

Phase-Locking and Amplitude Modulations of EEG Alpha: Two Measures Reflect Different Cognitive Processes in a Working Memory Task

Christoph S. Herrmann,¹ Daniel Senkowski,² and Stefan Röttger³

¹Institute for Biological Psychology, Otto-von-Guericke University, Magdeburg, Germany,

²Max-Planck Institute of Cognitive Neuroscience, Leipzig, Germany, and

³Institute for Psychology, Leipzig University, Germany

Abstract. It has been demonstrated in numerous experiments that oscillatory EEG responses in the alpha frequency band (8–12 Hz) increase with memory load during the retention interval in working memory tasks. However, the findings diverge with respect to which measurement of alpha activity is influenced by memory processes. Here, we differentiate between evoked and total alpha activity in order to separate effects of phase-locking and amplitude modulation. We present data from a delayed-matching-to-sample task (S1-S2 paradigm) for which we compared EEG alpha responses between a perception and a memory condition. Increased total alpha activity was found in the retention interval for the memory as compared to the perception condition. Evoked alpha activity, however, did not differentiate between memory and perception conditions but, instead, was increased for the more complex condition of processing non-Kanizsa figures as compared to Kanizsa figures. Thus, our results demonstrate a functional differentiation between evoked and total alpha activity. While alpha phase locking seemed to be influenced mainly by task complexity, alpha amplitude clearly reflected memory demands in our paradigm.

Key words: alpha, EEG, evoked, induced, phase-locking, working memory

Introduction

A vast amount of studies have indicated a close relationship between memory processes and oscillatory responses in the EEG (see Başar, Başar-Eroglu, Karakaş, & Schürmann, 2000; Klimesch, 1999, for reviews). Frequently, memory processes are associated with EEG activity in the theta-band (4–7 Hz: Tesche & Karhu, 2000; Klimesch, Doppelmayr, Rohm, Pollhuber, & Stadler, 2001), alpha band (8–12 Hz: Schack & Klimesch, 2002; Klimesch, 1997; Klimesch, Doppelmayr, Schimke, & Pachinger,

1996), and gamma band (30–80 Hz: Gruber & Müller, 2002; Fell et al., 2001; Herrmann & Mecklinger, 2001; Tallon-Baudry, Bertrand, Peronnet, & Pernier, 1998). Recently, also the interaction of different frequencies has been investigated with respect to its relevance for memory processes (Düzel et al., 2003; Sauseng et al., 2002; Stam, 2000; von Stein & Sarnthein, 2000). Here, we want to demonstrate how different aspects of the alpha frequency band reveal different aspects of cognitive processes. Two types of event-related changes occur in EEG oscillations in response to experimental conditions. On the one hand, the amplitude of an oscillation can increase or decrease in response to different memory demands (Jensen, Gelfand, Kounios, & Lisman, 2002). However, also the phase of an oscillation can be influenced by stimulation (Brandt, 1997) and is modulated by working memory demands (Rizzuto et al., 2003). In order to differentiate these two phenomena, evoked alpha oscillations, which result mainly from

We express our thanks to Bernward Winter who helped to prepare the experimental setup, to Jonathan Whittlock who helped during data acquisition and analysis, and to Maren Grigutsch for software development. Daniel Senkowski was supported by the German Research Foundation (DFG, grant HE3353/1) and the Max Planck Society.

phase locking, need to be differentiated from induced ones, which mainly reflect amplitude changes. Usually a simultaneous modulation of both measures results in the so-called alpha-paradox (Klimesch et al., 2000). We believe that it is important to understand the different mechanisms underlying oscillatory EEG changes within one frequency band before we can then address how the different frequency bands interact. Therefore, we use a differentiation between phase locking and amplitude modulations, which seems to be necessary when investigating EEG oscillations, and then demonstrate how the two measures are modulated by different cognitive processes.

Methods

Subjects

Twenty-two subjects with a mean age of 24.2 years (ranging from 19 to 33 years, 11 female, 7 left-handed) participated in the study. All subjects had normal or corrected-to-normal vision and showed no signs of neurological or psychiatric disorders and all gave written informed consent.

Stimuli

The stimuli used in this paradigm were composed of four inducer disks which either constituted a Kanizsa square due to their collinear arrangement or not. These assemblies of four disks were presented at three different rotation angles (11.25° , 22.5° and 37.5°).

