EEG Alpha Synchronization and Functional Coupling During Top-Down Processing in a Working Memory Task

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Abstract: Electroencephalogram (EEG) α (~10 Hz) is the dominant rhythm in the human brain during conditions of mental inactivity. High amplitudes as observed during rest usually diminish during cognitive effort. During retention of information in working memory, however, power increase of α oscillations can be observed. This α synchronization has been interpreted as cortical idling or active inhibition. The present study provides evidence that during top-down processing in a working memory task, α power increases at prefrontal but decreases at occipital electrode sites, thereby reaching a state in which α power and frequency become very similar over large distances. Two experimental conditions were compared. In the first, visuospatial information only had to be retained in memory whereas the second condition additionally demanded manipulation of the information. During the second condition, stronger α synchronization at prefrontal sites and larger occipital α suppression was observed as compared to that for pure retention. This effect was accompanied by assimilation of prefrontal and occipital α frequency, stronger functional coupling between prefrontal and occipital brain areas, and α latency shifts from prefrontal cortex to primary visual areas, possibly indicating the control of posterior cortical activation by anterior brain areas. An increase of prefrontal EEG α amplitudes, which is accompanied by a decrease at posterior sites, thus may not be interpreted in terms of idling or "global" inhibition but may enable a tight functional coupling between prefrontal cortical areas, and thereby allows the control of the execution of processes in primary visual brain regions. *Hum Brain Mapp 26:148–155, 2005.* © 2005 Wiley-Liss, Inc.

Key words: central executive; coherence; cortical inhibition; event-related synchronization (ERS); idling; prefrontal cortex

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INTRODUCTION

When for the first time Berger [1929] recorded the human scalp electroencephalogram (EEG), he observed rhythmic brain waves around 10 Hz that he termed α waves. In healthy humans, these high amplitude brain oscillations dominate the EEG during resting conditions, especially when subjects' eyes are closed. When the eyes are opened or under mental effort, the high α amplitudes diminish, which is termed α blocking or α desynchronization. Strong EEG α can thus be observed usually during relaxed wakefulness without higher cognitive load, whereas pronounced amplitude reduction reflects cortical activity [for a detailed review, see Klimesch, 1997]. During execution of several cog-

nitive or motor tasks, however, increased α activity is found in brain areas that are not involved in execution of this task, e.g., α synchronization (in terms of power increase) was found in sensorimotor areas during reading and in the visual cortex during execution of a motor task [Pfurtscheller, 1992]. This has led to the view that α might be an idling rhythm [Pfurtscheller et al., 1996] indicating cortical regions in a resting state in which no information is processed. Recent research, however, suggests that α synchronization does not reflect simple idling of brain areas but possibly active inhibition of task-irrelevant brain circuits [Busch and Herrmann, 2003; Cooper et al., 2004; Herrmann et al., 2004; Jensen et al., 2002; Klimesch et al., 1999; 2000]. Klimesch et al. [1999] reported a power increase of the upper α band (~10–12 Hz) in a working memory task when the digit span had been exceeded. Pronounced desynchronization of upper α oscillations is associated usually with semantic long-term memory activation. The increase of α amplitudes during a highly demanding working memory task (lacking semantic demands) was therefore interpreted in terms of active inhibition of neural circuits subserving long-term memory. Jensen et al. [2002] showed a linear increase of α activity with increasing memory load in a working memory task, which was also interpreted as active inhibition, thereby preventing the flow of information to brain areas retaining information in working memory. Alpha synchronization was reported not only for increased working memory load, however, but also during internal as compared to external attentional control [Cooper et al., 2004; Ray and Cole, 1985]. Von Stein et al. [2000] found synchronization of brain oscillations in the α frequency range between primary and higher visual areas in the cat brain to reflect top-down processing. In response to expected stimuli, α oscillations showed a clear latency shift between higher and primary visual areas, indicating a flow of information from higher visual cortices to V1. When unexpected stimuli were presented, no latency shifts were observable; however, this suggests that under certain conditions α synchronization might play an important role in information processing, going beyond simple idling and even beyond active inhibition of brain areas.

