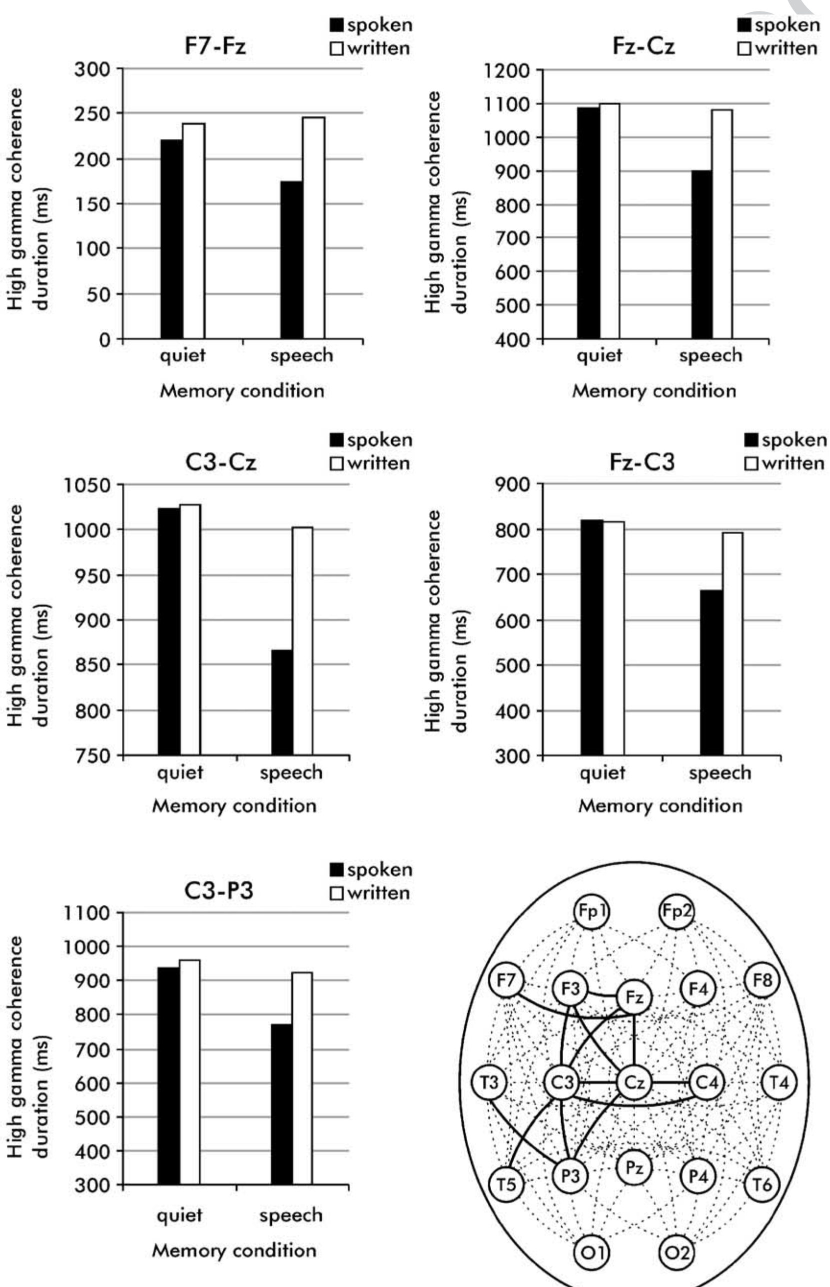

Fig. 4. Duration of high coherence in gamma (35–47 Hz). Solid lines in the bottom-right figure illustrate the network of electrode combinations that showed a consistent significant pattern which is represented for five selected electrode pairs by way of example. Faint lines in the bottom-right figure indicate all electrode combinations that were analyzed but did not reveal significant effects.

a promising procedure in our previous study (Kopp et al., 2004). Behavioral data of the present experiment revealed a pronounced irrelevant speech effect in *spoken* recall for all participants but showed some variation in recall performance in *written* recall: Only 10 out of 21 participants showed a strong decline of memory performance in the *irrelevant speech* condition whereas 11 participants showed only a weak or no decrease of behavioral performance from *quiet* to *speech* (see Table 1). We hypothesized that participants with a strong irrelevant speech effect in the *written* condition might possibly show a similar reduction of synchronization as in the *spoken* condition but this was actually not the case: A comparison between participants with weak and strong irrelevant speech effect revealed no significant differences of the coherence patterns in gamma. Thus, the formation of participant subgroups was not adequate to explain the difference between *spoken* and *written* recall mode.