Paradigm

In our paradigm, subjects had to either perform an easy perception or a more complex memory task (Figure 1). During each trial, two stimuli, S1 and S2, were presented sequentially. In the perception condition, subjects had to judge whether or not the S2 stimulus was maximally rotated (37.5°). In the memory condition, the task was to decide whether the stimulus S2 had the same rotation angle as S1. A manual yes/no response was required in every trial. Both stimuli, S1 and S2, were always identical in collinearity and could vary only in rotation angle. Each trial started with an initial warning tone, which indicated whether the perception condition (750 Hz) or the memory condition (3000 Hz) was to be per-

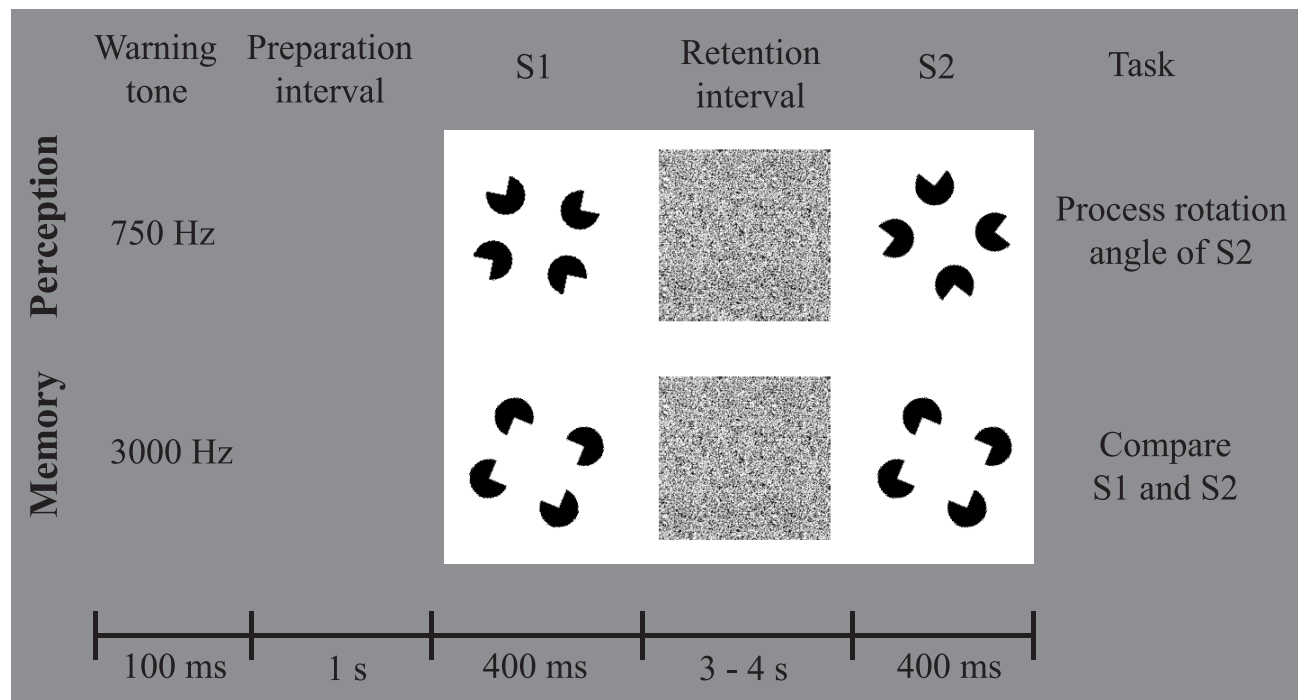


Figure 1. Illustration of the paradigm. After a warning tone, which indicates the condition to follow (perception or memory), and a 1 s preparation interval, the S1 stimulus was presented for 400 ms. During the retention interval of a random length between 3 to 4 s, a mask with randomly distributed black and white pixels was shown, followed by the 400 ms presentation of S2.

formed. Then, a 1 s preparation interval followed. Stimulus S1 was presented for 400 ms on a screen 1 m in front of the subjects. After a retention interval of 3 to 4 s (3, 3.25, 3.5, 3.75 and 4 s, randomly distributed), S2 was presented for 400 ms. The measurement of the reaction time started with the onset of S2.

Data Acquisition

The EEG was recorded with NeuroScan amplifiers using 19 Ag/AgCl-electrodes mounted in an elastic cap. Electrodes were placed according to the international 10–20 system. The ground electrode was C2 and all electrodes were referenced to the left mastoid (M1). Electrode impedance was kept below 5 k Ω . Horizontal and vertical EOG were registered with four additional electrodes. Data were sampled at 500 Hz and analog-filtered with a 0.05 Hz high-pass and a 100 Hz low-pass filter, and digitally filtered with a 50 Hz notch filter.

