

IN order to study the neurophysiological correlates of working memory for different types of information, event-related brain potentials (ERPs) were recorded during a visual spatial and visual as well as auditory duration memory tasks. From stimulus onset to 500 ms ERPs were distinguishable by allocation to visual or auditory modality. From 500 to 2000 ms after stimulus onset, the spatial task generated a parieto-occipital focused negative slow wave, while corresponding ERPs of the temporal task showed a negative slow wave with frontolateral focus. From 1200 to 5500 ms a large positivity was found for the auditory temporal task and for good performers of the visual temporal task. The data suggest a distinction of three processing phases: modality-specific encoding, information-specific encoding and retention in conjunction with modality-specific inhibition processes.

Key words: Event-related potential; Frontal lobe; Slow waves; Temporal/spatial information; Working memory; Visually/auditory

Electrophysiological correlates of temporal and spatial information processing

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Introduction

While studies on temporal information processing traditionally focused on psychophysical aspects,¹ more recent work on temporal information processing has concentrated on cognitive aspects such as memory and attention. Two main models of temporal information processing have evolved: 'storage size' models consider subjective sensation of duration to be a by-product of general information processing and reject the idea of an internal timing mechanism as well as the independent notion of temporal information.² According to this view, duration judgment is a function of the amount of (non-temporal) information processed during the to-be-judged interval, as it is shown to be affected by factors such as non-temporal information processing load³ or number of contextual changes in a judged interval.⁴ In contrast, proponents of 'attentional' models argue that duration is one of the attributes of any stimulus and, therefore, is information that can be selectively attended to.⁵ They stress the need for a specific timing mechanism⁶ that can be triggered by attention.^{7,8} This timing mechanism has recently been discussed in the context of the functional meaning of the prefrontal cortex.^{9–11}

It is generally agreed that on-line processing of temporal information, such as comparing two duration intervals, requires operations of the working memory.^{12–14} The notion of working memory used here refers to a modular account of a system conceptualized as consisting of several components: a central

executive for decision and control processes and at least two subsystems, specialized for phonological and visuo-spatial information processing.¹⁵ However, despite the extensive body of evidence in support of this multi-component model of working memory, the issue of the actual number of its substructures and their neurophysiological specificity requires further research. Additional subdivision of the so-called visuo-spatial sketch-pad, supporting visuo-spatial processing, into a 'what-system' supporting object processing and a 'where-system' responsible for processing spatial information,¹⁶ as well as that of the phonological loop supporting different aspects of phonological processing,¹⁷ are currently under discussion. The multi-component model of working memory and the timer model of temporal information processing were recently brought together by considering an additional component, the 'context timing signal', to explain particular time-related aspects during phonological processing.¹⁸

The present study addressed the issue of how duration as a specific type of temporal information is stored and manipulated in working memory. We recorded event-related brain potentials (ERPs) from healthy human subjects while they had to maintain either visuo-spatial or temporal information in memory for a subsequent memory test. If multi-component models of working memory are valid and basic informational dimensions are processed separately by domain-specific memory subsystems, as supposed, topographical differences in ERP activity should occur when subjects are holding either

visuo-spatial or temporal information in working memory. The question is whether the processing of a temporal feature of a stimulus, here duration, is realized by a specific neuronal circuitry or system, reflected in a distinct topography of the corresponding ERP waveforms. As different ERP topographies were observed as a function of the type of information held in working memory, we expected to find distinct ERP patterns for the processing of the duration and location of a given stimulus.

In behavioural pilot studies, subjects reported remembering durations of visual stimuli unintentionally either by hearing a tone or by producing a phoneme in their inner speech, while watching the stimulus. Therefore in the present study, durations were presented not only as visual stimuli but also as auditory stimuli, using tones and spoken phonemes.

Material and Methods

Twenty paid subjects (eight male; aged 19–27 years, mean 23 years; righthanded; students) participated in the experiment. They underwent a half-hour training-session a few days before the main experiment.

