Alpha oscillations as an indicator of dynamic memory operations — anticipation of omitted stimuli

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Abstract

Elaborating on a paradigm of Başar in experiments with periodically presented auditory or visual stimuli, 10 subjects performed tasks in which omitted stimuli had to be anticipated and their (virtual) onset time had either to be marked (a) mentally (‘mental marking’ MM) or (b) by pressing a button (‘button pressing’ BP). EEG was obtained from 11 sites in frontal, central, temporal, parietal and occipital areas. The experiments were carried out in triplets of MM, BP, MM measurements. Mean temporal errors of motor responses served as the basis for a functional interpretation of EEG patterns. Correlation analysis of sweeps for each individual revealed brief intervals of phase ordering of EEG patterns in the alpha range lasting approximately three periods. For frontal and vertex derivations a close congruence of the location of the phase-ordered patterns to mean errors of motor responding was shown. These results corroborate the claim that ‘emitted’ alpha oscillations represent intentional processing. The close agreement between temporal locations of phase-ordered EEG segments and those of the motor responses strongly suggests that EEG phases represent memory retrieval of period duration as a common functional component of MM and BP. A lack of topographical correspondence with results from a passive ‘missing stimulus’ paradigm underlines the specific intentional origin of the observed phase ordering. Theoretical implications of the results are discussed.

Keywords: Alpha-rhythm; Memory processes; Time interval reproduction; Phase-ordered alpha patterns

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1. Introduction

The analysis of functional correlates of alpha activity has again become attractive for EEG researchers. Mulholland (1995) used the expression ‘work-alphas’ to indicate that this activity does not only represent the ‘idling’ of the brain as over a long period was assumed by investigators. A good illustration of this change of attitude is provided by a recent collection of papers (Başar et al., 1997) about functional correlates of alpha activity. Among different types of alpha activity: spontaneous, induced, evoked and emitted (Galambos, 1992), emitted alpha activity is the most intriguing but less consistently observed. This activity has a pure endogenous origin, represents a manifestation of cognitive processes, and results in repeatable ‘phase-ordered alpha patterns’.

Phase-ordered alpha patterns emitted during cognitive performance have been reported by Başar and co-workers (Başar et al., 1988, 1989; Başar and Schürmann, 1996). The task in these studies was to predict mentally every fourth omitted stimulus in the sequence of rhythmic tones or light flashes. After the training of subjects a phenomenon of phase-reordering of oscillations, especially in the alpha range, was observed in their EEGs: superposition of filtered EEG signals showed a good phase congruence prior to the expected onset of ‘omitted stimuli’ (Fig. 1). These repeatable coherent oscillations have been interpreted as event-related rhythms reflecting brain activity in expectation and prediction of an event. Since they are emitted in the absence of physical stimuli they have to be considered as of purely endogenous origin (Başar et al., 1988).

That the deletion of expected stimuli is associated with so-called ‘omitted’ or ‘missing’ stimulus potentials was already shown in several earlier studies (e.g. Sutton et al., 1967; Klinke et al., 1968; Barlow, 1969; Picton et al., 1974; Simson et al., 1976). In these experiments the negative component of a ‘missing’ potential appeared synchronous with the point in time at which the missing stimulus would have occurred. Therefore, it has been suggested that this negative component is associated with anticipatory events. However, in these experiments that utilise the missing stimulus paradigm, the only task of the subjects was to detect the omission of stimuli. In contrast, the studies of Başar’s group apply to intentional components of behaviour during cognitive task performance. Subjects were asked to predict the moment of the onset of omitted stimuli, as if they were not actually omitted. To perform this task, subjects had to actively keep in memory and recall the duration of interstimulus intervals. This means that this version of the omitted stimulus paradigm can be interpreted as a memory paradigm. If this assertion is right, then it is reasonable to suppose that similar patterns of alpha activity that repeatedly occur reflect retrieval processes during time interval reproduction. How could this statement be examined experimentally?