Data Analysis

Prior to data analysis, filtered EEG data were scanned by an artifact scanning software for eye movements, drifts, and defective electrodes: All epochs containing amplitude standard deviations of more than 30 μ V (40 μ V for EOG channels) in any of the recorded channels within a moving 200 ms window were excluded from further analysis. In a second step, the remaining epochs were visually inspected for artifacts missed by the automatic rejection procedure. In order to analyze oscillatory alpha activity, a wavelet transform was applied to the data (for details, see Herrmann, Mecklinger, & Pfeifer, 1999; Herrmann & Mecklinger, 2000). This analysis yields evoked alpha activity which is strictly phase-locked to stimulation and total alpha activity which comprises evoked and induced activity, the latter not being phase-locked to stimulation. It is important to note that an increase of evoked alpha activity alone does not resolve how this increase comes about. It could either be caused by phase resetting or amplitude increase. Only if we consider both measures, evoked and total alpha activity, we can infer what kind of change of alpha activity happened. If only the evoked activity increases after stimulation while the total activity remains stable, a pure increase of phase locking across trials was the cause of this stimulus-related change.

If, instead, only the total activity increases while the evoked remains stable, a pure increase of amplitude was the cause. However, both measures can re-

act at the same time, indicating that both phase locking and amplitude vary in response to stimulation. The Morlet wavelets had a center frequency of 10 Hz. Epochs for wavelet transformation and signal averaging ranged from –1200 to 1000 ms relative to stimulus onset for S1 and S2 and from –1400 to 3400 ms relative to S1 offset for the retention interval. Oscillatory activity was computed relative to baselines that preceded the event of interest, i.e., the stimulus presentation or the beginning of the retention interval. To compensate for the effect of temporal smearing, which is particularly present in the alpha frequency of the decomposed EEG, baselines were chosen to end before the respective stimulus begins. These baselines were –400 to –200 ms relative to S1 and S2. The baseline for the retention interval was from –800 to –600, which is identical to the baseline of S1, since S1 lasted 400 ms. In order to avoid a loss of statistical power that is inherent when repeated measures ANOVAs are used to quantify multi-channel EEG data, selected electrode sites were pooled to an anterior and a posterior topographical region of interest (ROI). The anterior region consists of the electrodes FP1, FP2, FZ, F3, F4, F7, and F8, whereas the posterior region was comprised of electrodes PZ, P3, P4, P7, P8, O1, and O2. For the S1 stimulus and the retention interval, repeated measures ANOVAs with the factors condition (memory vs. perception), figure (Kanizsa figure vs. non-Kanizsa figure), and ROI (anterior vs. posterior) were computed. ANOVAs for the brain responses to S2 additionally included the factor Response (yes vs. no), with the maximally rotated stimuli requiring a yes response in the perception condition and S2 stimuli matching the preceding S1 stimulus requiring a yes response in the memory condition. ANOVAs were computed for the mean activity within a specified time interval. These time intervals were chosen to be 80 to 220 ms after onset of S1 and S2, as well as an early (0 to 500 ms) and a late (500 to 2500 ms) time period in the retention interval. When separate conditions are shown in figures, the data are collapsed across all other experimental conditions.

Results

Behavioral Data

An ANOVA of the RTs yielded no significant differences between the memory (800 ms) and the perception condition (780 ms). A significant main effect found for the factor figure, $F(1, 21) = 7.05$, $p < .05$, indicates longer RTs for non-Kanizsa figures (795 ms) as compared to Kanizsa figures (784 ms). Furthermore, a significant Figure \times Response in-

teraction was found, $F(1, 21) = 5.55, p < .05$. Post hoc analyses revealed longer reaction times for no-responses to non-Kanizsa figures (803 ms) as compared to no-responses to Kanizsa figures, 780 ms; $F(1, 21) = 9.48, p < .01$. An ANOVA for the yes-responses showed no effects for the factor figure.

For the analysis of error rates, a repeated measures ANOVA with the factors condition, figure and response was computed. In this analysis, significant main effects of the factors condition, $F(1, 21) = 65.08, p < .0001$, and response, $F(1, 21) = 7.32, p < .05$, were found. A higher error rate in the memory condition (15.3%) as compared to the perception condition (4.1%) indicates a higher difficulty of the memory condition. Finally, more errors were observed for the no-responses (11.1%) as compared to the yes-responses (8.4%).

Alpha Activity

All three stimuli, S1, the mask in the retention interval, and S2, elicited changes of evoked as well as total alpha activity. However, evoked activity increased in response to stimulation (see Figure 2A) while total alpha activity decreased (see Figure 2B).

