

Instruction differentiates the processing of temporal and spatial sequential patterns: evidence from slow wave activity in humans

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Abstract

Event-related potentials (ERPs) were recorded while subjects monitored a visually presented sequence of stimuli that provided information about both a temporal pattern (rhythm) and a spatial pattern, and responded to rhythmical or spatial deviants. A third task, which required the monitoring of the same sequence for screen flickers served as a perceptual baseline condition and controlled for response preparation effects. The monitoring of temporal and spatial sequential information elicited negative slow potentials (SPs) over distinct topographical areas. Thus, attention to the temporal and to the spatial domain of one and the same stimulus sequence are reflected by distinct ERP components, providing evidence for distinct cortical sources. © 1999 Elsevier Science Ireland Ltd. All rights reserved.

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Our sensation of time has long been considered by some researchers to be a mere by-product of general information processing [14]. In contrast, models arguing that temporal duration and temporal order are attributes of any stimulus or sequence of stimuli, and therefore can be selectively attended to, stress the need for a specific timing mechanism that can be triggered by attention [9]. Thus, more recent theories of temporal information processing have followed from theories in neurophysiological and neuropsychological research fields that suggest that holding on-line spatial, object or linguistic information partly rely on separate brain systems that can be dissociated by behavioral data, event-related potential (ERP) analysis or imaging techniques. Although now there is general agreement that the processing of temporal information requires operations of the short-term memory [4] too, the brain areas underlying the sense of time are still almost unknown.

Recently, temporal information processing has been discussed in the context of the functional role of the prefrontal cortex (PFC), as supported by lesion studies in animals [12]

and patient studies [17]. In neurophysiological research, frontal slow cortical potentials (SP), usually referred to as contingent negative variation (CNV) [1], are correlated with attention, response preparation, and expectancy [13], but because SP over frontal sites have recently been reported during both the mnemonic encoding and the production of temporal intervals [3,8], a timing or delay function revealed by frontal ERP-components is also implicated. Therefore, the assumption can be made that the manipulation of timing information in short-term memory depends primarily upon frontal systems, just as the manipulation of spatial information relies upon posterior systems [15].

The present study investigated short-term memory of temporal and spatial sequential information using a modified go/no-go paradigm, in which subjects had to monitor a series of standard stimuli (no-go) for infrequent deviants (go) and indicate deviant items, e.g. by button press. The hypothesis that the maintenance of temporal and spatial sequential information elicits negative SPs over distinct topographical areas, which therefore reflect continuous mnemonic functions in the temporal and the spatial domain, was tested. Slow wave activity was expected over frontal sites during the monitoring of temporal structures, and over

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parietal sites during the monitoring of visual-spatial structures.

Subjects monitored a visually presented series of standards, a short temporal and spatial pattern repeated several times, and responded to stimuli that were deviants either in terms of rhythmic or spatial features. By manipulating task instructions, attention was focused on one of these two features provided by one and the same series of stimuli. Thus, a short-term representation of a rhythm or a spatial pattern had to be maintained and rehearsed for an on-line comparison with the successive repetitions. ERPs corresponding to this mnemonic maintenance and comparison in both the rhythm task and the spatial pattern task were recorded. A physically identical, but purely perceptual baseline task was employed to control for perceptual and preparatory functions. Furthermore, to rule out any motor response contribution, only electrophysiological activity in no-go trials was analyzed. Verbalization strategies were not expected to play a role because subjects were engaged in monitoring without any temporal delay.

Twenty-four healthy, right-handed subjects (19–29 years, mean age 22.6 years, 12 male, 12 female) participated in this study. After giving informed consent, subjects sat comfortably in a dimly lit, acoustically attenuated chamber in front of a 17" Trinitron Color Graphic Display (distance: 1.1 m). Three tasks were presented in blocks in a counter-balanced order across subjects. In the rhythm task, subjects monitored the rhythm repetitions and indicated by button-press when this rhythm was violated. In the spatial pattern task, they monitored the spatial pattern for deviant spatial positions. In the baseline task, a screen flicker had to be indicated by button press.

Each trial consisted of 12 successive pictures, each showing a pair of blue 1×1 cm squares on a gray background (see also Fig. 2). The presentation time of each picture and the spatial positions of the squares varied between the first three pictures. Thus, a rhythm comprising three elements and a serial spatial pattern comprising six positions had to be maintained. This first set of three pictures was repeated three times. One trial lasted 9600 ms, without reaction time and feedback. Go and no-go conditions were combined crosswise between the relevant and the irrelevant information dimension (50% no-go/no-go, 20% no-go/go, 20% go/no-go and 10% go/go).

The electroencephalogram (EEG) was recorded with electrodes from 42 scalp locations of the extended 10–20 system. The reference electrode was positioned over the left mastoid (M1). The vertical electrooculogram (EOG) was monitored via electrodes 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 and digitized by a NeuroScan data acquisition unit (digitization rate: 250 Hz; lowpass: 30 Hz; no highpass).