Coherence results for the theta band are illustrated in Fig. 5. As one can see, mainly fronto-parietal electrode pairs form a consistent coherence pattern completed by left fronto-central and right centro-parietal and centro-temporal electrode combinations. Here we found a main effect of *distraction* [$F(1,20)$ range from 4.05 to 16.96 (2–4 s), $F(1,20)$ range from 4.98 to 14.22 (6–8 s)], a main effect of *recall mode* [$F(1,20)$ range from 4.22 to 33.65 (2–4 s), $F(1,20)$ range from 4.50 to 22.88 (6–8 s)], and a significant interaction of *distraction* and *recall mode* [$F(1,20)$ range from 4.59 to 15.44 (2–4 s), $F(1,20)$ range from 4.26 to 17.64 (6–8 s)] on coherence durations. Duration of high coherence increased significantly from *quiet* to the *speech* condition in *written* recall but not in *spoken* recall.

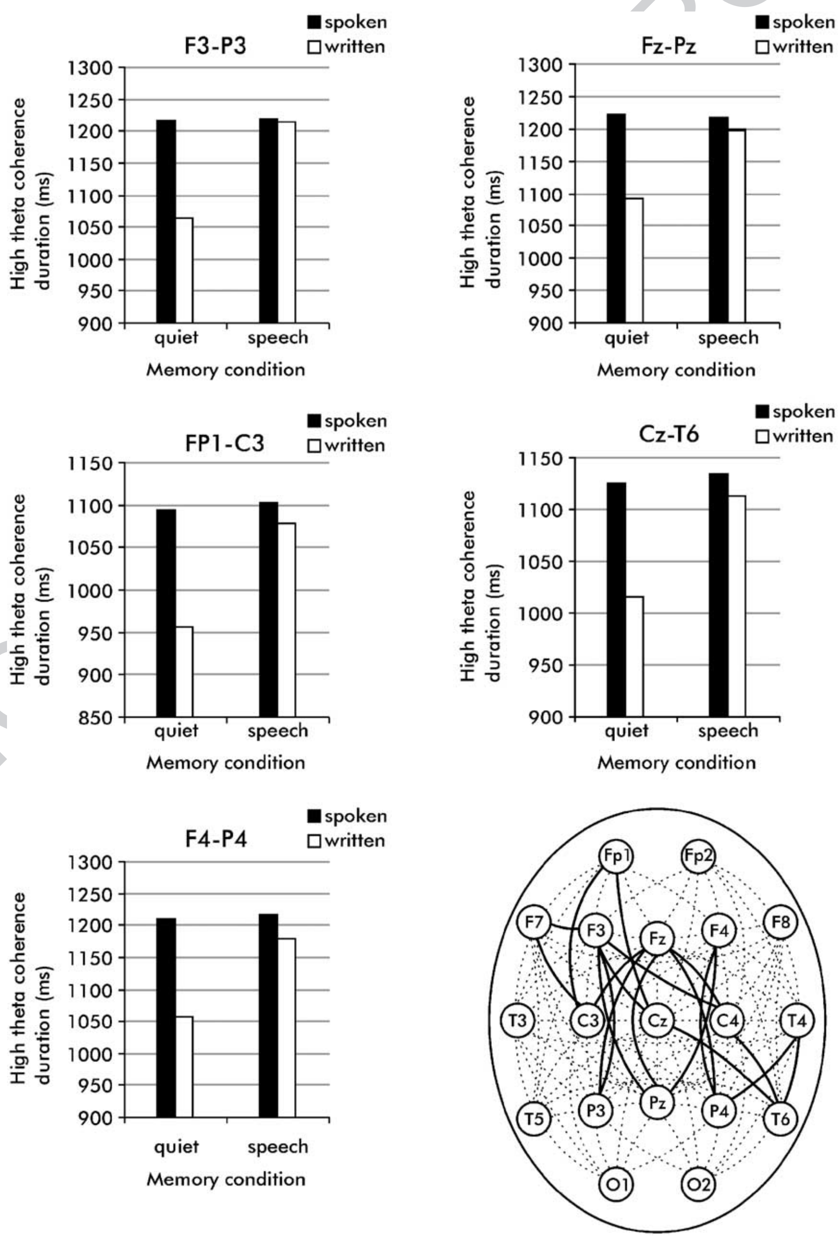

Fig. 5. Results of coherence analysis in theta (4–7.5 Hz). Examples of electrode combinations showing a significant pattern are illustrated in the graphs. The topographic map shows that predominantly fronto-parietal electrode pairs reveal this pattern (solid lines).