The present study was designed to investigate the role of α oscillations during top-down processing in a working memory task using a short-term memory task as control condition. In the short-term memory task, visuospatial information had to be retained, whereas in the working memory task the information had to be retained and manipulated. We assume that in this latter condition top-down processes plays an important role that is reflected by increased α activity and a stronger coupling between prefrontal and occipital areas. The reason for this assumption is that mental operations with visual stimuli can be carried out in occipitoparietal areas but that the initiation of these processes requires central execution/attentional control of frontal brain regions. Furthermore, as more top-down processing is required during the second experimental condition, we should find latency shifts from anterior brain areas to the primary visual cortex, as reported by von Stein et al. [2000] for the cat's visual system.

SUBJECTS AND METHODS

Participants

Thirty-one healthy volunteers participated in the experiment after giving written informed consent. Eight subjects had to be excluded from data analysis due to excess artifacts in the EEG; 15 of 23 remaining participants were female and 8 were male. Mean age was 22.6 years (standard deviation [SD] = 3.0 years). With the exception of two volunteers, all subjects were right-handed.

Tasks

At the beginning of the experiment, EEG was recorded during a 1-min baseline resting situation with eyes open. Subsequently, a visuospatial working memory task was run. In each trial, a 4 × 4 matrix containing three targets (colored squares) was presented for 500 msec. If the three targets were green, their positions had to be kept in memory for 2,500 msec and then had to be compared to three gray labeled matrix positions of a probe that were presented for 1,000 msec. The subjects had to indicate by a button press whether the target positions were the same as in the probe or not. If the color of the targets was red, however, their positions had to be mirrored around a vertical gap in the matrix and then retained in memory for 2,500 msec. Again, the new mental target positions had to be compared to the probe item, and subjects had to indicate whether the positions were identical. In both experimental conditions, *retention* and *manipulation*, half of the probes were positive and half were negative matches. Every participant carried out 80 trials, 40 retention and 40 manipulation trials, in randomly sorted order. The two conditions did not differ in memory load (memory load was three in every trial), but the manipulation condition demanded more top-down processing than did the retention condition. Visual stimulation was run with Presentation v. 0.71 (NBS, Albany, CA).

Data Acquisition

The EEG was recorded from 19 Ag-AgCl electrodes (positioned according to the international 10-20 system) against a linked earlobe reference. The vertical and the horizontal electrooculogram (EOG) were recorded from two additional channels to control for eye movements and blinks. Impedances were kept below 8 kOhms. A Neuroscan Synamps 32-channel amplifier was used for data acquisition. Sampling rate was 500 Hz. Frequencies between 0.15–70 Hz with a Notch-filter at 50 Hz were recorded.

Data Analysis

EEG recordings were offline-EOG corrected and visually inspected for remaining artifacts. All analyses described below were applied to epochs between 0–1,024 msec (1,024

msec represents 512 data points) after offset of the 4 × 4 target matrix. In this time range, there should be a difference in top-down processing between the retention and the manipulation conditions, as the mental rearrangement of the targets should be done in the latter condition during this interval. Additionally, the analyses were run with time segments covering most of the second half of the retention interval (1,024–2,048 msec after target matrix offset). Here, the two experimental conditions have been supposed not to show pronounced differences. The mental rearrangement should already have been determined at this stage of the task, and in both conditions solely the relevant information had to be kept in memory during the second half of the retention interval.

To obtain amplitude values in the frequency domain, fast Fourier transformation was applied. By averaging in the frequency domain, amplitude spectra were calculated separately for the two experimental conditions as well as for the resting baseline condition with eyes open. A minimum of 20 epochs in each condition was used for averaging. For the upper α frequency band, values between 9.8–12.7 Hz were averaged. In addition to the absolute power, upper α amplitudes of the two experimental conditions were normalized with respect to the baseline condition by using the event-related synchronization (ERS) transformation, which expresses EEG amplitudes as percentage of increase or decrease compared to the baseline ([experimental condition − baseline]/baseline × 100) [see Pfurtscheller and Aranibar, 1977].