The EEG epochs under investigation extended from 150 ms before the first set-picture until the last repetition-pic-

ture. The interval covering the first 150 ms of the epoch was used as a baseline for the averages. Epochs containing artifacts (eye movements and blinks, excessive bodily movement, electrode artifacts) were excluded from analysis. Low frequency artifacts in the EEG signal were corrected by means of a modified version of the linear regression approach. Single trial EEG epochs were averaged separately for each subject and condition. Only no-go-trials with correct responses, i.e. no button presses, were used for the average. Twenty-one frontal (FP1, FP2, FPZ, AF8, AF7, AF4, AF3, AFZ, F10, F9, F8, F7, F6, F5, F4, F3, FZ, FT10, FT9, FT8, FT7) and 21 parietal (TP8, TP7, CP6, CP5, CP4, CP3, CPZ, P10, P9, P8, P7, P6, P5, P4, P3, PZ, PO8, PO7, PO4, PO3, POZ) electrodes were used for statistical analysis. The criteria for electrode selection were hemispheric symmetry and equal number of electrodes for both regions of interest. The amplitude measures were collapsed across channels within regions of interest (ROIs). The mean values of the ERP measures in the whole trial epoch (0–9600 ms) were subjected to a repeated-measure ANOVA with the two level factors CONDITION (rhythm, spatial pattern) and ROI (frontal, parietal).

The performance level was defined as accuracy of answers, i.e. a reaction to go-items and no reaction to no-go-items. There were 7% false alarms and 39% misses in the rhythm task and 10% false alarms and 35% misses in the spatial pattern task. The P -value, i.e. hit rate corrected for false alarms, was 0.54 in the rhythm task and 0.55 in the spatial pattern task. They were statistically not different ($F(1,23) = 0.16$, $P = 0.7$). There were no errors in the baseline task.

As shown in Fig. 1, during the monitoring of both rhythm and spatial pattern sequences, negative SPs were generated. To get a better estimate of SP activity related to mnemonic processing, electrophysiological activity is represented here as difference waves in which the baseline activity is subtracted from the activity elicited by the rhythm or the spatial task. Relative to the perceptual baseline task activity, the negative SPs corresponding to the rhythm task had a frontal topography, whereas the SP evoked by the spatial pattern task showed a parietal scalp distribution. Statistically, there was a significant interaction between the factors CONDITION (rhythm, spatial pattern) and ROI (frontal, parietal) ($F(1,23) = 5.7$, $P = 0.02$). Before entering in the statistical analysis, the amplitude values from both conditions were scaled, so that amplitude differences between conditions were ruled out. Thus, the interaction indicated reliably that the topographical profiles were different for the two conditions.

As shown in Fig. 2, there was an amplitude shift in slow activity relative to the baseline task at the beginning of the first repetition (fourth picture), both in the rhythm monitoring condition (electrode F7) and in the spatial pattern monitoring condition (electrode P7). From this time point on, active rehearsal of the pattern is required to detect deviants in the relevant dimension. Thus, the enhanced activity

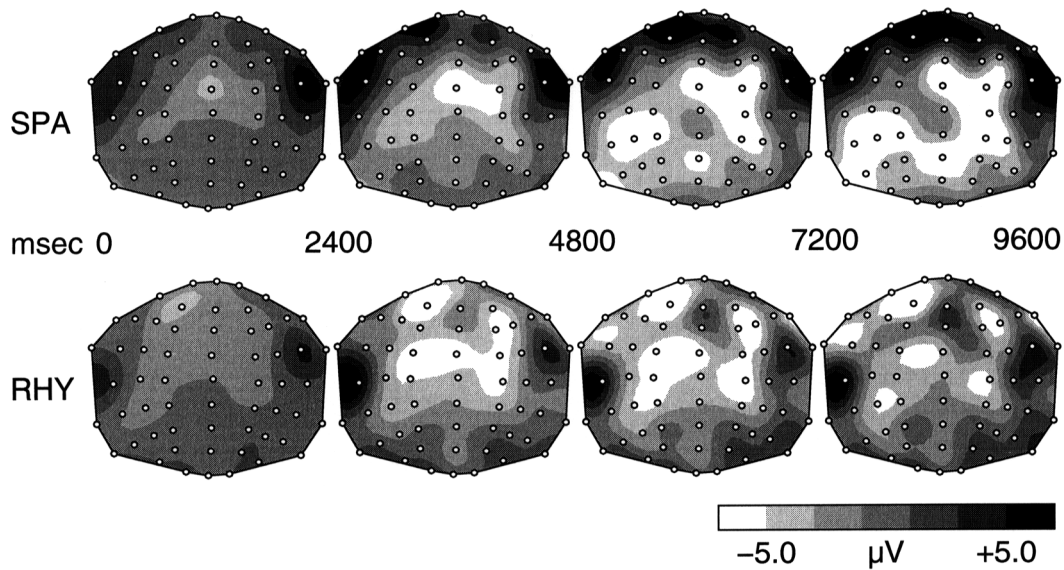


Fig. 1. Mapped topographical distributions of the electrophysiological activities, averaged over all subjects ($n = 24$), elicited by monitoring a spatial pattern (SPA, upper row) and monitoring a temporal rhythm (RHY, lower row). Perceptual and preparatory activity is removed by subtraction of the baseline activity. Motoric response activity is excluded by exclusively analyzing no-go trials, as plotted here. Rhythm monitoring elicits frontal negative SPs, whereas spatial pattern monitoring elicits negative SPs on parietal sites. Although visual inspection suggests laterality in the slow wave pattern, there were no statistically significant hemisphere effects neither for the spatial pattern nor for the temporal rhythm condition.

recorded at these regions reflects the maintenance and mnemonic rehearsal of temporal and spatial sequences.