Increased fronto-parietal coherence in theta has repeatedly been reported to occur in working memory tasks (Sarnthein et al., 1998; Sommerfeld et al., 1999; Weiss et al., 2000). These results are commonly interpreted as an indicator of working memory capacity or mental effort required to solve working memory demands. To explain the theta coherence pattern in our experiment and to relate our results to existing findings in literature we decided to investigate this pattern in more detail which led again to the formation of subgroups of participants. As a control indicator of working memory capacity we used the measure of digit span and divided participants into two groups: 11 participants with low digit span (five, six, or seven) and 10 participants with high digit span (eight or nine). The same principle was applied to the behavioral data of the easiest experimental condition – *quiet* in *written* recall – that we used as a kind of “baseline” measure of working memory capacity in this task to form again two subgroups: 13 participants with low and 8 participants with high performance in *quiet* with *written* recall. The classification according to “baseline” memory capacity was somehow arbitrary. Performance in *quiet written* was classified as high when it reached a level of 60% correctly recalled word lists or higher. It is important to note that the classification according to working memory capacity (digit span) and task-specific capacity (performance in *quiet written*) were not confounded with the subgroups according to strength of irrelevant speech effect (see results in gamma above), i.e., low-span participants were not more distracted by irrelevant speech than high-span participants and vice versa.

Participant groups based on digit span and those based on behavioral performance overlapped largely, and statistical analyses led to similar results for both types of group

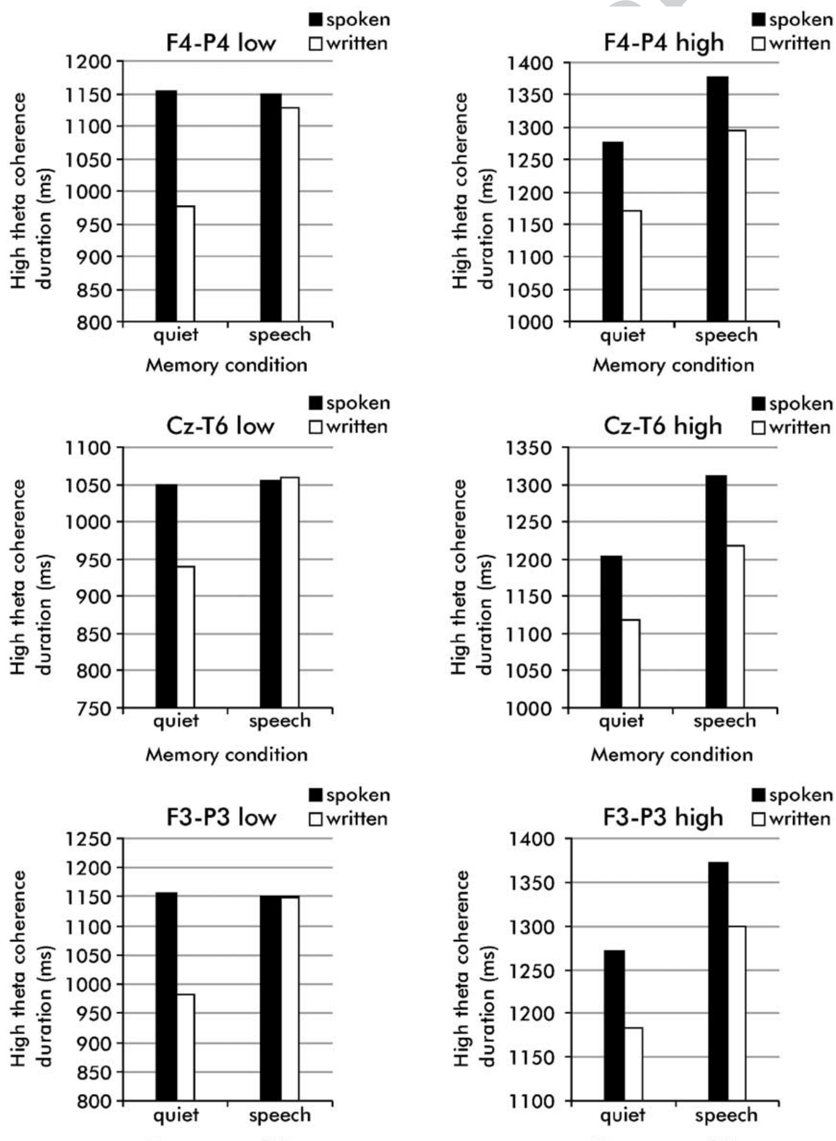

Fig. 6. Differentiation in theta (4–7.5 Hz) between participants with low and high working memory capacity. Three examples of electrode pairs were selected to illustrate that only participants with low working memory capacity showed an interaction between distraction and recall mode in theta suggesting processing differences compared to participants with high working memory capacity.