Procedure: The participants of the ERP study were seated comfortably in a dimly lit, acoustically attenuated, and electrically shielded cabin in front of a 17 inch Trinitron Color Graphic Display (distance: 1.1 m) with two 25 W loudspeakers at the left and at the right of the monitor. Two different memory tasks were combined with two presentation modalities (a visual spatial task, a visual and two auditory temporal tasks). Subjects were required to indicate whether two stimuli were the same with regard to duration of presentation or spatial location.

For the visual spatial task, a blue 1×1 cm square appeared on a grey monitor at one of 400 (20×20) possible positions in an area of 12×12 cm. There were four possible presentation times, corresponding to the presentation times of the visual temporal task: 275, 300, 570, or 650 ms. After presentation, the screen remained grey for 350 ms and then turned blue. The blue mask remained for 5000 ms. At 1000 ms before S2-onset the screen turned grey again. The second square appeared at the same or a slightly different position and remained as long as the first stimulus. The subject had to indicate whether the two squares had appeared at the same position or at different positions.

The visual temporal task used the same stimuli and procedure as the visual spatial task. The difference was that the position of the stimuli within a trial always remained the same, while the presentation times of the first and the second stimulus could be different. The subject had to indicate whether the two

squares had appeared for the same duration or for different durations.

For the first auditory temporal task a tone with the frequency of squared sine and a loudness of ~70 dB was presented via the loudspeakers for 236, 256, 313 or 360 ms. After a delay of 350 ms the subject listened to an auditory mask (pink noise; ~62 dB) for 5000 ms while the screencolor turned blue as in the visual tasks; 1000 ms before the second stimulus was presented the auditory mask ended and the screen turned grey again. After the second tone, the subject had to indicate whether the duration of presentation was the same for both tones or not.

The course of the second auditory temporal task was the same as the tone-task, but the stimulus material was different. Instead of a tone, one of four possible phonemes was presented ('bah', 'pah' and two artificially generated levels in between, like 'bpah' and 'pbah') at an intensity of ~65 dB, for 236, 256, 313 or 360 ms. The subject had to indicate whether the duration of presentation was the same or different for the two phonemes.

Tasks were presented in eight blocks (the order of the blocks was counterbalanced across subjects); the experiment consisted of two 1 h sessions with four blocks of tasks each and a 1 h break between the two sessions.

EEG-registration and analysis: The EEG activity was measured with tin electrodes from 64 scalp locations of the extended 10-20 system.¹⁹ The reference electrode was positioned over the left mastoid (M1). The vertical electrooculogram (EOG) was monitored above and below the right eye; the horizontal EOG was recorded from electrodes positioned at the outer canthus of each eye. The EEG was recorded continuously, amplified by an analogous amplifier close to source (factor: 150) and digitized by a NeuroScan Inc. data acquisition unit (digitization rate 250 Hz; bandpass 1–30 Hz). The EEG epochs analysed extended from 200 ms before study-stimulus onset (S1) until test-stimulus onset (S2). The first 200 ms of the epoch was used as a baseline for the averages. Epochs containing artifacts (eye movements and blinks, excessive bodily movement, electrode artefacts) were excluded from analysis; drift artefacts were corrected by detrending each epoch. From the edited set of raw data ERPs were extracted by averaging single trials separately for subjects and conditions (tasks and levels of difficulty). Only trials with correct responses were used for the average.

Electrodes used for statistical analysis on frontal effects were FP1, FPZ, FP2, AF7, AF3, AFZ, AF4, AF9, F9, F7, F5, F3, FZ, F4, F6, F8, F10, FT9, FT7, FC5, FC3, FCZ, FC4, FC6, FT8 and FT10 (26 electrodes); those used for analyses on centroparietal

effects were T7, C5, C3, CZ, C4, C6, T8, TP7, CP5, CP3, CPZ, CP4, CP6, TP8, P7, P5, P3, PZ, P4, P6, P8, PO7, PO3, POZ, PO4, PO8, O1 OZ and O2 (29 electrodes); effects focused on parieto-occipital areas were analysed on TP7, CP5, CP3, CPZ, CP4, CP6, TP8, P7, P5, P3, PZ, P4, P6, P8, PO7, PO3, POZ, PO4, PO8, O1 OZ and O2.