Psychological studies in human timing activities have given evidence that judgements of time can vary quite markedly when subjects reproduce target time intervals (Treisman, 1963; McConchie and Rutschman, 1971). This variability can, however, be reduced by practice. Prolonged practice is necessary to reach a stationary level of performance (Kristofferson, 1976). Phase-ordered alpha patterns were also obtained after long-term training of subjects, where they were found to be time locked to the moment of omitted stimulus onset (Başar et al., 1989). These results implied that after prolonged practice subjects could fairly precisely predict the time of the omitted stimulus onset, accurately reproducing interstimulus intervals, although no kind of behavioural control was included in the experimental design. Behavioural measurements give information about the accu-
racy of subjective reproduction of an omitted stimulus. If the phenomenon of alpha phase ordering reflects a subjective component of timing that depends on the representation of interstimulus interval in memory, it could be assumed that the time of phase-ordered patterns appearance and the time of motor responses are covarying. To check this assumption there is no necessity for long-term training of subjects.

The experiments reported in the present study were designed to explore the structure and functional significance of the phase-ordered alpha patterns arising in omitted stimulus situations. In order to control the accuracy of time interval reproduction behavioural measurements were added. Subjects were required to mark the expected onset of the omitted stimuli by pressing a button. It was hypothesised that a close correspondence between the time of appearance of the alpha patterning and mean errors in motor responding would be observed.

2. Materials and methods

2.1. Experimental methods

2.1.1. Subjects
Ten subjects (five male and five female, age 22–40) participated in the experiments. They were seated in a soundproof and dimly illuminated room with eyes open. They were requested to limit eye and head movements as much as possible.

2.1.2. Stimuli
Two types of sensory stimuli (auditory and visual) of 800 ms duration were presented regularly with an inter-stimulus interval of 2600 ms. Each series contained 100 signals. Every fourth signal was omitted. The auditory stimuli were 2000-Hz 80-dB SPL tones. The optic stimulator consisted of a 40-W commercial fluorescent lamp and driven by a DC power supply through a properly designed switching circuit which provides a rise time approximately 1 ms for the lamp, the DC source being gated by the pulses obtained from a pulse generator. The light stimulation was free of any acoustical ‘click’ artifact.

2.1.3. Tasks
Experiments contained two types of task. (1) Subjects were instructed to mark the omitted stimuli only mentally, avoiding any kind of movement activities or counting of stimuli. (2) Subjects were required to mark the expected time of each omitted stimulus by pressing a button. A series with button pressing was performed between two series with mental marking. The three series represented one experimental block. This arrangement was implemented so that during a relatively short performance time within one experimental block subjects would maintain approximately the same motivation, attention, and cognitive strategy. Mean estimates of time interval reproduction from button press measurements were used to evaluate the EEG data in which the subjects marked the omitted stimuli mentally. For comparison of behavioural and electrophysiological results, data from different measurements were used to avoid the interference of brain activity associated with movement when pressing the button.

There were two sessions for each subject with 2–7 days between them. Each session contained one auditory and one visual experimental block.

2.2. Data acquisition and processing
The EEG was recorded from F3, F4, C3, C4, Cz, T3, T4, P3, P4, O1 and O2 electrode position referred to the right ear. The filter bandpass during recording was 0.3–70 Hz. The EEG 800 ms prior and 800 ms after stimulus onset, including omitted one, was digitised with sampling intervals of 1.56 ms and stored on the hard disk. Trials with artefacts due to eye, head or electrode movement or scalp muscle contamination (EEG > 100 mV) were eliminated a posteriori. For further off-line analysis only EEG sweeps corresponding to the omitted stimuli were used.

For determination of the phase-ordered alpha patterns, 10 first and 10 last artifact-free sweeps of each measurement were digitally filtered in the alpha range (8–13 Hz) without phase shift (Başar,
and superimposed. Thus the data of each subject contained eight sets of 10 sweeps for each stimulus modality and each channel.

Previous studies have shown that superposition of filtered single sweeps makes visible a phenomenon of the phase locking of the alpha oscillations during mental task performance (Fig. 1). To quantify phase alignment of sweeps a suitable statistical method has to be applied. Averaging is a traditional method for the presentation of the phase-locked activity (e.g. EP). This method is reliable when a big number of sweeps are at hand. But for 10 sweeps this method of processing is sensitive to the amplitude of sweeps. It can cause enhancement due to the occasional presence of sweeps with a large amplitude. Correlation analysis estimates the similarity of the dynamics of different processes. It thus can reflect the specificity of the phenomenon under study without much disturbance by accidental amplitude variations. Therefore, this method was applied to estimate the similarity of oscillations within subsets of sweeps.