formation. Therefore only the results of the comparison of participants with low and high recall performance in the *quiet* condition with *written* recall are reported here (Fig. 6). Statistical analysis revealed a main effect of *recall mode* on theta coherence duration in both participant groups [$F(1,12)$ range from 4.73 to 20.69 (2–4 s), $F(1,12)$ range from 4.36 to 15.02 (6–8 s) in participants with low recall performance, $F(1,7)$ range from 4.31 to 8.46 (2–4 s), $F(1,7)$ range from 4.27 to 12.46 (6–8 s) in participants with high recall performance], but only participants with high performance showed a main effect of *distraction* [$F(1,7)$ range from 5.20 to 20.66 (2–4 s), $F(1,7)$ range from 4.69 to 12.96 (6–8 s)], and only low-performance participants showed a significant interaction of *distraction* and *recall mode* [$F(1,12)$ range from 4.56 to 14.59 (2–4 s), F (1,12) range from 4.31 to 8.75 (6–8 s)].

Fig. 7 shows results of the analysis of duration of high coherence in the alpha frequency band. The consistent coherence pattern found in alpha is similar to that in theta: there was a main effect of *recall mode* [$F(1,20)$ range from 4.88 to 16.21 (2–4 s), $F(1,20)$ range from 4.66 to 10.35 (6–8 s)], a main effect of *distraction* [$F(1,20)$ range from 3.91 to 17.85 (2–4 s), $F(1,20)$ range from 4.51 to 22.84 (6–8 s)], and a significant interaction of *distraction* and *recall mode* [$F(1,20)$ range from 4.34 to 7.38 (2–4 s), $F(1,20)$ range from 4.58 to 17.61 (6–8 s)] on duration of high coherence. As in theta, coherence duration increased from *quiet* to