Results and Discussion

The two auditory duration tasks showed no significant different ERPs for the whole time course whereas the visual tasks did. In the following we will only report the ERPs of the tone-task in comparison to the two visual tasks.

First time window (Fig. 1A): The grand average ERP waveforms showed significant differences between the auditory and the visual modality, but not within modality, up to about 500 ms after stimulus onset: ERPs from visual tasks were significantly more negative than those from the auditory task in the frontal area between 300 and 800 ms after stimulus onset (visual tasks *vs* auditory task, $t = 30.05$; $p < 0.0001$). ERPs from the auditory task were significantly more positive than those from the visual tasks in the centroparietal area between 200 and 500 ms after stimulus onset ($t = 9.17$; $p < 0.0069$). As expected,²⁰ the N1–P2 complex waveforms of the auditory task were slightly faster than those of the visual tasks (P2 peaked 35 ms earlier). Only distinguishable by allocation to task modality, these electrophysical processes were interpreted as correlates of modality-specific perception and first encoding activities.

Second time window (Fig. 1B): Between 400 ms (PZ) and 550 ms (P6) after stimulus onset, the spatial task started to generate a slow negative wave over parieto-occipital sites, peaking at about 750 ms after stimulus onset and declining until 2300 ms (Pz) and 3000 ms (P3), respectively. This slow negative wave was observed exclusively for the spatial task, and was highly significant in a time range of 700–2400 ms after stimulus onset (position *vs* duration, $t = 16.80$; $p < 0.0006$).

Around 1150 ms after stimulus onset, the ERP waves of both auditory and visual duration task showed a frontolateral negative peak, nearly simultaneously: 780 ms after stimulus onset the visual duration task generated a slowly rising frontolateral negative wave, peaking at about 1130 ms after stimulus onset and then declining until about 2000 ms. This frontolateral effect was marginally significantly more negative than the ERP wave of the position task in the latency range of 1100–1300 msec ($t = 4.24$; $p < 0.0535$). When tested statistically for all frontal