Alpha Topography

Alpha activity was not evenly distributed across all electrodes. In response to S1, an ANOVA for the evoked alpha activity yielded a significant main effect of ROI, $F(1, 21) = 7.14, p < .05$, indicating higher posterior amplitudes (1.69 μV) as compared to anterior amplitudes (1.13 μV). In addition, an ANOVA for the total alpha activity yielded a significant main effect for the factor ROI, $F(1, 21) = 10.08, p < .005$, indicating that the decrease of total alpha activity was significantly stronger in posterior electrodes ($-1.58 \mu\text{V}$) as compared to anterior ones ($-1.07 \mu\text{V}$).

Alpha in Response to S1

ANOVAs for the evoked and total alpha activity were calculated for the time interval from 80 to 220 ms after stimulus onset and yielded no significant effects of the factors condition or figure.

Alpha During the Retention Interval

ANOVAs for the evoked and total alpha activity were calculated for an early (0 to 500 ms after onset of

the retention interval) and a late time interval (500 to 2500 ms). In the early interval, a significant main effect of the factor figure, $F(1, 21) = 4.36, p < .05$, indicated that alpha responses evoked by non-Kanizsa figures (0.36 μV) were higher than those evoked by Kanizsa figures (0.24 μV). No significant effects were found for the total alpha activity during the early time interval.

During the late time interval no significant effects were found for the evoked alpha activity. However, for the total alpha activity, a significant effect of the factor condition was found in the late time interval, $F(1, 21) = 4.58, p < .05$. Total alpha amplitudes were higher in the memory (0.1 μV) as compared to the perception condition ($-0.16 \mu\text{V}$). Finally, a three-way interaction of the factors ROI, figure, and condition was observed, $F(1, 21) = 5.04, p < .05$. Separate ANOVAs for the anterior and posterior ROI revealed that only for posterior electrode sites, a Figure \times Condition interaction was present, $F(1, 21) = 6.32, p < .05$. Post hoc tests showed that in posterior regions, the factor condition had no effect whenever Kanizsa figures were presented, whereas non-Kanizsa figures induced higher alpha activity in the memory condition as compared to the perception condition, 0.39 μV vs. $-0.18 \mu\text{V}$; $F(1, 21) = 7.89, p < .05$.

Alpha in Response to S2

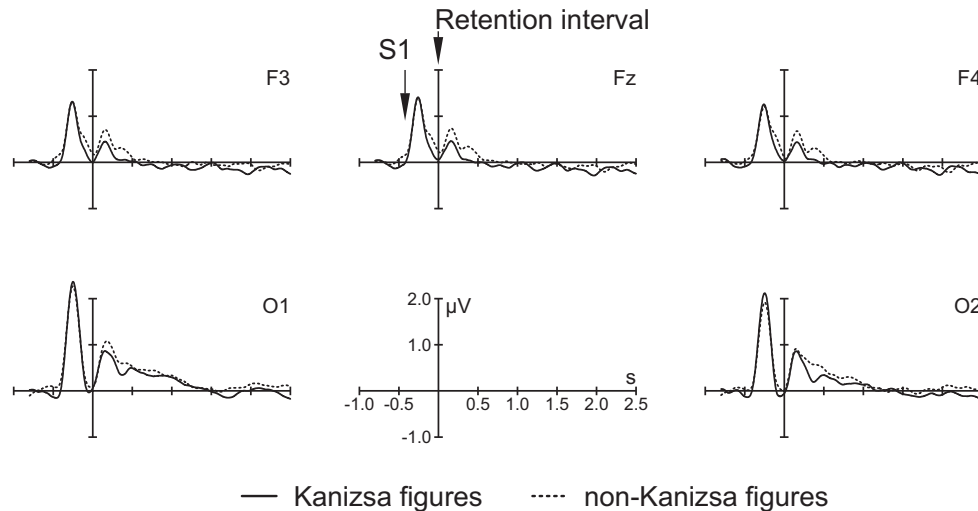
For the responses to the presentation of the second stimulus, ANOVAs of the evoked alpha activity yielded a significant ROI \times Response interaction, $F(1, 21) = 6.14, p < .05$ in a time interval from 80 to 220 ms after onset of S2, indicating that yes-responses evoked stronger alpha activity in posterior ROIs (1.52 μV) as compared to anterior ROIs (1.18 μV). The post-hoc analysis testing this hypothesis, however, missed significance.

Discussion

Behavioral Data

The error rates in our experiment were higher for the memory condition than for the perception condition. The main difference between the memory and the perception condition results from a different memory load during the retention interval. Thus, the higher error rate for the memory condition probably results from subjects delivering false responses due to incorrectly remembering S1 in short-term-memory (STM). In addition, subjects made more errors in case of no-responses than in case of yes-responses.