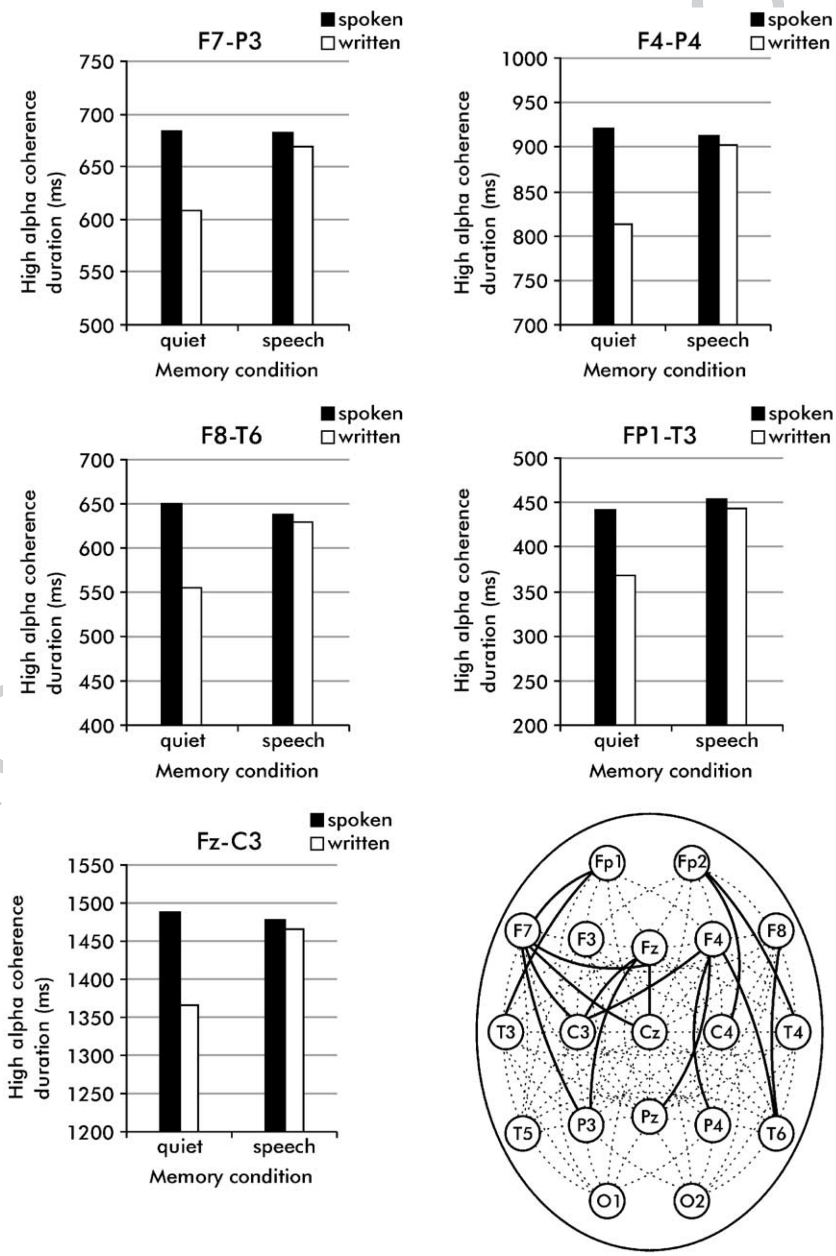

Fig. 7. Duration of high coherence in alpha (8–12 Hz). The pattern and electrode pairs illustrated here are similar to those of theta (see Fig. 5). Electrode combinations showing the significant coherence pattern as selectively represented in the graphs are more laterally distributed (solid lines in the topographic map) than in theta.

speech in the *written* but not in the *spoken* condition. The electrode combinations involved were also similar to those in theta, i.e. fronto-parietal and left fronto-central electrode pairs, but altogether more laterally distributed than in theta.

Results for coherence duration in the beta frequency band are presented in Fig. 8. No main effect of *distraction* was found, but there was a main effect of *recall mode* [$F(1,20)$ range from 4.97 to 15.56 (2–4 s), $F(1,20)$ range from 4.40 to 13.97 (6–8 s)], and a significant interaction of *distraction* and *recall mode* [$F(1,20)$ range from 4.96 to 13.64 (2–4 s), $F(1,20)$ range from 4.19 to 10.04 (6–8 s)] on durations of high coherence. *Spoken* and *written* recall differed significantly under the condition of *irrelevant speech* with *spoken* revealing shorter beta coherence duration at left-hemispheric leads.

4. Discussion

4.1. Gamma coherence and memory rehearsal

In a previous experiment (Kopp et al., 2004) we investigated the disruptive effect of irrelevant speech in a highly similar delayed serial recall paradigm with spoken recall only. As the most important result we found gamma coherence decreases at central and left frontal electrode combinations during the retention interval. These results were fully replicated in the