With the same epochs that were used for calculating amplitude spectra, EEG coherence was calculated for all 171 electrode pairs (resulting from 19 electrode sites) in each experimental condition. Coherence is a normalized measure of coupling between signals of electrode pairs. It is calculated by normalizing the squared cross-spectrum from two signals by the product of their auto-spectra ($K_{xy} = |C_{xy}|^2 / C_{xx} \times C_{yy}$). Coherence coefficients thus can range from 0 to 1, with $K_{xy} = 0$ meaning no similarity and $K_{xy} = 1$ indicating maximal similarity between the two signals [for further detail see Rappelsberger, 1998].

Finally, latency shifts of α activity between electrode pairs and thus the direction of information flow was assessed. The EEG raw data were bandpass filtered between 9.8–12.7 Hz (96 dB/oct roll-off; zero-phase shift). The filtered data were epoched between 0–1,024 msec (or 1,024–2,048 msec for the second half of the retention interval) with respect to 4 × 4 target matrix offset for the experimental conditions. For the baseline condition, nonstimulus locked epochs of 1,024-msec length were made. Cross-correlations for all 171 electrode pairs were calculated on a single-trial basis and then averaged for each pair and each condition. Next, for every electrode pair, condition, and subject, the latency of the positive peak correlation nearest to time zero was detected. This procedure allowed the direction of the latency shift (indicated either by a positive or a negative latency of the peak correlation) to be determined [for further detail see Sauseng et al., 2004]. As differences in α peak frequency between

anterior and posterior sites could account for latency shifts in the EEG, we also determined the frequency of maximal power between 8–12 Hz for prefrontal and occipital sites for each experimental condition. EEG data analyses were run with Scan 4.3 (Neuroscan) and BrainVision Analyser (Brain Products, Inc.).

Statistical Analysis

The same statistical analyses were carried out on the data obtained in the first and the second halves of the retention period.

Two-way analysis of variance (ANOVA) was calculated with ERS values to find out whether the two experimental conditions (retention and manipulation) differed in the amount of α power change compared to that at baseline. The factors were *condition* (retention and manipulation) and *site* (the 19 electrode bins). Greenhouse-Geisser correction was applied and the significance level was $P < 0.05$. The same analyses were run with absolute power values.

For statistical analysis of the coherence values, the coefficients were first Fisher Z transformed. Next, data were tested for normal distribution with Kolmogoroff-Smirnov tests. Only 3 of 684 variables (2 time frames × 2 conditions × 171 electrode pairs) were not normally distributed. Parametric statistics were therefore used for analyzing further the Fisher Z-transformed coherence values. To assess differences of coherence between the experimental conditions, two-way ANOVAs with factors condition (retention and manipulation) and *pair* (171 electrode pairs) were calculated. Greenhouse-Geisser correction was applied and the significance level was $P < 0.05$.

To assess latency shifts, one-sample *t* tests (test value = 0) were calculated for every electrode pair and condition to determine electrode pairs with a stable latency shift across all 23 subjects. Effects were considered reliable when *P* was <0.005.

Two further two-way ANOVAs were calculated with α peak frequency as dependent measure. Peak frequencies of prefrontal (F7, F3, Fz, F4, and F8) sites and occipital electrodes (O1 and O2) were averaged, separately. The factors of the ANOVAs were site (frontal vs. occipital) and experimental condition (retention vs. manipulation).

RESULTS

The task was not very difficult and all subjects performed near ceiling. The mean percentage of correctly responded trials was 97.2% (SD = 3.3%) and 92.0% (SD = 4.8%) for retention and manipulation, respectively.

First Half of the Retention Interval

The two-way ANOVA calculated with ERS values yielded a significant main effect for factor SITE ($F_{18/396} = 5.52$; $P < 0.01$), indicating anterior α power increase and occipital power decrease with respect to the baseline condition. Most importantly, there was a significant interaction between the factors condition and site ($F_{18/396} = 9.49$; $P < 0.01$). Verified

by post-hoc Scheffé tests, there was a stronger α power increase at prefrontal sites accompanied by a larger power decrease at occipital sites in the manipulation condition compared to that in the retention condition (Fig. 1a).