2.3. Statistical evaluation

Correlation analysis was used for the statistical estimation of the covariance of oscillations within each subset of 10 sweeps. Fig. 2 illustrates the method (cf. also Appendix A). The covariance of oscillations in the subset of 10 sweeps was estimated within a 300-ms time window which was shifted along the time axis in steps of 100 ms. For example, the interval from −800 ms to −500 ms was selected for analysis. Each of 10 sweeps was presented by a discrete time series of the amplitudes \( A_t \), \( t = 1, 2, 3, \ldots, 192 \), in this interval. Correlation coefficients were computed for each pairwise combination of such time series. That means that 45 correlation coefficients were obtained. They were converted into Fisher’s Z-values

\[
Z = \frac{1}{2} \ln \left( \frac{1 + r}{1 - r} \right)
\]

and then averaged. The arithmetic mean of Fisher’s Z-values was considered to be a measure of similarity for the behaviour of the alpha oscillations in the interval of analysis. The same procedure was applied to intervals from −700 ms to −400 ms, from −600 ms to −300 ms, etc., up to the last interval from 500 ms to 800 ms. From this analysis 14 estimates of mean Z-values were obtained for each subset of sweeps; these values reflect the dynamics of intersweep relationships along the time axis. In Fig. 2 they are plotted against the midpoints of the intervals of analysis. It is seen, that the mean Z-values are approximately 0 in the parts of superimposed sweeps, where sweeps have accidental behaviour. When the oscillations get phase-aligned the mean Z-values increase. This means that the method is suitable for estimation of similarities in the behaviour of sweeps.

Fig. 3 presents different examples of the phase-ordered alpha patterns.

For further analysis, one set of sweeps for each stimulus modality was selected for each subject. The set of sweeps with the highest mean Z-value in one of the derivations was considered to be the set with the most marked phase tuning. This set of sweeps was used for comparison with the behavioural data.

Estimation of significance of the relationships between sweeps was performed using a criterion
Fig. 3. Examples of individual phase-ordered alpha patterns and their statistical estimation. At the top of each picture (a–c), 10 filtered superimposed EEG sweeps (8–13 Hz, F3) are shown. The lower curve presents the dynamics of the inter-sweep correlation. Arrows indicate mean errors of time interval reproduction in behavioural measurement. (a) Subject SH, auditory stimulus. (b) Subject CE, visual stimulus. (c) Subject MM, auditory stimulus.

from correlation analysis. As it was mentioned before, for the calculation of correlation coefficients between two sweeps in the interval 300 ms, 192 discrete time series were used. For n = 192 and P = 0.01 the corresponding Pearson correlation coefficient is r = 0.1855 and the corresponding Z-value is Z = 0.1877. This value was used as a criterion for the estimation of significance of the relationships between sweeps. Mean Z-values exceeding this criterion were considered as having significant relations between sweeps (Fig. 2). Fig. 4 shows the derivations in which mean Z-values exceeded this criterion.

3. Results

3.1. Characteristics of phase-ordered alpha patterns — individual variability

For each subject eight sets of 10 sweeps were obtained for each modality of the signal. Phase-ordered alpha patterns were not observed in every set, but as a minimum two–three sets of sweeps contained these patterns in some of the derivations in each subject. Fig. 3 presents typical examples of phase-ordered alpha patterns and their assessment with the correlational method described above. At the top of each figure, 10 superimposed filtered (8–13 Hz) single sweeps are shown. The lower curve illustrates the variation of correlation coefficients for the discrete epochs of the analysis. Fig. 3a illustrates the case of a pronounced phase-ordered pattern appearing in the middle of superimposed sweeps between −300 ms and 300 ms.

The duration of this pattern (the congruent part of superimposed sweeps) is relatively long and the correlation among sweeps is high. Fig. 3b exhibits a very pronounced overlapping of sweeps, but in this case the duration of the phase-ordered pattern is relatively short. Another example is presented in Fig. 3c. Here the congruence between sweeps is weak in comparison to those of Fig. 3a,b. However, the curve describing the dynamics of correlation exceeds the critical level of Z = 0.1877 in the vicinity of −300 ms. The degree of congruence between sweeps in the alpha patterns can be considered as an indicator of stability in the performance of time interval reproduction. Note that irrespective of a broad interindividual variation in duration, degree of congruence and probability of appearance of effects of phase ordering were observed in all subjects in spite of the relatively small number of experiments with each of them.