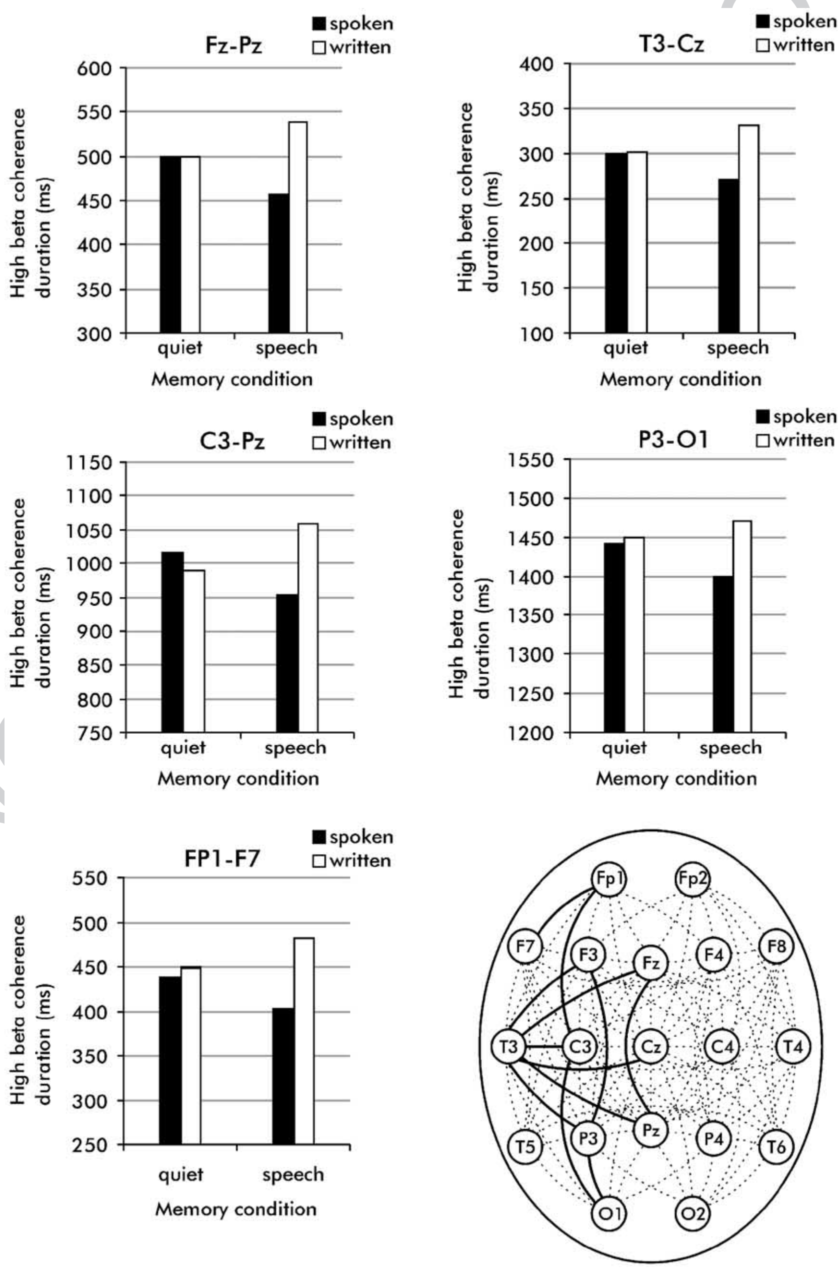

Fig. 8. Beta (13–20 Hz) coherence durations. A left-hemispheric network of electrode combinations showed a significant difference between the recall modes in the speech condition. The graphs again illustrate this pattern for five selected electrode pairs whereas the topographic map shows all electrode pairs revealing these significant effects (solid lines).

spoken condition of the present experiment. The neural basis for the classic irrelevant speech effect well studied in behavioral research (Colle and Welsh, 1976; Salamé and Baddeley, 1982, 1989) seems to be a disruption of left frontal and central networks in gamma. EEG coherence turned out to be a reliable measure in our study, particularly duration of high coherence — a rather rarely applied measure. This is an important outcome since reliability is a prerequisite for acceptance of coherence results (Harmony et al., 1993).

Regarding gamma coherence in *written* recall, however, no decrease in central or left frontal electrode combinations was found from *quiet* to *irrelevant speech*. Behavioral data suggest that written recall is somehow easier to accomplish than spoken recall. This view is supported by all participants, who reported subjectively easier written conditions. There may be several reasons for this effect. First, following the participants' reports, one may postulate a sort of facilitation of executive functions while writing down the to-be-remembered items. Second (see also Introduction), Craik (1970) who found a superiority of written recall performance hypothesized that writing down the answers allows simultaneous rehearsal of the last items that are then better recalled. In contrast, in spoken recall articulating the first few items may interfere with the information retained in short-term memory. Third, Brimer and Mueller (1979) assume that participants review their written outputs and could use them as retrieval cues to access unrecalled items. All explanations relate to the recall process. By using online measures in our experiment, however, we were able to demonstrate that interference due to recall mode is already present at the stage of rehearsal.

The behavioral superiority effect of written recall as found in this and in other studies (Craik, 1970; Murray, 1965) raises the question of whether or not written recall is too easy to reduce high gamma coherence in irrelevant speech at all. Our behavioral data argue against this view: A pronounced irrelevant speech effect was found in *written* as well as in *spoken* conditions. Formation of subgroups in coherence analysis of gamma activity did not clarify the problem of absence of effects in the gamma range. Participants with a strong irrelevant speech effect in *written* did not show any decrease in the duration of high gamma coherence from *quiet* to *speech* either. Inspection of the EEG data did not reveal the opposite coherence pattern at other electrode sites or frequency bands, i.e., a decrease of high gamma coherence in *written* from *quiet* to *speech* with simultaneously constant coherences in *spoken* recall.