The ANOVA with absolute power as dependent measure yielded a significant interaction between the factors condition and site ($F_{18/396} = 7.43$; $P < 0.01$). Absolute upper α power during manipulation was higher at anterior and lower at posterior sites for the manipulation condition compared to that for the retention condition (Fig. 1b). During manipulation, prefrontal and occipital α power was of about the same magnitude, whereas during retention occipital power remained higher compared to that at prefrontal sites.

For peak frequency, the ANOVA showed a significant interaction between the factors site and condition ($F_{1/22} = 7.31$; $P < 0.05$). As depicted in Figure 1c, there was no difference in peak frequency between prefrontal and occipital areas for the manipulation condition, whereas prefrontal α was slower and occipital α was faster during retention.

In Figure 2, stable α latency shifts ($t_{22} > 3.12$; $P < 0.005$) are indicated by black arrows. During manipulation (Fig. 2a), all significant latency shifts were in an anterior-to-posterior direction. There was information flow from (prefrontal) brain areas showing strong α power increase to sites exhibiting α power decrease, namely the primary visual areas. This pattern of information flow could not be seen in the retention condition (Fig. 2b). In general, there were fewer electrode pairs showing significant latency shifts during simple retention (6 in contrast to 14 in the manipulation condition), and not all of them were in an anterior-to-posterior orientation. For the baseline condition, only one reliable latency shift (from Fp2 to O1) was found (not shown in Fig. 2). This indicates that during rest there was hardly any stable propagation of information.

In accordance with the results of the cross-correlation analyses, we found stronger long-range coherence between prefrontal and occipital areas in the manipulation compared to that in the retention condition (Fig. 3a). This is indicated by a significant interaction between the factors condition and pair ($F_{170/3740} = 4.19$; $P < 0.01$) of the two-way ANOVA calculated with Fisher Z-transformed coherence values. During retention, short-range connections, mainly between central and frontal electrode sites, were stronger than they were during manipulation. This was also evident after an additional exploratory analysis where we carried out pairwise comparisons between the two experimental conditions for every electrode pair. In general, of course, short-range coherence values were higher than were values for long-range connections, evident from a significant main effect for the factor pair ($F_{170/3740} = 88.10$; $P < 0.01$) in the ANOVA.

Second Half of the Retention Interval

The ERS analysis for the second half of the retention interval yielded a significant interaction between the factors condition and site ($F_{18/396} = 5.94$; $P < 0.01$). In contrast to the first half of the retention interval, however, there was no difference in prefrontal α synchronization between manip-

ulation and retention, as shown by post-hoc Scheffé-tests. At posterior electrode sites, stronger α suppression was obtained in the manipulation condition (Fig. 1d).

The same pattern was found with absolute power values (Fig. 1e). The interaction was significant between the factors condition and site ($F_{18/396} = 8.54$; $P < 0.01$), with no power difference at prefrontal sites and lower power estimates at occipital leads.

The ANOVA with peak frequency as the dependent measure resulted in no significant interaction between the factors site and condition ($F_{1/22} = 0.01$; not significant). The main effect for the factor site was significant ($F_{1/22} = 10.49$; $P < 0.01$) indicating higher α frequency at occipital than at prefrontal sites for both experimental conditions (Fig. 1f).

During the second time frame, no significant latency shifts from prefrontal to occipital brain areas were obtained in any condition (Fig. 2c,d). Instead, manipulation and retention both yielded short-range latency shifts in a posterior-to-anterior direction ($t_{22} > 3.12$; $P < 0.005$).

A two-way ANOVA with Fisher Z-transformed coherence values showed a significant interaction between the factors condition and pair ($F_{170/3740} = 3.06$; $P < 0.01$). Post-hoc pairwise comparisons between the two experimental conditions revealed that the retention condition elicited higher fronto-central short-range coherence. In contrast to the first time frame, there was no difference between the two conditions regarding fronto-occipital coupling (Fig. 3b).