Fig. 4 represents the scalp distribution of phase-ordered alpha patterns in individual data obtained for auditory and visual stimuli. It shows that patterns may appear at all scalp locations. Large individual differences are observed in the topography of phase-ordered alpha patterns. The distribution of patterns ranges from sharply lo-
calised presentation in one lead (subject CE, auditory stimulus; subject RQ, visual stimulus) to appearance at all points of the EEG record (subject SH, auditory stimulus). Stimulus modality has an influence on the topographical distribution of phase-ordered patterns only within subjects. For example, subject SH had pronounced patterns at every point under study for auditory signals, but expectation of visual stimuli induced phase-ordered patterns only in the frontal area and at the vertex. For subject MM phase-ordered patterns were observed in the left hemisphere for visual stimulation. When tones were used as a target, congruent patterns were recorded only in frontal areas. But considering the data of the whole group there was no consistency across individuals in relation to the type of applied stimulation. In general, the data of Fig. 4 indicate that phase-ordered patterns appeared more often in frontal and central areas.

Because all subjects demonstrated phase-ordered alpha patterns in frontal areas, derivations F3 and F4 were chosen to assess the duration of these patterns. For each subject, the duration of the phase-ordered alpha pattern was measured as a period in which the mean Z-values exceeded the critical level. Mean durations of the congruence patterns were found to be 288 ms (S.D. = 102 ms) and 338 ms (S.D. = 99 ms) for auditory and visual stimuli, respectively, no reliable difference between them was observed in the t-test (t = 0.91, P > 0.35). The average for both types of stimuli was 313 ms (S.D. = 101 ms).

In order to describe the amplitude within the phase-ordered alpha patterns compared with the amplitude characteristics of superimposed sweeps outside these patterns the envelopes were used. In most cases phase tuning was accompanied by a decrease in amplitude. For the auditory stimulus three subjects showed amplitude enhancement. Only one subject showed an increase of the amplitude for visual stimulation. In one subject the

Fig. 4. Brain topography of the phase-ordered alpha patterns in the individual data of 10 subjects for visual and auditory signals. '●' marks leads in which mean Z-values exceeded level $Z = 0.1877$. 
amplitude did not change for both types of stimuli.

3.2. Phase-ordered alpha patterns and behavioural errors of timing

Mean errors in the reproduction of omitted stimuli by button pressing varied from \(-465\) ms to \(384\) ms for auditory stimulus and from \(-398\) ms to \(463\) ms for visual stimulus. The average time for errors across subjects was found to be negative for auditory (\(-84\) ms, S.D. = \(231\) ms) and positive for visual stimulus (11 ms, S.D. = \(214\) ms), but the difference is not significant. Only two subjects showed a stable tendency to underestimate the stimulus time interval, i.e. in button pressing they constantly produced time intervals that were shorter than the stimulus intervals. All other subjects exhibited positive as well as negative errors for both types of stimuli.

Comparison of the data obtained in measurements with mental marking and button pressing was performed by correlation analysis. For each channel the interval with the largest intersweep correlation was selected. The values corresponding to the middles of the selected intervals were compared with mean errors of timing in measurements with button pressing. Significant correlation coefficients were obtained for F (\(r = 0.909, P < 0.0001\)), F (\(r = 0.378, P = 0.1\)) and C (\(r = 0.732, P < 0.0001\)). Most subjects showed alpha phase patterns in these scalp locations.

Because all of the subjects exhibited pronounced phase ordering of alpha oscillations in the frontal area, these data were compared with behavioural errors of timing. In Fig. 3, arrows indicate arithmetic mean of errors obtained in the corresponding control experiments with button pressing. For all of the subjects correlation coefficients between sweeps were found to increase in close correspondence to the mean errors found in the behavioural measurements. For the F derivation the relationships between errors of performance and parameters of time intervals with the best correlation among sweeps were reliable for auditory (\(r = 0.884, P = 0.001\)) and visual (\(r = 0.948, P < 0.0001\)) stimuli. Fig. 5 illustrates the combined relationship by plotting the central value of the critical intervals with maximal intersweep correlation coefficients for F against the mean errors obtained in the motor responding situation on the abscissa.