Although behavioral performance in this study (main effect of *recall mode* without interaction between *distraction* and *recall mode*) points to the idea that rehearsal processes in *spoken* and *written* recall tasks – though different in quantity – are qualitatively similar, synchronization patterns of brain activity give another picture. Results show a clear interaction between *distraction* and *recall mode* in duration of high gamma coherence. There might be a fundamental difference in the way how participants retain items in *written* compared to *spoken* recall. Walker and Hulme (1999) found significant effects for word length and concreteness of nouns on recall performance in a serial recall task. However, these effects occurred both in spoken and in written recall mode. Walker and Hulme concluded that word length and concreteness affect memory tasks at a processing stage prior to the point where written and spoken recall become separate processes. Our data suggest that the influence of recall mode begins at a relatively early stage, i.e. irrelevant speech and recall mode already interact during the rehearsal interval.

An important factor is how people rehearse items. In this serial recall task we prompted participants to rehearse subvocally by using a relatively short presentation time per item. This procedure limits the possibility of constructing more elaborative representations or developing visual strategies like memorizing in a visuo-spatial way or forming visual or other kinds of associations. Participants indeed confirmed this.

Nevertheless, coherence patterns suggest that there must have been some difference between *written* and *spoken* during rehearsal. A promising idea is the assumption of a parallel visual code that contributes to recall performance as well. Logie et al. (2000) found a visual similarity effect for visually presented words and its interaction with the articulatory suppression effect. They concluded that participants rely on subvocal rehearsal but when this is disturbed, the visual code remains available to support recall. A similar model came from Rönnberg and Nilsson (1987) who hypothesized that the visual system has a "richer" spectrum of processing options than the auditory system and when auditory pathways are disrupted, people can still choose between different visual processing options. This fact, for example, allows deaf people to compensate better in verbal short-term memory tasks than blind people (Rönnberg and Nilsson, 1987). Penney (1989) reviewed studies that investigated short-term storage of auditory and visual items and suggested a separate-stream hypothesis: Visual items, in contrast to auditory items, are retained both in a phonological and in a visual code. Some evidence for a dual-route theory (Coltheart et al., 1993) comes from neuroanatomical studies. Specific structures in the brain were identified that show enhanced activity when visual word forms are stored directly from sensory visual input whereas a separate stream goes via phonological recoding (Fiebach et al., 2002; Jobard et al., 2003). These kinds of mechanisms can be transferred to the present experimental situation. With visual presentation and written recall, a parallel visual code, operating in addition to phonological rehearsal, may remain more strongly activated than with spoken recall.

Finally, recall in the non-spoken mode may be easier because interference by auditory distraction (irrelevant speech) is attenuated or compensated. Considered that irrelevant speech meets the auditory modality of spoken recall while it does not with written recall the difference may be explained in an attentional context. Differential effects of visual and auditory attention within and between modalities are in line with this explanation (Alho et al., 2003; Talsma and Kok, 2001, 2002; Vorobyev et al., 2004). One possibility to further explore the interaction of recall mode and distraction by irrelevant speech, and the main effect of recall mode is the random presentation of trials with written and spoken recall (in contrast to our block by block design). Participants would not be able to anticipate recall mode which should affect rehearsal. Moreover, it is necessary to compare results with auditory presentation of memory items and with visual presentation of distractor items.

4.2. Fronto-parietal theta/alpha coherence and working memory demands

As for theta, fronto-posterior synchronizations have been found to be associated to working memory demands (Sarnthein et al., 1998; Sauseng et al., 2004; Sommerfeld et al., 1999) and are often interpreted as an indicator of capacity or task difficulty with increasing working memory load. This interpretation is again confirmed in our analysis of subgroups according to digit span and according to behavioral "baseline" performance. Considering patterns of the duration of high theta synchronizations in this study, participants with high working memory capacity or high behavioral performance seem to be able to decrease fronto-posterior theta coherence values in the condition *quiet* in *spoken* recall, whereas participants with low digit span or low performance are not able to do so but need to maintain the high level of theta synchronization in this difficult experimental condition. An alternative explanation could be that condition *speech* in *spoken* recall is such a difficult and demanding one (confirmed by behavioral performance and subjective reports) that participants with low working memory capacity have some kind of ceiling effect in their theta synchronization and are not able to increase this synchronization anymore in case of a further increase of working memory demands or at least they may not be able to maintain high theta synchronizations for a long period of time.