DISCUSSION

The task used in this experiment allowed dissociation between simple short-term memory and working memory demands, with the latter requiring more top-down control. Task-related differences were expected primarily for the first half of the retention interval, when subjects actually were involved in mental manipulation of visuospatial information. No differences in brain activation between the two experimental conditions were therefore expected for the second time period.

The most interesting results were found for the first half of the retention interval. During manipulation, the event-related increase in α power at prefrontal sites was larger than it was during retention; occipital α suppression was also stronger during manipulation. Absolute α power, however, shows that during manipulation, brain activation reflects a state of "α equilibrium," where α power exhibits a topographically flat distribution. Surprisingly, this effect was found not only with α power but also with α frequency. As depicted in Figure 1c, α frequency for prefrontal areas becomes very similar to the frequency at occipital sites during manipulation. In contrast, in the retention condition occipital α is clearly faster than is prefrontal α. As evident from the cross-correlation and coherence analysis during this α equilibrium, increased long-range integration between distant cortical areas occurs. It thus seems that a state of α equilibrium enhances or enables cortico-cortical communication.

The alignment of α power and frequency between prefrontal and occipital electrode sites theoretically could be
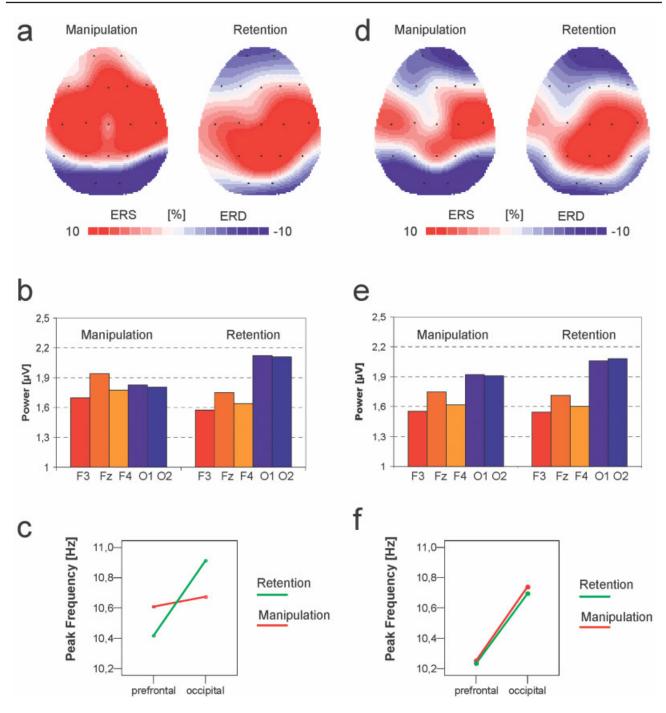
Figure 1.

Comparison of event-related synchronization (ERS), α power, and α frequency between manipulation and retention. Results for the first half of the retention interval are depicted in **a–c**; **d–f** represent results for the second time window. During the first half of the retention period, stronger prefrontal α synchronization (warm colors) accompanied by larger α suppression (cold colors) at occipital sites was found for manipulation than for retention (a). Absolute power values (b) indicate that during manipulation the prefrontal power increase and the posterior power decrease cause a state in which α power assimilates between large distant brain areas. Additionally, α peak frequency over prefrontal and occipital brain areas aligns in the manipulation condition whereas during retention faster α at occipital and slower α at prefrontal sites was found (c). During the second half of the retention interval, both experimental conditions exhibit ERS (d), absolute power values (e), and α peak frequency (f) very similar to that in retention during the first time frame.
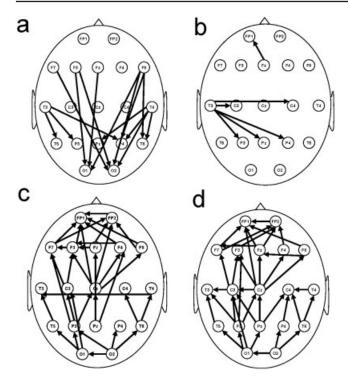
Figure 2.