Task instructions produced parallel changes in the behavioural and EEG parameters. One subject (ST) underestimated the target interval during all measurements of the first session. Before the second session she was instructed to take into account the onset of the first stimulus of the next trial that followed the omitted stimulus for self-control of accuracy in performance. Behavioural measurements of the second session showed that, apparently using a new cognitive strategy, she could perform more accurately. The position of the alpha patterns changed accordingly. Fig. 6a,b illustrates this case. The phase-ordered pattern related to the performance with underestimation appeared in the range between \(600\) ms and \(300\) ms, whereas the EEG signals in other areas showed disordered behaviour. In the next measurement the best congruence of sweeps appeared at approximately \(0\) ms on the time scale.

Comparison of the EEG data obtained in measurements with mental marking with those obtained in behavioural measurements therefore indicates that coherent patterns of alpha activity appear at a time that corresponds to the errors in motor performance. This means that during the reproduction of the interstimulus interval alpha
oscillations become locked to the moment of the subjective representation of the omitted stimulus in memory. It happens fairly often that subjective estimation of the interstimulus interval is different from an objective one. In these cases phase-ordering of alpha oscillations appears in the corresponding area on the time scale. Instruction or additional self-control increases accuracy of interstimulus interval estimation and reproduction and, as a result, phase locking of alpha oscillations becomes visible near the objective onset of the omitted stimulus. The same takes place after long-term training of subjects. In this case ordering of the alpha oscillations seems to be phase locked to the objective onset of the omitted stimulus, as it was already reported (Başar et al., 1988, 1989; Başar and Schürmann, 1996). Taking into account the findings of the present study this result may be interpreted in the following way: training reduces the errors in time interval reproduction and, as a result, ordering of alpha oscillations appears to be phase locked to the onset of the omitted stimulus, indicating an adequate reproduction of the interstimulus interval by the subject.

4. Discussion

Patterns of phase-ordered alpha activity were analysed in the present study. These patterns appeared during mental marking of the omitted stimuli. They represent the covariance (similarity of wave shape) over EEG segments of 300 ms duration or approximately three periods of the alpha rhythm. Cognitive task performance required mental anticipation of the omitted stimuli and instigated phase ordering of alpha oscillations. Phase reordering (tuning) in general denotes alignment of single alpha sweeps with respect to the time axis resulting in reproducible alpha patterns. The present findings demonstrate that phases become locked to the time of subjective representation of the target (omitted stimuli) in memory.

In spite of a variety of individual differences of phase-ordered patterns, all subjects demonstrated phase tuning of alpha activity in frontal and central areas during performance of the cognitive task. Visual and auditory stimuli produced different topographies of the phase-ordered patterns within each subject, but no consistent topographical differences between modalities were found across subjects. Tuning by phase was in most cases accompanied by amplitude attenuation. The time of appearance of these patterns corresponded to time errors in experiments with motor responding by button pressing. This implies that endogenous processes manifested by phase reordering of the alpha waves are strongly associated with subjective stimulus evaluation and probably reflect operations of memory in action.

In a number of earlier studies it has been stated that the phase of the alpha activity imposes temporal limitations on data processing. It was
hypothesised that there is a parallel between phase changes in the cycle of the alpha activity and behaviour (Lindsley, 1952; Callaway and Yeager, 1960; Dustman and Beck, 1965; Nunn and Osselton, 1974; Varela et al., 1981; Rice and Hagstrom, 1989). In these studies it was shown that the phase of alpha activity in which a stimulus input arrives may influence the time characteristics of output reactions. The present experiments show, in addition, that the phase characteristics of ongoing EEG are relevant indicators of the output of mental activity during timing.