A: Evoked alpha activity



B: Total alpha activity

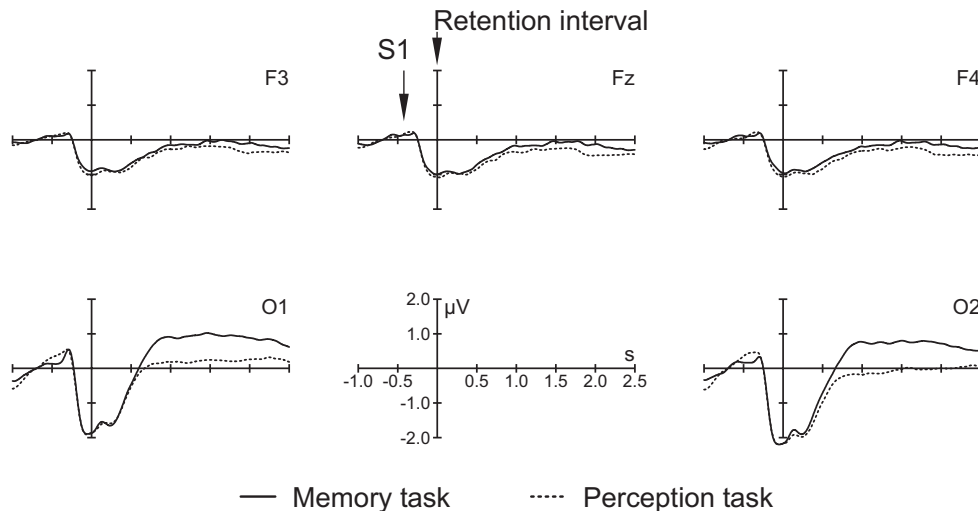


Figure 2. A: Grand averages of evoked alpha activity reveal two peaks. The first one was evoked by the onset of the first stimulus (S1, see arrow). The second peak was evoked by the onset of the mask in the retention interval which occurs at time point 0 in this graph. B: Grand averages of total alpha activity. During the retention interval there was an increase after an initial decrease. The increase was significantly larger for the memory condition.

In the memory task, yes-responses are required for S2 stimuli that match the S1 stimulus. Thus, it is plausible to assume that such repeated items are easier to process in this paradigm, since repetition facilitates the processing of the stimuli (Buckner et al., 1995).

The reaction times of our experiment were longer for non-Kanizsa figures than for Kanizsa figures,

which probably indicate that the non-figural stimuli are harder to process. Especially the non-Kanizsa figures, which required a no-response, yielded the longest reaction times irrespective of whether they had to be memorized or their rotation angle had to be judged. However, it was not relevant for the task at hand whether or not the presented stimuli constituted Kanizsa figures or not. Figure 3 shows which