Stable latency shifts during manipulation and retention. **a, b:** Stable latency shifts for the first half of the retention interval. **c, d:** Stable latency shifts for the late time window. At the beginning of the retention interval, stable latency shifts from prefrontal to occipital electrode sites are exhibited in the manipulation condition (a). This indicates top-down flow of activation from anterior to visual brain areas. There is a lack of this pattern during retention (b). Prefrontal to occipital long-range latency shifts cannot be found during the second half of the retention interval. Here, manipulation (c) and retention (d) both show a propagation of α activity from posterior to anterior. No prefrontal–occipital long-range connections were found to be significant in the second time window.

manipulation in the first time window, however, there are no fronto-occipital long-range connections and there is no top-down flow of activation from anterior to posterior sites. Furthermore, coherence analysis reveals that prefrontal-to-occipital long-range coupling does not dissociate the two experimental conditions during the second half of the retention period (Fig. 3b). It thus seems that brain activation patterns obtained by the manipulation condition during the first time window actually reflect visuospatial top-down processing.

Our data suggest that increased α power is associated with a selective and active cognitive process. Jensen et al. [2002] proposed that EEG α synchronization might prevent the flow of information into areas retaining memory items. The present data, however, suggest that during pronounced α synchronization, activity in posterior regions (including the visual cortex) is modulated (top-down) by anterior brain areas, although this is only true for the condition where the visual information had to be rearranged (manipulation). As in this latter condition, the rearranged information had to be visually imagined, one would expect activation over posterior cortical areas as shown by Kosslyn et al. [1999] in a mental imagination task. In our study, this is reflected by a strong upper α desynchronization over posterior areas, as it
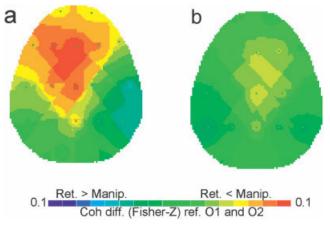

Figure 3.

Fronto-occipital coherence differences between retention and manipulation. The difference between manipulation and retention in Fisher Z-transformed coherence values between the two occipital electrode sites (O1 and O2) and the respective lead is mapped. The color/grayscale code at any electrode position gives the condition-related difference of coherence between this respective electrode site and the occipital cortex. Warm colors/dark shadings indicate stronger coherence for the manipulation condition; cold colors/pale shadings indicate higher coherence values for retention. During the first half of the retention interval (a), manipulation elicits stronger functional coupling between prefrontal and occipital bins. This is in accordance with the results yielded by the latency shift analyses (Fig. 2a). During the second half of the retention interval, there is no significant difference between the experimental conditions (b). [Color figure can be viewed in the online issue, which is available at www.interscience.wiley.com.]

explained by a common, central α source; however, the fact that α coupling is characterized by latency shifts between prefrontal and occipital sites (Fig. 2a) argues against this interpretation.

During the second half of the retention period for both manipulation and retention ERS, α power and α frequency show a similar topography as retention in the first time frame (Fig. 1). The larger occipital α suppression during manipulation might be a residual effect from the first half of the retention interval or might reflect higher task demands than are required in the retention condition. In a similar way, as for power and frequency, we would also expect different findings for cross-correlations between the first and the second half of the retention interval. As depicted in Figure 2c and 2d, α propagates from posterior to anterior regions during the second half of the retention interval with no differentiation between the two conditions. In contrast to

has been shown that mental imagery modulates α activity in sensory brain areas [Tesche et al., 1995]. We suppose that this activity in visual processing areas is modulated by prefrontal brain areas. This is reflected by latency shifts between prefrontal and occipital sites. Von Stein et al. [2000] described similar activation patterns in the cat visual system during top-down processing.