In the present study, we explored the nature of negative SPs elicited while subjects monitored visually presented sequences of stimuli for deviants in the temporal or in the spatial domain. In a third condition, subjects monitored the same sequence of stimuli in a purely perceptual way for a short screen flicker. In contrast to the perceptual baseline task, the two experimental tasks involved mnemonic function in that a rhythmic or spatial pattern set had to be memorized and compared across several repetitions. Due to the fact that only no-go trials were analyzed, motor response activity was not involved in slow cortical activity in any of the three conditions.

Relative to the perceptual baseline, the rhythm task elicited negative SPs over frontal sites, whereas the spatial pattern task elicited negative SPs over parietal sites. As shown by the interaction between the factor CONDITION and ROI, absolute electrophysiological activity revealed that the two tasks elicited ERPs with different topographical distributions. Thus, short-term memory processes in the temporal and the spatial information domain were reflected by different ERP components [2], which are defined in terms of their latency range, their scalp distribution and their sensitivity to experimental variables [11].

These findings indicate that different cortical sources underlie temporal and spatial mnemonic functions. While negative frontal SPs classically are conceived of as reflecting attention, expectation and response preparation [19], recent investigations strongly indicate that frontal SP activity also reflects timing functions [3,8,10,16]. This is in accordance with the interpretation that one of the cognitive

functions that the CNV reflects is the temporal synchronization of responses to expected stimuli [20]. In the present

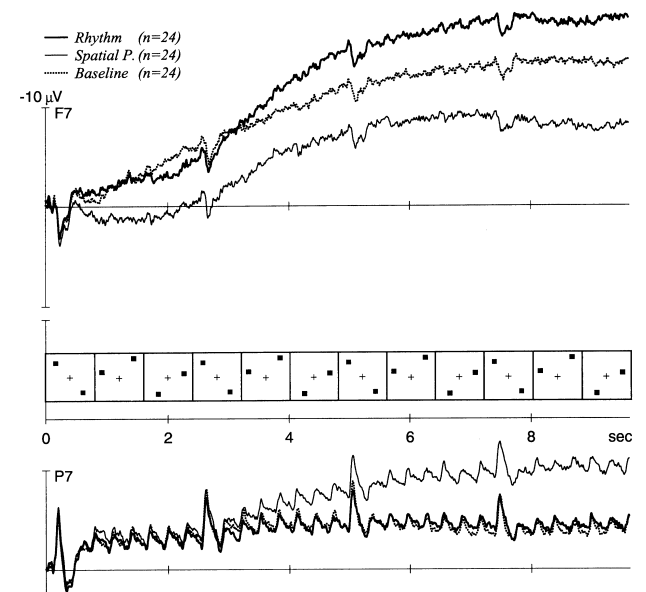


Fig. 2. ERP waveforms (absolute amplitude) averaged across all subjects, plotted for a frontal (F7) and a parietal (P7) electrode. An example of the stimulus presentation in one trial is given in the middle of the figure. In relation to the baseline condition (dotted line), spatial pattern monitoring (thin solid line) elicited a negative SP over parietal sites. This SP began during the first repetition (2400–4800 ms), reflecting spatial mnemonic rehearsal required from this time point until the end of the trial (9600 ms). In contrast, the rhythm monitoring (thick solid line) elicited a negative SP over frontal sites, which started during the first repetition. This component is thought to reflect mnemonic rehearsal in the temporal domain that is required from this time point on until the end of the trial epoch.

study, SPs were elicited over frontal areas during monitoring of visually presented sequences, both in the spatial pattern and the rhythm conditions and in the perceptual baseline task. However, as shown by the comparison between slow wave activity during the rhythm and the spatial pattern task, frontal ERPs could not be attributed to attentional and preparatory effects, but to the short-term mnemonic representation of temporal structures, as required by continuously monitoring a rhythm.

In conclusion, the present results indicate that the frontal SP elicited during the go/no-go monitoring of sequences reflects both anticipatory as well as timing functions of the frontal cortex. An explanation for how the PFC is in the position to serve temporal organization of perception and action might be based on its neuroanatomical characteristics. Single-cell studies in non-human primates have shown that frontal delay neurons [6] fire only during the delay between two stimuli in a memory paradigm [7]. This delay-function in the primate brain has been demonstrated several times in lesion studies and reversible lesion studies using cooling-technique [5], as well as in human PET-studies [18]. Thus, the high density of delay neurons in prefrontal areas might provide a basis for the temporal phasing and sequencing of various motor and perceptual behaviors.

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