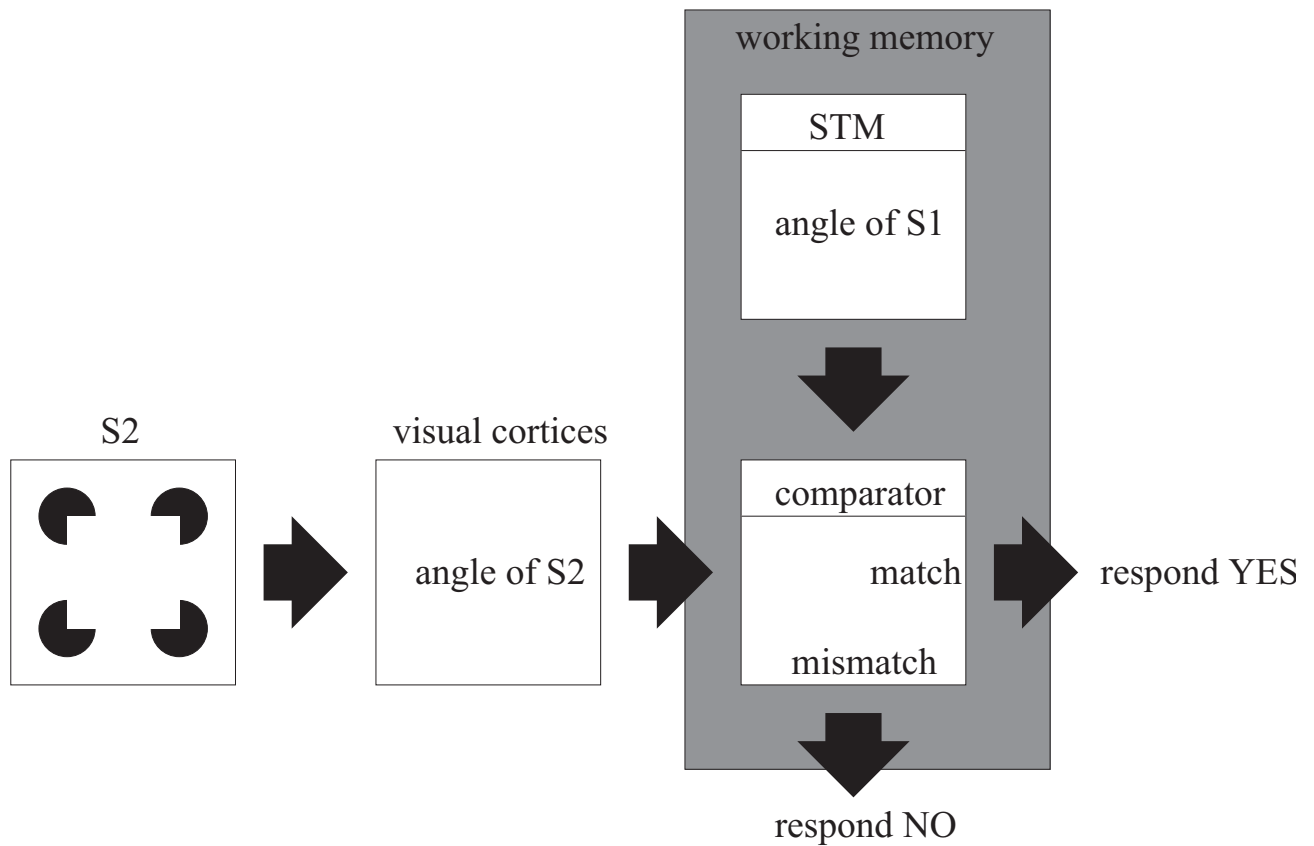


Figure 3. A model of the processes involved in our paradigm after S2 presentation. S2 needs to be visually processed and the rotation angle has to be detected. Then, this angle has to be compared to an angle in STM. This is either the angle of S1 (memory condition, shown) or a fixed angle of 37.5° (perception condition, not shown). Finally, a manual response can be given depending on whether the S2 angle does or does not match the angle in STM. It is important to note that memory demands only vary between conditions at S1 presentation and during the retention interval but not at S2 presentation.

cognitive processes are involved in the memory condition and could potentially influence reaction times. It is important to note that recording of the reaction times started with presentation of S2. Thus the differences of memory load during the retention interval probably did not influence the reaction times. Both the memory and the perception condition required a comparison of the rotation angle of S2 with an angle held in STM. In case of the memory condition this was the angle of S1. In case of the perception condition, it was a fixed angle of 37.5° . This explains why there was no difference in reaction times between these two conditions. However, error rates already indicated that non-matching S2 stimuli (no-responses) are harder to process than matching S2 stimuli (yes-responses) due to the lack of repetition priming. Also the three-way interaction of total alpha activity in the retention interval indicated that non-Kanizsa figures are harder to be maintained in memory than Kanizsa figures. In addition, a previous study showed that the processing of non-Kanizsa fig-

ures leads to longer reaction times than that of Kanizsa figures, indicating that non-Kanizsa figures are also hard to process (Proverbio & Zani, 2002). Thus, it seems plausible to assume that when a difficult non-matching S2, at the same time, represents a non-Kanizsa figure, this leads to the longer reaction times due to higher processing effort in visual cortices.

Alpha Responses

In response to S1 presentation, no significant differences were found in evoked or total alpha activity. This was surprising, since S1 stimuli had to be stored in STM during the memory condition while they could be ignored during the perception condition. Thus, the differences either occurred in other frequency bands or the stimuli were for some reason equally processed in both conditions.

At the beginning of the retention interval, evoked alpha activity was significantly stronger in response