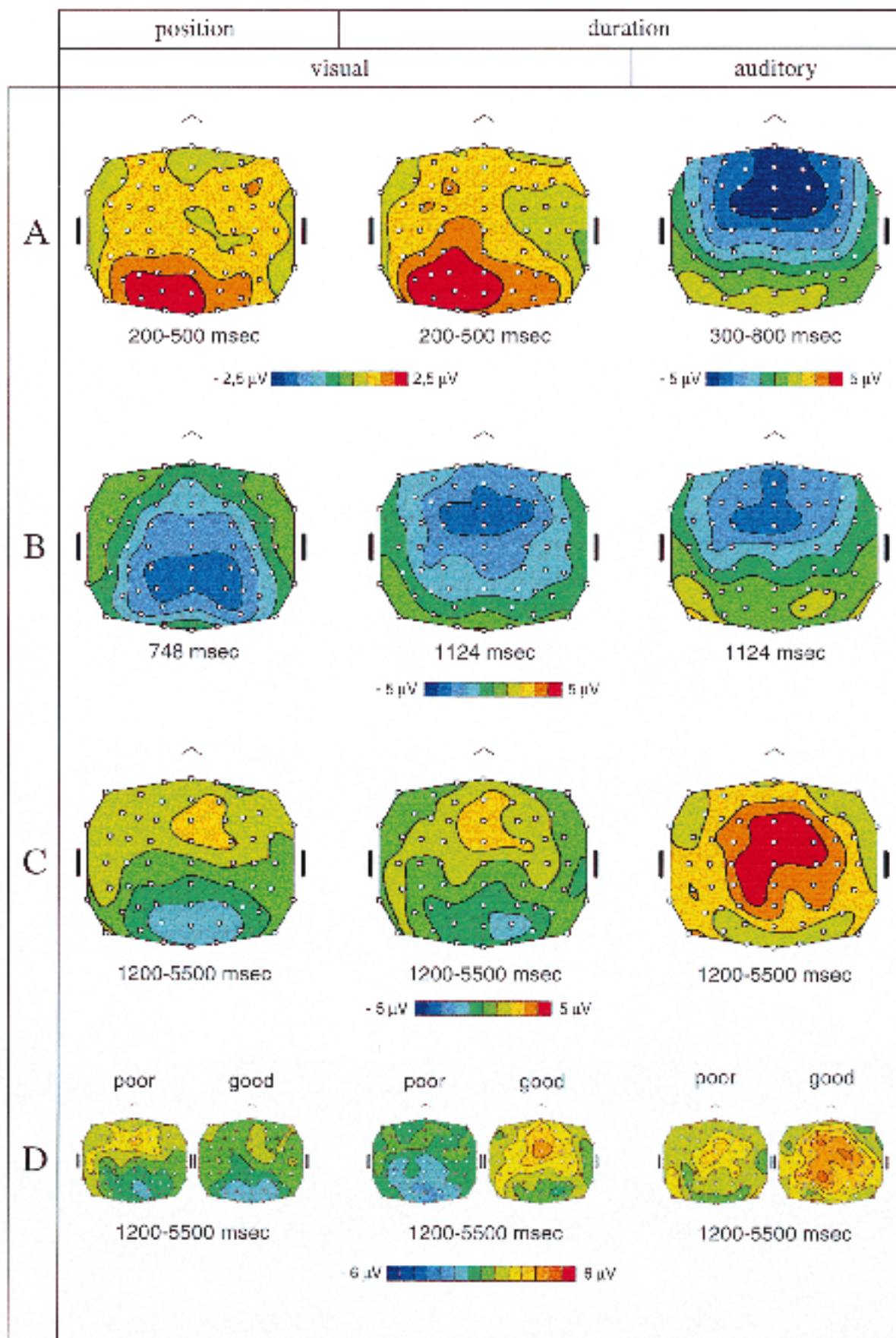
electrodes without the midline electrodes, this effect became significant ($t = 5.13$; $p < 0.0355$) and showed an even broader time range of 1050–1350 ms after stimulus onset ($t = 4.47$; $p < 0.0479$). The auditory duration task generated a frontolateral negative peak at about 1180 ms after stimulus onset ($t = 10.76$; $p < 0.0039$), significantly more negative than ERPs generated by the position task in the same time range (1050–1350 ms).

When the ERP waveforms of the tasks were compared by type of information (position *vs* duration), this frontal effect was highly significant (all frontal electrodes, latency range 1100–1300 ms: $t = 9.18$; $p < 0.0069$ and without midline $t = 9.51$; $p < 0.0061$; without midline, 1050–1350 ms: $t = 7.68$; $p < 0.0122$).

The slow waves elicited in the time range of about 500–3000 ms after stimulus onset, when subjects are supposed to be engaged in storage and retention operations, showed remarkable differences in time course and scalp topography, depending on the type of information to be retained. When subjects were holding either duration information (which is assumed to be correlated with a frontolateral slow negative waveform) or spatial position information (with the corresponding electrophysical activity mapped by a parietal slow negative waveform), ERPs seemed to reflect information-type specific processes of storage and retention. This is in accordance with recent ERP studies showing that negative slow waves in the ERP vary in temporal and topographical pattern as a function of the type of information held in working memory.²¹ In particular, parietally focused negative slow waves have been reported to be associated with the storage of visuo-spatial information.²²

The ERPs of the auditory task also showed a large negative wave form peaking at about 945 ms, with a parietal focus. A further average was performed, time locked to stimulus offset to synchronize the onsets of the visual and the auditory mask. Since there was a smaller peak with the same latency (simultaneous to the auditory tasks) and polarity for the visual task waveforms, the negative waveform of the auditory task was interpreted as a P2 elicited by onset of the auditory mask. To test this hypothesis, four subjects performed the auditory task without auditory mask and the visual tasks with auditory mask. The finding that this auditorily unmasked auditory task generated no parietal negative going wave, whereas the auditorily masked visual tasks did, is in agreement with the above hypothesis.