An alternative interpretation of the present results would be to assume that information actually is transferred between anterior and posterior brain areas. There is recent research reporting phase or latency shifts between distant brain areas to reflect exchange of information. As an example, during processing of verbal information phase shifts from posterior to anterior sites were reported by Schack et al. [2003]. They suggested that phase shifts actually reflect the flow of information from posterior to anterior brain areas. Halgren et al. [2002], however, observed alternation of phase shifts from visual association cortex to parietal and central structures and propagation back to the occipital cortex in a broad frequency range from 4 to 12 Hz in a working memory task. This was interpreted as rapid change between bottom-up and top-down processing. Similar findings were obtained by Sauseng et al. [2002], who could show that the interaction between working and long-term memory is reflected by a change in the direction of traveling θ (around 5 Hz) waves, first propagating from anterior to posterior and then reversing, which triggered the beginning of upper α power suppression. Generally, in working memory tasks coupling between brain areas or memory systems is found primarily within the θ frequency range [Halgren et al., 2002; Sarnthein et al., 1998; Sauseng et al., 2002, 2004]. All of these findings can very well be interpreted in terms of bottom-up and top-down processes (or an interaction of both); thus, our interpretation of the present findings is not in contradiction with the above-mentioned literature.

There is also current evidence that central executive functions in working memory are reflected by EEG θ long-range coupling of frontal and parietal brain areas [Sauseng et al., 2005]. In the present study, however, no such effects were found. We ran the same analysis as reported above for the θ band (4–7 Hz), and found no difference in θ power between manipulation and retention and no increased θ coherence between prefrontal and occipital electrode sites for the manipulation condition. A possible explanation is that long-range integration in the θ band might in particular reflect the interfacing between working and long-term memory [Sauseng et al., 2002]. The present experiment did not require long-term memory activation.

Recently, it was emphasized that evoked (phase-locked) α activity might reflect memory processes [Klimesch et al., 2004]. Brain activation patterns as described above could thus actually reflect evoked α activity that is superimposed on the ongoing EEG. This seems implausible in the present study, however, as during the analyzed time windows the visual stimulus had already disappeared. The event-related potentials (ERPs) for the analyzed epochs in this study only show a very weak stimulus offset effect and some slow cortical potentials, with hardly any evoked α activity visible. We compared the ERPs, evoked α power, and coherence of evoked α activity between the two experimental conditions without finding any task-related differences. Furthermore, no significant evoked α latency shifts were found for either condition. We thus conclude that our findings reflect ongoing and not evoked α activity.

To summarize, the present study does not support the idea that EEG α is a simple idling rhythm, nor does it indicate that α synchronization reflects general or global inhibition of task-irrelevant neural circuits when working memory load is increased. We found that during retention and manipulation of visuospatial information, a strong prefrontal α power increase can be observed. At the same time, at occipital sites, α suppression is elicited. This activation pattern reflects an equilibrium between prefrontal and occipital areas with respect to absolute α power. Additionally, α frequency also becomes aligned between prefrontal and occipital sites, resulting in a state of α equilibrium in which anterior and posterior brain areas exhibit a nearly identical level of α power and α frequency. During this state of α equilibrium prefrontal and occipital brain areas show a stronger functional coupling than in a condition in which no top-down processing was required. There is a directed activation pattern from prefrontal to occipital cortices as indicated by α latency shifts.

Prefrontal α synchronization can hardly be interpreted in terms of general or global inhibition. Nonetheless, our findings would be consistent with the idea of selective top-down inhibition in the sense that frontal areas must not become involved in (distracting) new activities as long as an ongoing working memory task is carried out. This is consistent with the idea by Jensen et al. [2002] that α synchronization could prevent incoming external input from disturbing ongoing memory processes. It may be argued that during α activity, cortical areas are in a less excitable state in which only a few selective processes survive inhibition. In other words, during the working memory condition in our task prefrontal areas operate (top-down) to control other areas, but at the same time remain inactive for other processes and in this sense, α synchronization facilitates or enables top-down processes. This is in line with findings of Nunez et al. [2001], who report global binding of local networks at human α frequency.

The suggested interpretation is well in line with findings from Hummel and Gerloff [2005], who were able to show that increased long-range coherence in the α band is functionally relevant and modulated by performance on a visuomotor integration task. It is also consistent with the hypothesis of a selective inhibition of specific brain areas [Hummel et al., 2002] and with findings indicating that a period of pronounced α activity preceding the performance of a task enhances performance [Klimesch et al., 2003].

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