to non-Kanizsa figures than to Kanizsa figures. At the same time, total alpha activity decreased and showed no significant differences between experimental conditions. Therefore, non-Kanizsa figures lead to an enhanced phase locking across trials. It has to be noted that at this time neither of the two figures were visible on the screen. Instead, the noisy pixel mask was shown during the retention interval. Therefore, we assume that even though the type of figure was not relevant for the subject's task, non-Kanizsa figures were harder to process as already indicated by the longer reaction times following S2. The enhanced evoked alpha response might reflect this difference in processing demands. However, this increase of evoked alpha activity appeared after the non-Kanizsa stimulus was shown and thus processing of the non-Kanizsa figure probably interacted with the processing of the pixel-mask due to a longer processing of non-Kanizsa figures as compared to Kanizsa figures. Previous studies had already demonstrated that alpha activity is related to task demands (Cooper, Croft, Dominey, Burgess, & Gruzelier, 2003; Earle, 1988). Our results are in line with data showing that the processing of non-objects leads to an increase of alpha activity as compared to objects (Vanni, Revonsuo, & Hari, 1997). However, we were able to show that the phase locking of alpha activity is enhanced for non-Kanizsa figures, while the decrease of amplitude following stimulation shows no differences with respect to whether Kanizsa figures or non-Kanizsa figures are presented. This, again, is in line with data showing that specifically the phase of alpha oscillations is sensitive to task processing (Kolev, Yordanova, Schürmann, & Başar, 1999). Due to the high degree of phase locking to the stimulus, evoked alpha activity is also visible in the visual evoked potential (VEP). In fact, it has been argued that phase-resetting may be one of the main mechanisms leading to evoked potentials in addition to pure amplitude changes (Makeig et al., 2002). Changes which are only visible in the total but not in the evoked alpha activity and thus reflect induced activity will, however, not influence the VEP very much.

The total alpha activity during the retention interval was significantly stronger for the memory condition as compared to the perception condition while evoked alpha activity revealed no significant differences between conditions. Thus, an increase of alpha amplitude reflects the increased memory demands of the memory condition. This finding replicates earlier findings of other experiments (Jensen et al., 2002; Schack & Klimesch, 2002). However, it is noteworthy to mention that not the initial decrease of total alpha activity reflects the increased memory demands but a later increase of total alpha activity.

Conclusions

Interestingly, memory demands only affected error rates, while task complexity only affected reaction times. This pattern of results is well explained by our model, which demonstrates that memory load is only crucial during the retention interval and does not influence S2 processing. Since reaction times are recorded following presentation of S2 no effects of memory load should be observed.

We were able to demonstrate that alpha phase resetting and alpha amplitude changes reflect different cognitive processes. Processing the figural aspects of the stimuli resulted in enhanced evoked activity while memory demands enhanced total activity. Thus, it seems that phase resetting is predominantly occurring during cognitive processes that don't relate to memory retention. At the same time, the amplitude of alpha oscillations as measured by the total alpha activity clearly reflected the enhanced memory load during the memory condition.

We don't want to exclude the possibility that alpha phase may be affected by memory aspects in other experimental conditions than the ones used here. However, we want to stress the fact that it is necessary to investigate both measures of event-related alpha activity, i.e., evoked and total alpha activity, in order to find out whether event-related alpha changes are due to phase locking or due to amplitude changes.

References

- Başar, E., Başar-Eroglu, C., Karakaş, S., & Schürmann, M. (2000). Brain oscillations in perception and memory. *International Journal of Psychophysiology*, *35*, 95–124.
- Brandt, M. E. (1997). Visual and auditory evoked phase resetting of the alpha EEG. *International Journal of Psychophysiology*, *26*, 285–298.
- Buckner, R. L., Petersen, S. E., Ojemann, J. G., Miezin, F. M., Squire, L. R., & Raichle, M. E. (1995). Functional anatomical studies of explicit and implicit memory retrieval tasks. *Journal of Neuroscience*, *15*, 12–29.
- Cooper, N. R., Croft, R. J., Dominey, S. J. J., Burgess, A. P., & Gruzelier, J. H. (2003). Paradox lost? Exploring the role of alpha oscillations during externally vs. internally directed attention and the implications for idling and inhibition hypotheses. *International Journal of Psychophysiology*, *47*(1), 65–74.
- Düzel, E., Habib, R., Schott, B., Schoenfeld, A., Lobaugh, N., McIntosh, A. R., Scholz, M., & Heinze, H. J. (2003). A multivariate, spatiotemporal analysis of electromagnetic time-frequency data of recognition memory. *Neuroimage*, *18*, 185–197.
- Earle, J. B. (1988). Task difficulty and EEG alpha asymmetry: an amplitude and frequency analysis. *Neuropsychobiology*, *20*(3), 95–112.