Studies of memory retrieval processes with ERP and records from single neurons reported involvement of frontal areas in memory processes (Pratt et al., 1989; Goldman-Rakic, 1992; Meclinger et al., 1992). John et al. (1996) discuss the role of ‘the frontal comparator’ for matching of information items in memory. These recent studies bear upon the fundamental theory about the role of frontal lobes in memory and attention functioning (Luria, 1973). Though each subject had a particular topography of phase-ordered alpha patterns in the present study, these patterns appeared more often in frontal and central areas. A systematic effect of phase tuning was observed in the frontal area only. The results provide additional support for the suggestion that phase-ordered alpha patterns are indicators of memory processes.

An influence of stimulus modality on brain activity was reported when the subject had to recognise missing stimuli (Simson et al., 1976). Topographic distributions of negative component of ‘missing’ potentials were different in the visual and auditory modalities and were similar to the respective evoked potentials topographies. Therefore it was suggested that involvement of modality-specific association areas may be a sufficient condition for the detection of stimulus deletion. In the present study no significant dependence on the topography of phase-ordered alpha patterns was found across the group of subjects in relation to stimulus modality. This result yields additional evidence that active reproduction of omitted stimuli involves brain mechanisms that are different from those in the passive perception of omitted stimuli.

To summarise, the topographical distributions found in the alpha range do not exhibit the modality specific patterning found in sensory tasks. From the comparison with behavioural results it seems rather that the arising topographical structures are typical of the purely internal, intentional character of the task. The evidence from the above topographical analysis is consistent with the view that the task under consideration involves components of working memory in which frontal processing plays a prominent role.

The appearance of phase-ordered alpha patterns corresponded to time errors in behavioural experiments that require the reproduction of the stimulus time intervals by button pressing. This result provides a provisional basis for the discussion of the functional meaning of phase-ordered alpha patterns. The reproduction of the time interval is an elementary cognitive task permitting the measurement of individual differences while minimising the variance attributable to specific knowledge and acquired intellectual skills. The present findings indicate that phase-ordered patterns may reflect the brain dynamics involved in the recollection of stimulus properties.

One of the possible explanations of the origin of repetitive alpha patterns can be found in a model by Lebedev (1980, 1990). In this model reference to alpha activity is part of a broader ‘dynamic memory approach’ in the physiological study of short-term memory functioning (John, 1968; Livanov, 1977; Başar et al., 1989).

The basic assumption of the model is that discrete brain oscillations in the alpha range represent elements of memory codes, where each oscillation can carry information about some feature of the object, that is of importance under given circumstances. All oscillations bearing information on the same object are supposed to have the same frequency and to be linked together with certain phase lags. Such an ensemble of alpha waves therefore forms a subpopulation which oscillates synchronously. Phase characteristics of the resulting oscillatory activity depend on the particular combination of phases between discrete alpha waves forming a code. Thus each memory code obeys particular phase and frequency properties.

Within the framework of this general hypothe-
sis, processing in experiments using omitted stimuli during each of the repetitive trials can be considered as consistent with the assumption of three steps of processing that together determine the subjects’ accuracy of interval reproduction. (1) Different memory codes are formed when a subject perceives the interval between the first and the second stimulus. These codes can contain information about physical characteristics of the expected stimuli and about the target interval. (2) The memory code is strengthened by information available from the perception of the interval between the second and the third signal. (3) The subject repeats the target interval by retrieving it from memory. The decision about the moment of mental marking may be considered as equivalent to activating and reading out a memory code represented by alpha waves of identical phase and frequency, which beside other characteristics of the stimulus itself carry information about its temporal relations to other stimuli.

Subjective representations of stimulus interval duration can differ from objective ones under conditions where there is no feedback and the subjects perform on the basis of self-referential impressions only. In several instances in the present study the mean error of performance exceeded 300 ms, although subjects in their interviews reported that according to their impressions their performance was very accurate. We suppose that in these cases subjects involuntarily estimated invalid parameters of their performance such as the level of their attention during task performance. They actually were able to work with great stability during the experiment despite regularly occurring systematic errors in the estimation of time intervals and, as a result, phase-ordered alpha patterns appeared in the corresponding time intervals.

Recent studies showed that analysis of oscillatory activity in the alpha range gives a key to the understanding of mechanisms of memory processes supporting a ‘dynamic memory approach’ (John, 1968; Livianov, 1977; Başar et al., 1989).