A similar pattern of coherence was found in the alpha band with similar statistically significant results and similar electrode positions. This is not surprising considering findings of co-occurring theta and alpha coupling in synchronization studies (Von Stein et al., 2000; Von Stein and Sarnthein, 2000). Sauseng et al. (2005) report a parallel increase of theta long-range coherence and a decrease of upper alpha short-range connectivity correlated to executive demands in working memory. Schack et al. (2005) found a load dependent increase in phase coupling between theta and upper alpha in a memory scanning task. These results and findings from Klimesch et al. (1999) suggest that a further refinement in lower and upper alpha could be effective to explain alpha activity in the memory paradigm in more detail.

4.3. Left-hemispheric beta coherence increase with irrelevant speech in written recall

The role of beta EEG responses is of increasing interest in cognitive processes, for example in face recognition (Özgören et al., 2005), mental arithmetic (Mizuhara et al., in press), in retention of sentences (Haarmann and Cameron, 2005), and semantic–pragmatic integration in sentence comprehension (Weiss et al., 2005). In our study coherence results of the beta band might reflect language-specific processes. This view is supported by several coherence studies reporting specific left-hemispheric beta coherence changes as a function of modality-independent language processes or search processes in semantic memory (Supp et al., 2004; Weiss and Rappelsberger, 1996). Furthermore, beta activity is also closely related to motor learning and motor preparation and execution (Alegre et al., 2004; Andres and Gerloff, 1999; Kilner et al., 2004; Stancak and Pfurtscheller, 1996, 1997). The significant effect of *recall mode* in our study leads to the assumption that different preparatory mechanisms are started for different motor actions (*spoken* vs. *written* recall) during the retention interval. The pronounced difference between the recall modes under the condition of irrelevant speech indicates a stronger involvement of left-hemispheric activities in preparing writing sequences. Auditorily presented irrelevant speech could possibly interfere more in *spoken* than in *written*. In order to relate left-hemispheric activity changes to motor processes we analyzed handedness of participants post hoc (Edinburgh inventory, Oldfield, 1971). Having excluded left-handed (one) and ambidextrous (one) participants (for individual handedness see Table 1) the remaining right-handed participants were found to show the observed beta coherence pattern, whereas left-handed and ambidextrous people did not. However, results of only two participants are not representative and should be analyzed explicitly in further experiments.

4.4. Conclusion

To summarize, we found that EEG coherence during short-term verbal rehearsal and distraction of rehearsal by irrelevant speech depends on recall mode. The written mode is easier than the spoken mode as behavioral data show. Behavioral measures were not sensitive to the differential influence of recall mode on the irrelevant speech effect. Nevertheless, coherence patterns show pronounced interactions between recall mode and distraction in gamma, theta, alpha and beta frequency bands reflecting clear processing differences prior to recall. With respect to psychological theories of the irrelevant speech effect our results confirm the idea that irrelevant speech affects phonological rehearsal of to-be-remembered items (Baddeley, 2000) and/or their serial order (Jones et al., 1992). Importantly, EEG coherence as an online measure of brain activity revealed that the effects extend from the early period of irrelevant speech presentation (2–4 s) until late periods (6–8 s). Moreover, the present results revealed that irrelevant speech exerts its effects in several ways as indicated by differential effects in gamma, theta/alpha, and beta bands. This suggests that there is not a single mechanism underlying the irrelevant speech effect or, instead, the irrelevant speech effect is instantiated in a rather complex manner involving many sub-processes. The influence of recall mode on the effects of irrelevant speech support this notion.

On a more general level, the present data deliver additional evidence that induced and evoked gamma band activity at a single site (Herrmann et al., 2004; Tallon-Baudry et al., 1999) and gamma coherence between different sites (e.g. Miltner et al., 1999) are related to basic memory operations such as encoding, rehearsal and retrieval. Aspects of working memory demand, however, were reflected in fronto-posterior synchronization of theta and alpha band being consistent with previous studies (e.g. Sarnthein et al., 1998; Sauseng et al., 2005). Note that networks involved in different aspects of this memory task may even overlap (left fronto-central electrode combinations in gamma, theta, and alpha). Thus, within the same task the brain processes different aspects not only in different brain areas as neuroimaging studies indicate (e.g. Gisselgard et al., 2003) but codes these different processes in the frequency domain as well.

5. Uncited reference

Lisman and Idiart, 1995

Acknowledgements

We thank Esther Herrmann, Jan Peters, and Frank-Michael Schleif for their assistance in data acquisition and analysis and Erdmute Sommerfeld and Bärbel Schack for helpful comments on EEG coherence. This work was supported by DFG.

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