- Fell, J., Klaver, P., Lehnertz, K., Grunwald, T., Schaller, C., Elger, C., & Fernandez, G. (2001). Human memory formation is accompanied by rhinal-hippocampal coupling and decoupling. *Nature Neuroscience*, 4(12), 1259–1264.
- Gruber, T. & Müller, M. M. (2002). Effects of picture repetition on induced gamma band responses, evoked potentials, and phase synchrony in the human EEG. *Brain Research: Cognitive Brain Research*, 13, 377–392.
- Herrmann, C. S. & Mecklinger, A. (2000). Magnetoencephalographic responses to illusory figures: Early evoked gamma is affected by processing of stimulus features. *International Journal Psychophysiology*, 38(3), 265–281.
- Herrmann, C. S. & Mecklinger, A. (2001). Gamma activity in human EEG is related to highspeed memory comparisons during object selective attention. *Visual Cognition*, 8(3/4/5), 593–608.
- Herrmann, C. S., Mecklinger, A., & Pfeifer, E. (1999). Gamma responses and ERPs in a visual classification task. *Clinical Neurophysiology*, 110(4), 636–642.
- Jensen, O., Gelfand, J., Kounios, J., & Lisman, J. E. (2002). Oscillations in the alpha band (9–12 Hz) increase with memory load during retention in a short-term memory task. *Cerebral Cortex*, 12, 877–882.
- Klimesch, W. (1997). EEG-alpha rhythms and memory processes. *International Journal of Psychophysiology*, 26(1–3), 319–340.
- Klimesch, W. (1999). EEG alpha and theta oscillations reflect cognitive and memory performance: a review and analysis. *Brain Research Review*, 29, 169–195.
- Klimesch, W., Doppelmayr, M., Rohm, D., Pollhuber, D., & Stadler, W. (2000). Simultaneous desynchronization and synchronization of different alpha responses in the human electroencephalogram: a neglected paradox? *Neuroscience Letters*, 284(1–2), 97–100.
- Klimesch, W., Doppelmayr, M., Schimke, H., & Pachinger, T. (1996). Alpha frequency, reaction time, and the speed of processing information. *Journal of Clinical Neurophysiology*, 13, 511–518.
- Klimesch, W., Doppelmayr, M., Yonelinas, A., Kroll, N. E., Lazzara, M., Röhm, D., & Gruber, W. (2001). Theta synchronization during episodic retrieval: neural correlates of conscious awareness. *Brain Research: Cognitive Brain Research*, 12, 33–38.
- Kolev, V., Yordanova, J., Schürmann, M., & Basar, E. (1999). Event-related alpha oscillations in task processing. *Clinical Neurophysiology*, 110, 1784–1792.
- Makeig, S., Westerfield, M., Jung, T. P., Enghoff, S., Townsend, J., Courchesne, E., & Sejnowski, T. J. (2002). Dynamic brain sources of visual evoked responses. *Science*, 295, 690–694.
- Proverbio, A. M., & Zani, A. (2002). Electrophysiological indexes of illusory contours perception in humans. *Neuropsychologia*, 40, 479–491.
- Rizzuto, D. S., Madsen, J. R., Bromfield, E. B., Schulze-Bonhage, A., Seelig, D., Aschenbrenner-Scheibe, R., & Kahana, M. J. (2003). Reset of human neocortical oscillations during a working memory task. *Proc Natl Acad Sci USA*, 100 (13), 7931–7936.
- Sauseng, P., Klimesch, W., Gruber, W., Doppelmayr, M., Stadler, W., & Schabus, M. (2002). The interplay between theta and alpha oscillations in the human electroencephalogram reflects the transfer of information between memory systems. *Neuroscience Letters*, 324, 121–124.
- Schack, B., & Klimesch, W. (2002). Frequency characteristics of evoked and oscillatory electroencephalographic activity in a human memory scanning task. *Neuroscience Letters*, 331, 107–110.
- Stam, C. J. (2000). Brain dynamics in theta and alpha frequency bands and working memory performance in humans. *Neuroscience Letters*, 286, 115–118.
- Tallon-Baudry, C., Bertrand, O., Peronnet, F., & Pernier, J. (1998). Induced γ -band activity during the delay of a visual short-term memory task in humans. *Journal of Neuroscience*, 18(11), 4244–4254.
- Tesche, C. D., & Karhu, J. (2000). Theta oscillations index human hippocampal activation during a working memory task. *Proc Natl Acad Sci*, 97, 919–924.
- Vanni, S., Revonsuo, A., & Hari, R. (1997). Modulation of the parieto-occipital alpha rhythm during object detection. *Journal of Neuroscience*, 17(18), 7141–7147.
- von Stein, A. & Sarnthein, J. (2000). Different frequencies for different scales of cortical integration: from local gamma to long range alpha/theta synchronization. *International Journal of Psychophysiology*, 38(3), 301–313.

Received February 19, 2004

Revision received March 4, 2004

Accepted March 10, 2004

Prof. Christoph Herrmann

Otto-von-Guericke-Universität Magdeburg

Fakultät für Naturwissenschaften

Lehrstuhl Biologische Psychologie

Postfach 4120

D-39016 Magdeburg

Germany

Tel.: +49 391 671 8477

Fax: +49 391 671 1947

E-mail: Christoph.Herrmann@Nat.Uni-Magdeburg.de