Studies from Klimesch’s group (Klimesch et al., 1990, 1994; Klimesch, 1996, 1997) using different memory paradigms present convincing evidence that the alpha range of the human EEG plays an important role in the brain mechanisms of memory. It was found that the alpha frequency varies as a function of memory performance. The evaluation of changes in band power revealed that the upper alpha band is particularly sensitive to semantic memory demands. Studies of Lebedev’s group (Lebedev, 1980, 1990; Markina and Maltseva, 1992; Maltseva and Masloboev, 1997) presented experimental data about the dependency of the individual capacity of short-term memory on step-type behaviour of oscillations in spontaneous alpha rhythm. In this report it was found that phase ordering of the alpha oscillations can serve as an index for retrieval processes.

Recent studies provide a lot of evidence that besides alpha, delta and theta rhythms also take part in memory processes (Meclinger et al., 1992; Klimesch et al., 1994; Lisman and Idart, 1995; Geissler, 1997). It is suggested that higher frequencies such as beta and gamma (Klimesch, 1996; Jensen and Lisman, 1996; Geissler, 1991, 1997) may be involved in the encoding and retrieval of information. Involvement of other EEG bands in cognitive processing during time interval reproduction will be under discussion in further studies.

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Appendix A

In this appendix, we illustrate how the data points that are plotted in Fig. 2 were calculated. In the set of 10 sweeps \(sw_1\ldots sw_{10}\) for each interval of analysis of 300 ms duration a correlation matrix \(r_{ik}\) was obtained. Pearson correlation
Table 1
Correlation coefficients between 10 sweeps in the 300-ms interval of analysis \((N = 192)\)

<table>
<thead>
<tr>
<th></th>
<th>sw1</th>
<th>sw2</th>
<th>sw3</th>
<th>sw4</th>
<th>sw5</th>
<th>sw6</th>
<th>sw7</th>
<th>sw8</th>
<th>sw9</th>
<th>sw10</th>
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<td>sw10</td>
<td>0.3065</td>
<td>−0.1032</td>
<td>−0.1741</td>
<td>0.0180</td>
<td>0.1828</td>
<td>0.4110</td>
<td>−0.3943</td>
<td>−0.4663</td>
<td>−0.1982</td>
<td>1.0000</td>
</tr>
</tbody>
</table>

Coefficients \(r_{nk}\) between two signals \(sw_n\) and \(sw_k\) were defined as

\[
r_{nk} = \frac{m \sum_{i=1}^{m} X_n X_{ki} - \left( \sum_{i=1}^{m} X_n \right) \left( \sum_{i=1}^{m} X_{ki} \right)}{\sqrt{ \left[ m \sum_{i=1}^{m} X_{ki}^2 - \left( \sum_{i=1}^{m} X_{ki} \right)^2 \right] \left[ m \sum_{i=1}^{m} X_{ni}^2 - \left( \sum_{i=1}^{m} X_{ni} \right)^2 \right]}}
\]

\(m\) denoting the number of points in the interval of analysis (in our case \(m = 192\), which corresponds to an interval of analysis of 300 ms duration), \(X_{ki}\) and \(X_{ni}\) are time series of amplitudes of signals \(sw_k\) and \(sw_n\) \((k = 1 \ldots 10, n = 1 \ldots 10)\).

Table 1 represents an example of a correlation matrix, computed to estimate the strengths of associations between 10 sweeps in the interval of analysis from \(-800\) ms to \(-500\) ms for the set of sweeps shown in Fig. 2.

As the value of the correlation coefficient is not a linear function of its variables, correlation coefficients cannot be simply averaged, but have first to be converted into additive measures. We converted correlation coefficients into Fisher's \(Z\)-values, which are additive, using the following equation:

\[
Z_{nk} = \frac{1}{2} \ln \left( \frac{1 + r_{nk}}{1 - r_{nk}} \right)
\]

As a result of such a transformation a new matrix of \(Z\)-values was obtained for each interval of analysis.

Table 2 represents an example for the conver-
sion of the correlation coefficients from Table 1 into Z-values.
Averaging of Z-values was carried out according to the expression
\[
Z = \frac{1}{N(N-1)} \sum_{n \neq k} Z_{nk}.
\]

We consider the resulting mean Z-value to be the estimate of the relationships between the 10 sweeps in the current interval of analysis. This value was plotted as the first point in the graph in Fig. 2.

References