The frontolateral negative peak generated by the auditory duration task had a latency delay of about 40 ms relative to the visual duration task. As this peak delay disappeared in the auditorily unmasked task



(peak delay averaged 1133 ms after stimulus onset vs 1128 ms for the visual task), the peak asynchrony observed between the (masked) auditory and the visual duration task was explained as a delay caused by the auditory mask.

Third time window (Fig. 1C): The ERPs of the auditory duration task showed a large global positive waveform with centroparietal focus, rising immediately after the frontal negative peak, i.e. about 1200 ms after stimulus onset. This effect was highly significant over centroparietal regions with a latency ranging from 1100 ms to 5650 ms ($t = 22.98$, $p < 0.0001$). The ERPs corresponding to the position task, though tending to a slight slow negative shift, showed no significant effect.

In order to determine whether the positivity was an effect of modality or of informational content of the task, we had to make a special control for the visual duration task, intending to monitor possible overlapping effects of modality and information. Therefore, good and poor performers were compared. When split into two groups, compared with the poor performers, subjects with good performance and reaction times also showed positivity in the visual duration task (Fig. 1). This effect was interpreted as reflecting inhibition processes, occurring when the system has to keep the amount of further visual input as small as possible to avoid interference. In the case of the position task, inhibition of additional visual processing is, of course suggestive, but at the same time it would be not very economical to shut down visual processing to the lowest level, for a certain readiness status has to be maintained and focused on the expected visual stimulus (see Fig. 1D). For the auditory duration task, suppression of visual information processing should reach a maximum, because visual input is entirely irrelevant to meet the task demands (see Fig. 1D). Performance on the visual duration task, however, depends on a somewhat more elaborate effort. As already described above, subjects had mostly reported remembering durations of visual stimuli non-deliberately by hearing a tone or a phoneme while watching the visual stimulus. On the one hand, the system has to be ready for visual input when a visual duration task is performed, so inhibition of visual input should be limited only to some extent. On the other hand, if the format in which visually perceived duration held in the memory bears a close relation to that of duration perceived in an auditory manner, inhibition processes may be advan-

tageous. While this appears to be a rather tentative explanation, it can be connected to the subjects' statements about how they remembered duration.

Conclusion

Our data support the view that the processing of stimuli differing in their underlying informational content is associated with different event-related activity. ERPs recorded during the performance of a temporal duration memory task and a spatial location memory task indicate that the processing of temporal information and that of spatial information is realized in topographically distinct neuronal structures. With regard to similar results in recent research outcomes,^{11–13,23–25} we propose that the prefrontal lobe is involved in temporal information processing. Temporal and topographical characteristics of the ERPs recorded suggest the distinction of three discrete processing phases: modality-specific encoding, information-specific encoding, and inhibitory accompanied retention of information.

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ACKNOWLEDGEMENTS: This work was supported by the Berlin-Brandenburgische Akademie der Wissenschaften, Germany.

Received 18 March 1997;
accepted 5 April 1997

FIG. 1: Mapped topographical distributions of the electrophysiological activities, averaged over all subjects ($n = 20$), during the performance of the three memory tasks: visual spatial position memory task, visual temporal duration memory task, and auditory temporal duration memory task.

General Summary

The present event-related potential study contributes to the issue of how temporal information (duration) is encoded and held in working memory in contrast to spatial information (location). For the temporal memory task, two presentation modalities (auditory and visual) were engaged to monitor modality-specific influences on temporal information processing. Negative slow wave activities with parietal focus corresponding to the spatial memory task and with frontal focus corresponding to the temporal memory task were observed. These significant topographical and structural differences of ERPs elicited by either a spatial memory task or a temporal memory task suggest that different cortical areas are activated during the retention of different types of information in working memory. The present findings are consistent with recent neuropsychological research, proposing prefrontal cortical structures to support the processing of temporal information and parietal cortical areas to be activated during visuo-spatial information storage.